Freshwater macroinvertebrate communities on exotic and native plants

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Abstract

Aquatic plants play an important role in the survival and proliferation of invertebrates in freshwater ecosystems. Exotic plants are now common in North American lakes and rivers, where they may displace native plants, thereby potentially altering epiphytic invertebrate communities. Differences in aquatic invertebrate communities on native and exotic plants are examined here through (1) a meta-analysis of published data, and (2) two field surveys in northeastern North America that compared invertebrates on the exotic *Myriophyllum spicatum* and *Potamogeton crispus* to those on their native congeners. The meta-analysis revealed that exotic plants generally support lower invertebrate abundance than do natives, while invertebrate taxa richness tends to be similar on exotic and native plants. The field surveys demonstrated that *M. spicatum* and *P. crispus* support significantly different invertebrate densities and lower taxa richness than their structurally similar native congeners. These results suggest that the replacement of native plants by exotics – even those with similar morphology – may cause concomitant changes to aquatic ecosystems.

Résumé

Les plantes aquatiques sont importantes pour la survie et la reproduction des invertébrés dans les écosystèmes d'eau douce. Les plantes exotiques d'eau douce se retrouvent maintenant dans plusieurs lacs et rivières en Amérique du Nord et peuvent, dans certains cas, remplacer les espèces indigènes. Ce remplacement peut entraîner des changements au sein des communautés épiphytes d'invertébrés. Cette recherche compare les communautés d'invertébrés aquatiques vivant sur les plantes indigènes et exotiques à l'aide d'une méta-analyse et d'un inventaire dans le nord-est de l'Amérique du Nord. L'inventaire a comparé les communautés d'invertébrés présentes sur deux espèces exotiques, *Myriophyllum spicatum* et *Potamogeton crispus*, et leurs congénères indigènes. Les résultats de la méta-analyse ont démontré que les plantes exotiques supportent généralement moins d'invertébrés que les plantes indigènes, tandis que la richesse taxinomique des invertébrés inventoriés est similaire entre les plantes exotiques et indigènes. L'inventaire a démontré que la densité et la richesse taxinomique d'invertébrés retrouvés sur *M. spicatum* et *P. crispus* sont inférieures à celles retrouvées sur leurs congénères indigènes. Ensemble, ces résultats suggèrent que le remplacement des plantes indigènes par les plantes exotiques (incluant celles qui possèdent une morphologie semblable) pourrait entraîner des changements au sein des écosystèmes aquatiques.

Contribution of Authors

Preface

This thesis was prepared in accordance with the Faculty of Graduate and Postdoctoral Studies Office's "Thesis Submission Guidelines"

"Candidates have the option of including, as part of the thesis, the text of one or more papers submitted, or to be submitted, for publication, or the clearly-duplicated text (not the reprints) of one or more published papers. These texts must conform to the "Guidelines for Thesis Preparation" with respect to font size, line spacing and margin sizes and must be bound together as an integral part of the thesis. (Reprints of published papers can be included in the appendices at the end of the thesis.)

The thesis must be more than a collection of manuscripts. All components must be integrated into a cohesive unit with a logical progression from one chapter to the next...As manuscripts for publication are frequently very concise documents, where appropriate, additional material must be provided (e.g., in appendices) in sufficient detail to allow a clear and precise judgment to be made of the importance and originality of the research reported in the thesis.

In general, when co-authored papers are included in a thesis the candidate must have made a substantial contribution to all papers included in the thesis. In addition, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. This statement should appear in a single section entitled "Contributions of Authors" as a preface to the thesis."

My thesis was completed under the supervision of Dr. Anthony Ricciardi at McGill University. Funding was provided by a Natural Science and Engineering Research Council PGS-M, granted to S. J. Wilson in winter 2005, and a McGill University Philip Carpenter Fellowship in Biology, granted to S.J. Wilson in winter 2005. I planned and executed field seasons in 2005 and 2006 in which I located sites and sampled plants, and completed all laboratory work including identifying invertebrates and measuring epiphytic algae. I also analyzed the data and wrote the original manuscript. Dr. A. Ricciardi assisted with project design, as well as with the design and editing of the final manuscript.

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GENERAL INTRODUCTION:

Macroinvertebrates on native and exotic freshwater plants

Aquatic plants and invertebrates in freshwater ecosystems: interactions and introductions

Aquatic plants play multiple roles in the structure and function of aquatic ecosystems. As major source of primary productivity in aquatic systems, aquatic plants are consumed directly by fish, waterfowl, and invertebrates (Johnson et al. 2000, Lake et al. 2002, Noordhuis et al. 2002). Aquatic plants provide substrate for epiphytic algae, an important food source for many herbivorous invertebrates including snails (Bronmark 1989, Cattaneo et al. 1998). They also provide refugia and colonization space for smaller organisms (Engle 1988, Kershner and Lodge 1990, Toft et al. 2003), and are thus capable of supporting abundant and diverse invertebrate communities (Krull 1970, Keast 1984, Strayer et al. 2003). Given that aquatic invertebrates play vital roles in processing detritus, and are a major food source for fish and waterfowl (Krull 1970, Vannote et al. 1980, Kovecses et al. 2005), changes to the invertebrate communities associated with plants may thus affect aquatic food webs, and may have impacts on species of ecological or economic importance.

Aquatic plant invasions are becoming frequent on a global scale (Myers and Bazely 2003). Human activities, such as recreational boating and distributing ornamental plants through the aquarium trade, play a large role in introducing and subsequently spreading exotic plants, herein defined as plants that have become established outside their native range (Reichard and White 2001, Myers and Bazely 2003). Furthermore, adding nutrients to aquatic systems via agricultural run-off or sewage effluents may promote the establishment and growth of exotic plants (Hobbs and Atkins 1988). Once established, exotic plants may alter the physical and chemical properties of freshwater systems (Cattaneo et al. 1998, Strayer et al. 2003). They often form dense monospecific stands, which can impede water flow, alter nutrient cycling, reduce oxygen levels, and increase sedimentation within plant beds, thereby changing both their physical and chemical environment (Dale and Gillespie

1977, Madsen 1997, Cattaneo et al. 1998, Caraco and Cole 2002). Highly invasive exotic plants such as water chestnut (*Trapa natans*) and Eurasian milfoil (*Myriophyllum spicatum*) may also out compete and replace native plants (Boylen et al. 1999, Myers and Bazely 2003).

Different species of aquatic plants support invertebrate communities that differ in abundance, diversity, and species composition (Krull 1970, Chilton 1990, Cheruvelil et al. 2002). Plant structure has been identified as an important determinant of invertebrate abundance: in general, structurally complex plants with finely divided leaves support higher densities of epiphytic invertebrates than do plants with simple leaves (Krull 1970, Cheruvelil et al. 2000, Cheruvelil et al. 2002). In addition, aquatic plants exude biological chemicals (Wium-Andersen et al. 1982, 1983, Pip 1992, Gross et al. 1996) and nutrients (McRoy and Goering 1974, Carignan and Kalff 1982) that may influence epiphytic invertebrate communities both directly and indirectly. Some biochemical exudates attract specific invertebrates (Marko et al. 2005). Biochemicals can also influence the growth of epiphytic algae (Gross et al. 1996), which is an important invertebrate food source (Cattaneo 1983, Lodge 1986). As such, differences in chemical exudates could lead to differences in epiphytic invertebrate communities between aquatic plant species, even between plants with similar structure.

As different species of aquatic plants often support different invertebrate communities, it follows that exotic plants may support different invertebrate communities than the native plants. In terrestrial systems, incidences of co-evolved mutualisms between plants and insects have been well documented (Janzen 1966, Hossaert-McKey et al. 1994), but in aquatic systems these relationships are less certain. However, several studies examining the relationships between freshwater gastropods and their host plants have found evidence to suggest that gastropods feed preferentially on certain plants (Pip and Stewart 1976, Sheldon 1987), or that gastropod distribution is partially based on differences in epiphyte communities on different plants (Lodge 1986, Bronmark 1989). Because of the potential for co-adaptation of native invertebrates and native aquatic plants, it is hypothesized here that native plant communities support more abundant and diverse macroinvertebrate communities than do exotic plants, provided that native invertebrates are more abundant in a given system than exotic invertebrates. If this is true, even native plants that are similar in structure to exotic plants should support more abundant and diverse invertebrates. Furthermore, exotic invertebrates are also present in many aquatic systems in North America, and some of these live on aquatic plants. Simberloff and Von Holle (1999) proposed that the presence of an exotic species in a system facilitates the establishment of other exotic species, a process termed “invasional meltdown”. For example, exotic aquatic plants might facilitate the establishment and population growth of aquatic invertebrates, particularly if these species shared an evolutionary history. Exotic plants may also act as a vector for the dispersal of exotic invertebrates (Johnson et al. 2001, Toft et al. 2003). Thus exotic invertebrates may be more commonly associated with exotic plants in aquatic systems, just as we might expect native plants to support more native invertebrates.

General trends in invertebrate abundance and diversity on native and exotic plants

To identify general trends, I compared the differences in the density and diversity of aquatic macroinvertebrates on exotic and native plants in freshwater systems, through a quantitative synthesis of data from multiple studies.

METHODS

Data selection

My analysis considered published studies that examined macroinvertebrate communities on submerged or floating aquatic plants including at least one exotic plant species and one native plant species in the same body of water. Published studies were located using computer databases (Aquatic Sciences and Fisheries Abstracts, Ecology Abstracts). Following Cheruvelil et al. (2002), I included only peer-reviewed studies that contained all of the following information: 1) sampling date, 2) sampler used, 3) plant species sampled, 4) lake(s) sampled, 5) country, 6) results for either a single exotic and native species or separate sites dominated by exotic and native macrophytes, 7) type of invertebrates sampled, and 8) results in the form of abundance of invertebrates per unit plant biomass, invertebrate taxa richness, or invertebrate Shannon-Wiener diversity.

Data Treatment

To control for variability between studies arising from differences in lakes and rivers (nutrient levels, temperature, location) and in sampling methods, I calculated an overall dimensionless effect size for each study. The ratio of the average invertebrate density or diversity on native and exotic plants was calculated, and this ratio was natural log transformed to create a dimensionless effect size:

Effect size (*E*) = ln (average parameter on native plants/average parameter on exotic plants)

For example, the effect size for density:

E **= ln (mean number of invertebrates per unit plant biomass on native plants/mean number of invertebrates per unit plant biomass on exotic plants).**

This technique minimizes interstudy variability and normalizes the data (Gurvitch and Hedges 1999, Hedges et al. 1999). Five separate effect sizes for either invertebrate density or diversity were calculated:

1) The ratio of the mean density of aquatic invertebrates on all native and exotic plants in each study;
2) The ratio of invertebrate density on native and exotic plants with similar leaf morphology. [This variable was used to minimize the influence of leaf morphology on invertebrate density. Plants were classified according to leaf type (floating, dissected, or simple leaves). Each exotic plant in the system was compared to native plants with similar leaf morphology. In studies where more than one native plant with similar leaf morphology was present, the average invertebrate density on native plants with similar structure to the exotic was used];
3) The ratio of the mean taxa richness of aquatic invertebrates on all native and all exotic plants in each study;
4) The ratio of taxa richness on native and exotic plants with similar leaf morphology using previous method (number 2, above).
5) The ratio of mean Shannon-Wiener diversity of invertebrates on all native and exotic plants in each study. The relative scarcity of studies that examined Shannon-Wiener diversity prohibited comparisons of plants with similar leaf morphology.

Studies included

I found 18 studies from four continents that fit the aforementioned criteria (Table 1). Schramm et al. (1987) found that invertebrate density was several orders of magnitude smaller on *Nuphar* sp. than any other plant species, and so this plant species was excluded from the analysis. As not all studies identified all the invertebrates to the species level, taxa richness and Shannon-Wiener diversity were based on the lowest level of identification used in each study.

Statistical analysis

For each of the aforementioned parameters, the mean response ratio and 95% confidence intervals were calculated. Results were considered significant if the zero line, equivalent to the one to one line, did not fall within this confidence interval. In studies that included invertebrate counts for multiple sites within a lake or river, rather than for on an individual plant species, data from sites dominated by native and exotic plants were used. When data were presented only in figure form, I enlarged the figures on a photocopier, calibrated a scale for the enlargement, and used a ruler to estimate values. When samples were taken over several months or years, I calculated the mean invertebrate density or diversity over all months or years for each plant species when they co-occurred. In studies that sampled in more than one lake or river, each lake or river was treated as a separate effect size (Schramm et al. 1987). Because some values for variance were not reported, the studies in this analysis were unweighted.

RESULTS and DISCUSSION

Invertebrate Density

The mean density of invertebrates was higher on native plants than on exotic plants in both comparisons ($p < 0.05$, Fig 1 a, b). Native plants had 1.8 times greater invertebrate density when all native and all exotic plants in each study were compared, and 1.7 times greater invertebrate density than exotic plants with similar leaf structure. This result suggests that in addition to leaf structure, the evolutionary context or non-structural attributes of the plant may influence the density of invertebrates it supports. Thus, when an exotic plant replaces a structurally similar native plant, the exotic may not fulfill the same role in the ecosystem, thereby reducing the number of invertebrates available as a food source for fish, waterfowl, and other invertebrates.

In some studies, exotic plants supported greater invertebrate densities than did native plants (Schramm et al. 1987). This was especially likely when an exotic with complex structure was compared to native plants with simple structure (as in Keast 1984, Strayer et al. 2003). When an exotic with complex structure is introduced into a system where the dominant natives have simple structure, the exotic may increase available colonization space and food for invertebrates (Strayer et al. 2003). However, on average, native plants supported greater invertebrate densities than exotic plants.

Invertebrate Diversity

Taxa richness was not significantly different on exotic and native plants in either comparison (Fig 2 a, b). Shannon-Wiener diversity was also not significantly different on exotic and native plants for either comparison; however, exotic plants tended to have higher Shannon-Wiener diversity than native plants (Fig 3).

The Shannon-Wiener diversity index accounts for both the number of taxa in a system and how evenly the abundance of invertebrates is distributed across taxonomic groups. Since taxa richness was similar between exotic and native plants, the tendency toward higher values of the Shannon-Wiener diversity index suggest that invertebrate abundance on exotic plants was more evenly distributed. These results should be treated with caution, however, as different studies identified invertebrates to different taxonomic levels. The patterns in invertebrate diversity on native and exotic plants may not be the same for family richness as for species richness, and so by comparing diversity in this way some of the resolution is lost. To create a clearer picture, ideally all invertebrates should be identified to the species level, which would account for the rare and perhaps endemic species that may be overlooked by identifying only to the genus or family level.

Sources of Bias

As with any meta-analysis of this type, there is the "file drawer" problem where authors do not report non-significant findings; however, the studies I found reported a wide range of results, so this might not be an important bias here. Differences between studies, such as the species of native plant chosen for study (not all studies included all the native plants in a system) may arbitrarily produce different results in different studies. I also did not account for the time since introduction of each exotic plants species, as this data was not available for all study sites; however, this may be an important variable to consider, as native invertebrates may adapt to exotic plants if given the time to do so. Finally, due to the small number of studies available on this topic, this analysis is also limited in its power to detect significant results.

Field studies of epiphytic invertebrates on native and exotic plants

This literature synthesis suggests that invertebrate communities on exotic plants differ from those on native plants. However, to the best of my knowledge, no one has yet conducted an in-depth analysis of the invertebrate communities on closely related, morphologically similar exotic and native plants. I therefore conducted two field studies, in which I compared invertebrate abundance, diversity, and community composition on two widespread exotic plants with those on their structurally similar native congeners. The two studies were similar in their execution, but deal with two genera that have different morphology and invasion histories.

In Chapter 1, I compared invertebrates on the exotic *Myriophyllum spicatum* to those on the native *M. sibericum* and *M. alterniflorum,* with an emphasis on the invertebrates' community composition. In Chapter 2, I compared invertebrates on another exotic plant, *Potamogeton crispus*, with those on the native *P. richardsonii* and *P. perfoliatus*. I also examined this second data set to see if a causal mechanism for differences in invertebrates on native and exotic plants might be identified: I compared epiphyte biomass on exotic and native *Potamogeton* species and related this to the abundance of invertebrates on each (Chapter 2).

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Table 1: Studies included in meta-analysis. In each study, exotic and native plants with similar structure are in bold

ID	Study	Lake	Country	Sampling Year(s)	Parameter	Native plants	Exotic plants
1	Krecker 1939	Lake Erie	USA	1935-36	taxa richness	***Elodea canadensis, Potamogeton pectanus, P. compressus***	***Myriophyllum spicatum, Potamogeton crispus***
2	Bownik 1970	Mikolajskie Lake	Poland	1967	density	*Potamogeton perfoliatus, P. lucens,* ***Myriophyllum spicatum***	***Elodea canadensis***
3	Korinkova 1971	Radov	SW Bohemia	1964-1965	density	*Batrachium aquatile, Potamogeton lucens*	*Elodea canadensis*
4	Soska 1975	Mikolajskie Lake	Poland	1970	density	*Potamogeton perfoliatus, P. lucens,* ***Myriophyllum spicatum***	***Elodea canadensis***
5	Biggs and Malthus 1982	Upper Clutha Valley	New Zealand	1980	abundance, taxa richness, diversity	***Myriophyllum propinquum, Potamogeton cheesemanii***	***Lagarosiphon major, Elodea canadensis, Ranuculus fruitans***
6	Keast 1984	Lake Opinicon	Ontario, Canada	1979	density	*Potamogeton robbinsii, Vallisneria americana*	*Myriophyllum spicatum*
7, 8	Schramm et al. 1987	Henderson Lake	Florida, USA	1983	density	*Utricularia* sp., *Ceratophyllum demersum, Nuphar luteum, Panicum hemitomon*	*Eichhorina crassipes*
9	Talbot and Ward 1987	Lake Alexandra, Lake Grasmere, Upper Clutha valley	New Zealand	1982-1985	abundance, taxa richness, biomass	*Chara fibrosus,* ***Myriophyllum triphyllum,*** *C. globularis*	***Elodea canadensis***
10	Kornijow 1989	Lake Piaseczno	Poland	1984	diversity, density, taxa richness	***Ceratophyllum demersum, Myriophyllum alterniflorum,*** *Potamogeton praelongus*	***Elodea canadensis***
11	Chilton 1990	Lake Onalaska	Wisconsin, USA	1983	diversity, density	***Ceratophyllum demersum***	***Myriophyllum spicatum***
12	Cattaneo et al. 1998	Lago di Candia	Italy	1995	density, taxa richness, diversity	*Myriophyllum spicatum, Ceratophyllum demersum, Najas marina.*	*Trapa natans*
13	Mastrantuono and Mancinelli 1999	Lake Monterosi	Italy	1995-94	species richness, diversity	*Myriophyllum spicatum, Ceratophyllum demersum, Chlorophyta* sp.	*Nelumbo nucifera*
14	Cheruvelil et al. 2000	Heron Lake, 1998	Michigan, USA	1998	density	***Ranuculus*** **sp.,** ***Potamogeton pectinatus***	***Myriophyllum spicatum***
15	Masifwa et al. 2001	Lake Victoria	Uganda	1996-1997	density, diversity	*Cyperus paprus*	*Eichhorina crassipes*
16	Balci and Kennedy 2003	Man made earthen ponds	Texas, USA	1998	taxa richness	*Heteranthera dubia*	*Myriophyllum spicatum*
17	Strayer et al. 2003	Hudson River	New York, USA	2000	taxa richness	*Vallisneria americana*	*Trapa natans*
18	Toft et al. 2003	Sacramento-san joaquin delta	California	1998	taxa richness, diversity	***Hydrocotyle umbellata***	***Eichhorina crassipes***

FIGURE CAPTIONS

Figure 1: Effect size for the ratio of mean invertebrate density on a) all native plants to all exotic plants in each waterbody, and b) on native and exotic plants with similar leaf morphology. An effect size > 0 indicates native plants have a higher density than exotic plants. Numbers refer to study used: 2. Bownik 1970; 3. Korinkova; 1971 4. Soska 1975; 6. Keast 1984; 7. Schramm et al. 1987, Orange Lake; 8. Schramm et al. 1987, Henderson Lake; 10. Kornijow 1989; 11. Chilton 1990; 12. Cattaneo et al. 1998; 14. Cheruvelil et al. 2000.

Figure 2: Effect size for the ratio of mean invertebrate taxa richness on a) all native plants to all exotic plants in each waterbody, and b) on native and exotic plants with similar leaf morphology. An effect size > 0 indicates that native plants have a higher taxa richness of invertebrates than exotic plants. Numbers refer to the study used: 1. Krecker 1939; 5. Biggs and Malthus 1982; 7. Schramm et al. 1987, Orange Lake; 9. Talbot and Ward 1987; 10. Kornijow 1989; 12. Cattaneo et al. 1998; 13. Mastrantuono and Mancinelli 1999; 16. Balci and Kennedy 2003; 17. Strayer et al. 2003; 18. Toft et al. 2003.

Figure 3: Effect size for the ratio of mean Shannon-Wiener diversity on all native plants to all exotic plants in each waterbody. An effect size > 0 indicates that native plants have a higher Shannon-Wiener diversity of invertebrates than exotic plants. Numbers refer to study used: 5. Biggs and Malthus 1982; 10. Kornijow 1989; 11. Chilton 1990; 12. Cattaneo et al. 1998; 13. Mastrantuono and Mancinelli 1999; 15. Masifwa et al. 2001; 18. Toft et al. 2003

Figure 1

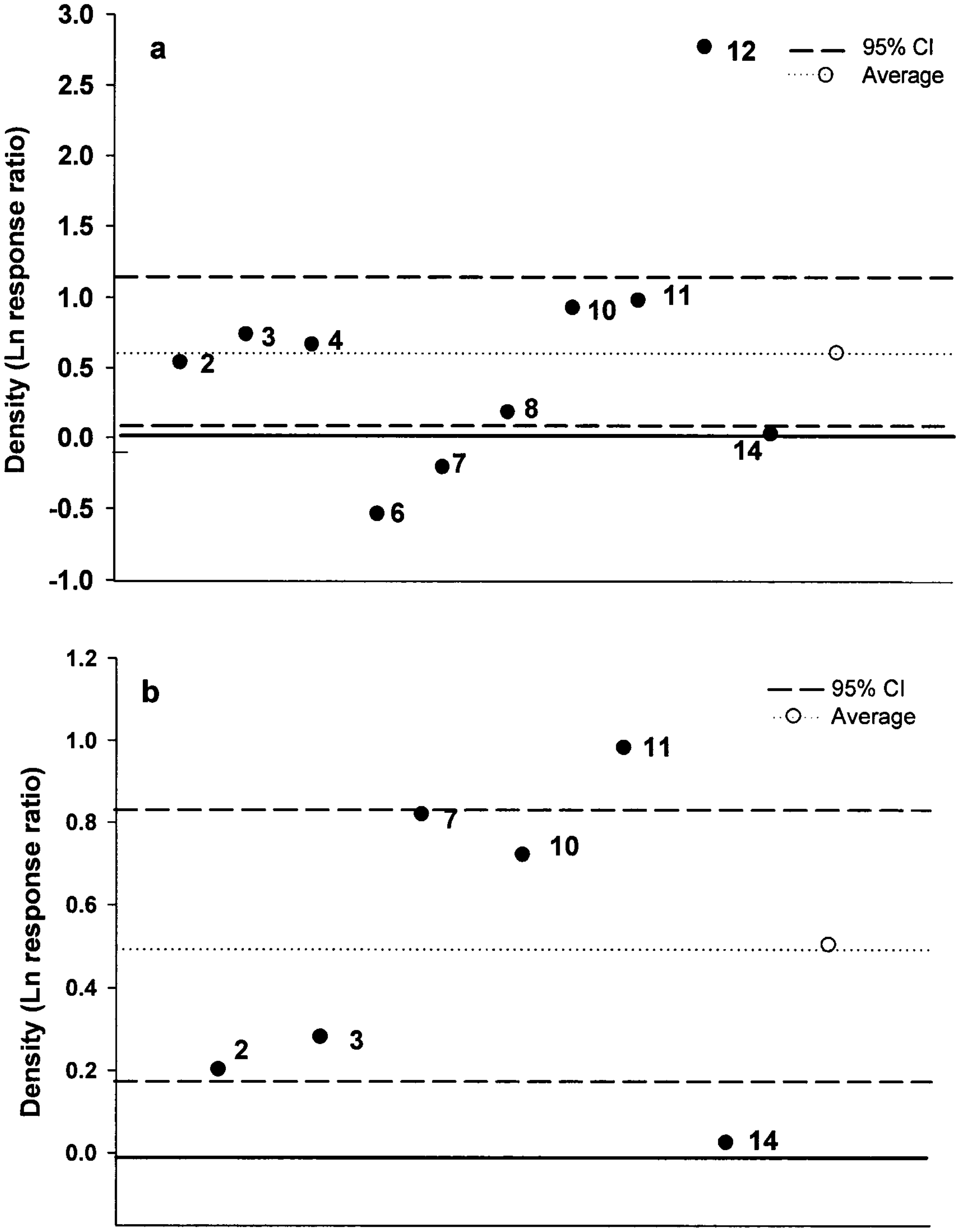
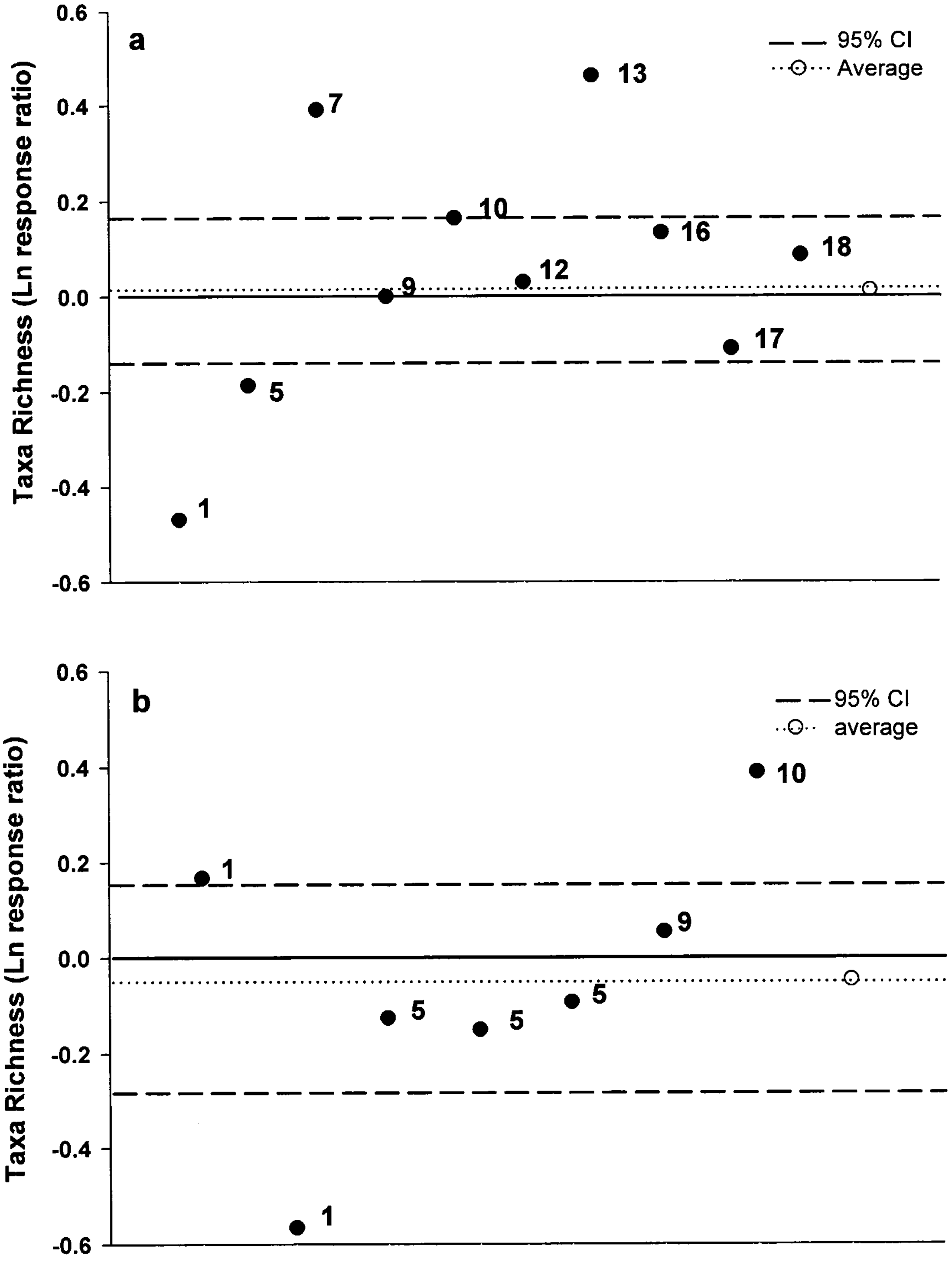

a
3.0
2.5
2.0
1.5
1.0
0.5
0.0
-0.5
-1.0
Density (Ln response ratio)
95% CI
Average
2
3
4
6
7
8
10
11
12
14
b
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Density (Ln response ratio)
95% CI
Average
2
3
7
10
11
14

Figure 2


a
— — 95% CI
··○··· Average
Taxa Richness (Ln response ratio)
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
13
7
10
16
18
12
9
17
5
1
b
— —95% CI
··○·· average
Taxa Richness (Ln response ratio)
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
10
1
9
5
5
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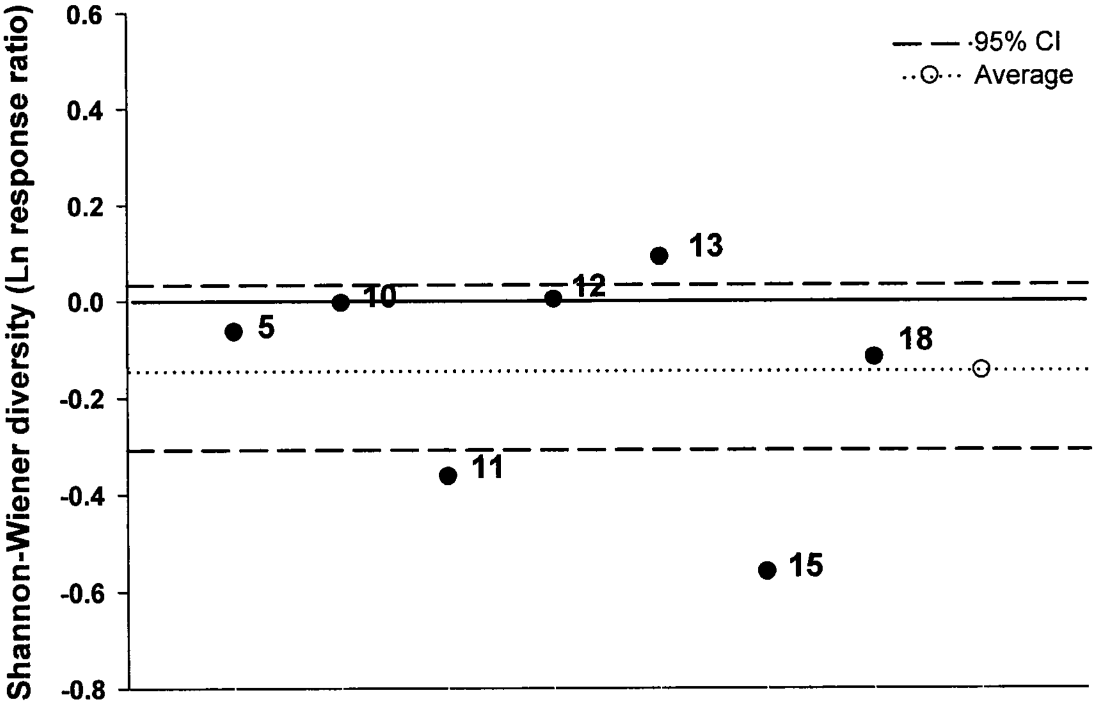
1

Figure 3


Shannon-Wiener diversity (Ln response ratio)
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
95% CI
Average
5
10
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12
13
15
18

Epiphytic macroinvertebrate communities on Eurasian milfoil and native milfoils in Eastern North America

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ABSTRACT

Aquatic plants play an important role in the survival and proliferation of invertebrates in freshwater ecosystems. Epiphytic invertebrate communities may be altered by the replacement of native plants by exotic plants, even if the latter are close relatives of the former. This research compared freshwater macroinvertebrate communities on native and exotic plants of similar leaf morphology and overall structure. Eurasian milfoil (*Myriophyllum spicatum)* and native milfoils (*M. sibericum* or *M. alterniflorum*) were sampled in four bodies of water in southern Quebec and upstate New York throughout the summer of 2005. Within each water body, we compared the density, biomass, diversity and community composition of epiphytic invertebrates on exotic and native *Myriophyllum*. We found differences in invertebrate communities on native and exotic *Myriophyllum* that varied with the sampling date and site. Both native *M. sibericum* and *M. alterniflorum* had higher invertebrate diversity and supported more gastropods than exotic *M. spicatum*, and both of these native *Myriophyllum* species also generally supported greater invertebrate biomass than *M. spicatum*. In late summer, invertebrate density was higher on *M. sibericum* than on *M. spicatum*, but lower on *M. alterniflorum* than on *M. spicatum*. The results demonstrate that *M. spicatum* supports invertebrate communities that differ from those on structurally similar native plants. Thus, the replacement of native *Myriophyllum* species by *M. spicatum* may have indirect effects on aquatic food webs.

INTRODUCTION

Aquatic plants play key ecological roles in lakes and rivers, both as a source of primary productivity, and as a structural component capable of supporting abundant and diverse invertebrate communities (Engle 1988; Kershner and Lodge 1990; Toft et al. 2003). Currently, aquatic plant communities are being transformed by introductions of exotic plants, which can replace or dominate native plant species (Boylen et al.1999, Myers and Bazely 2003). Researchers are now aware that plant invasions often alter the physical and chemical environment of invaded aquatic systems, as invasive plants often grow in dense stands (Dale and Gillespie 1977, Carpenter and Lodge 1986, Madsen 1997, Cattaneo et al. 1998, Caraco and Cole 2002); however, the effects of plant invasions on epiphytic invertebrate communities is still largely unknown (but see Keast 1984, Strayer et al. 2003, Toft et al. 2003). In particular, it is not clear if exotic plants provide similar habitat for invertebrates to that fostered by closely related, morphologically similar native plants.

Within a given ecosystem, native plants and their associated native invertebrates may have interacted over the course of their evolution, potentially leading to coadaptation. If shared evolutionary history matters, then we might expect native plants to support more abundant and diverse invertebrate communities than exotic plants, given that the vast majority of freshwater invertebrate species in North America are native (Pennak 1989; Merritt and Cummins 1996). By similar logic, Simberloff and Von Holle (1999) proposed that the presence of exotic species in a system might facilitate the establishment of other introduced exotic species, a process termed "invasional meltdown." For example, exotic freshwater plants might facilitate the establishment and population growth of aquatic invertebrates, particularly if these species have shared an evolutionary history. Furthermore, exotic plants may also act as a vector for the introduction of exotic invertebrates, for both short- and long-range dispersal events (Johnson et al. 2001, Toft et al. 2003). Thus we might expect to find more exotic invertebrates living on exotic plants.

The physical and chemical properties of aquatic plants may influence the abundance, diversity, and community composition of the invertebrates associated with them, potentially resulting in different invertebrate communities on different species of plants (Krull 1970, Cyr and Downing 1988, Chilton 1990, Cheruvelil et al. 2002). Plant structure has been identified as an important determinant of invertebrate abundance, as structurally complex plants with finely divided leaves tend to support higher densities of epiphytic invertebrates than do plants with simple leaves (Krull 1970, Cheruvelil et al. 2000, Cheruvelil et al. 2002). The chemicals exuded by aquatic plants may also directly affect the abundance of certain invertebrates (Marko et al. 2005), while other plant exudates may influence the growth of epiphytic algae, an important invertebrate food source (Wium-Andersen et al. 1982, Cattaneo 1983, Pip 1992, Gross et al. 1996). It therefore follows that even plants with similar structure may support different invertebrate communities (Cyr and Downing 1988).

Myriophyllum spicatum is an invasive plant that was introduced into North America in the early 1900s, reaching the St. Lawrence River by 1957 (Aiken et al. 1979, Smith and Barko 1990). It is now present in a wide range of aquatic ecosystems across North America, where it often outcompetes native plants including species of native *Myriophyllum* (Boylen et al. 1999). Most milfoils have finely divided, feather-like leaves arranged in whorls of four around the stem; in particular, the native *M. sibericum* and exotic *M. spicatum* have very similar leaf morphology, including their specific leaf area (surface area/biomass of leaf) (Gerber and Les 1994, Crow and Hellquist 2000).

The overall objective of this study was to determine if the exotic *M. spicatum* supports invertebrate communities equivalent to those on structurally similar, native species of *Myriophyllum*. To meet this objective, we address the following hypotheses: If leaf structure (i.e. complex versus simple leaves) largely determines epiphytic invertebrate abundance and diversity, structurally similar plants should support similar invertebrate communities. However, if biochemical or other subtle differences between these species influence epiphytic invertebrates, we hypothesized that native species of *Myriophyllum* would support more abundant and diverse invertebrate communities than would the exotic *M. spicatum* due to potential coadaptation between native invertebrates and native *Myriophyllum* species. Under the invasional meltdown model, we also hypothesized that the exotic *M. spicatum* would support more abundant and diverse exotic invertebrates than would the two native species of *Myriophyllum*. To test these hypotheses, we compared the density, biomass, diversity, and community composition of epiphytic invertebrates on the exotic *M. spicatum* to invertebrate communities on native *M. sibiricum* and *M. alterniflorum*, and also compared the density of exotic invertebrates on these plants.

METHODS

Study sites

Macrophytes and their associated epiphytic invertebrates were sampled on multiple occasions at four sites in Eastern North America: the Richelieu River and Lac Saint-Louis, in southern Quebec, and Upper Saranac Lake and Upper Chateaugay Lake in the Adirondack Park, in upstate New York (Fig 1). These lakes and rivers represent a range of freshwater habitats in which native and exotic *Myriophyllum* co-occur (Table 1). Prior to sampling, we informally surveyed macrophytes in each waterbody, and selected a site within each where the relative abundance of both native and exotic *Myriophyllum* species was approximately equal. All subsequent samples were then taken from the same site, although we sampled different individual plants on each sampling date. We could not find a site where all three plant species were present, and so in Lac St-Louis and the Richelieu River we sampled the native *M. sibericum* and exotic *M. spicatum*, and in Saranac and Chateaugay Lake we sampled the native *M. alterniflorum* and exotic *M. spicatum*. At the time of sampling, Saranac Lake was undergoing a milfoil control program wherein *M. spicatum* was hand-harvested at discrete periods. As a result, the relative abundance of the two species varied throughout the season at this site. At all four waterbodies, we sampled two to three times at one month intervals throughout the summer of 2005.

Epiphytic invertebrate sampling

At each site, a snorkeler or SCUBA diver collected plants and epiphytic invertebrates using a modified Downing box sampler, a plexiglas box that encloses plant material and associated invertebrates in six litres of water (Downing 1986, Rasmussen 1988, Appendix A). On one side of this box is a screen (0.5mm) to drain out water while keeping macroinvertebrates and plants inside. Within each site we limited the depth variation at which samples were taken to within one meter. Plants were identified in the field prior to sampling. Because *M. spicatum* and *M. sibericum* are often difficult to distinguish (Crow and Hellquist 2000), we only sampled at sites where morphological differences between the two species were sufficiently distinct to ensure correct identification (Fig 2). At each site, six to 10 replicate samples of each plant species were collected. At Saranac Lake, we took additional samples as there were very few invertebrates on the plants. The number of samples taken depended on the density of invertebrates and the availability of plants. Although at each site samples were taken from scattered locations within a mixed stand of macrophytes, we made an effort to take a native and exotic plant from similar locations within each site. At each site on each sampling date, we measured water temperature and depth, identified the other macrophyte species present, and took water samples, which we refrigerated for less than 48 hours prior to testing water pH using a digital pH meter (AP63 pH meter, Accumet Portable Laboratory, Fisher Scientific).

Sample processing

In the field, we placed plants from each sample in plastic tubs and removed loose invertebrates from both the tray and sampler using forceps. Invertebrates were immediately preserved in 70% ethanol. The plants from each sample were then stored in separate plastic bags and transported to the lab in a cooler, where they were refrigerated and processed within 48 hours of collection. We removed the remaining invertebrates from the plants using forceps and preserved them in 70% ethanol. As plant dry weight is less variable than plant wet weight, the plants were subsequently rinsed of debris and epiphytic algae, blotted to remove excess water, dried in an oven at 65°C for 16 hours until a stable weight was reached, and finally weighed on an electronic balance (± 0.01g).

We identified preserved invertebrates to the lowest taxonomic level possible under a dissection microscope. Because the mass of individual species and genera was often insignificantly small, we measured the wet weight (± 0.001g) of every order of invertebrates in each sample. Although preservation alters the wet weight of invertebrates, for each date at each site all samples were stored in the same conditions (i.e. temperature and light) and weighed within the same week to minimize error due to desiccation.

Statistical analysis

Invertebrate density (number of invertebrates per gram of plant dry weight) and biomass (wet weight of invertebrates per gram of plant dry weight) were calculated for each sample and log-transformed prior to statistical analysis to meet assumptions of normality. We tested for homogeneity of variance across sampling groups at each site using Levene's test. We then used two-factor ANOVA to compare the mean invertebrate density on native and exotic *Myriophyllum* at each site, with date and plant type (native or exotic) as the two factors, and did the same for invertebrate biomass. Densities of each exotic invertebrate species on native and exotic *Myriophyllum* were compared using ANOVA when the abundance of an exotic invertebrate species was normally distributed across a site. If a two-factor ANOVA was inappropriate for including date as a factor, we used two-tailed t-tests on each date where exotic invertebrate density was normally distributed. All of the above statistical tests were preformed using SPSS version 14.0 for Windows (SPSS Inc., Chicago, Illinois).

To measure diversity, we calculated taxa richness and two other diversity indices, the Shannon-Wiener index and the inverted Simpson index. Both the Shannon-Wiener and inverse Simpson diversity indices measure taxa richness as well as how evenly invertebrate abundance is distributed across invertebrate taxa, but the Shannon-Wiener index is influenced more by taxa richness and less by evenness than the Simpson index (Magurran 2004). For each site, we created individual-based Coleman rarefaction curves for taxa richness, and accumulation curves for Shannon-Wiener and inverse Simpson diversity on native and exotic *Myriophyllum* (Colwell 2005). The curves were generated separately for native and exotic plants at each site. These were then used to compare invertebrate diversity on two species of plants while controlling for differences in the total abundance of invertebrates on the different plant species. Shannon-Wiener and inverse Simpson diversity were calculated based on 50 randomizations sampled with replacement to generate error bars (Colwell 2005). We also used detrended correspondence analysis (DCA) to reveal trends in invertebrate community composition at each site using CANOCO version 4.5 (Biometris, Wageningen). Before running a DCA we excluded rare taxa, defined as those present in fewer than three replicate samples at a site throughout the season.

RESULTS

Invertebrate Abundance

Invertebrate Biomass

At three out of the four sites, during at least part of the summer invertebrate biomass was significantly higher on the two native *Myriophyllum* species than on exotic *M. spicatum* (ANOVA, $p < 0.05$, Figure 3). In early to mid summer, invertebrate biomass was higher on native *M. sibericum* than on exotic *M. spicatum* in Lac St-Louis by a factor of 2.2, while from June to August total invertebrate biomass declined on both species of plant. In the Richelieu River, *M. spicatum* supported slightly higher invertebrate biomass than *M. sibericum* in early summer, while in late summer *M. sibericum* had 2.3 times greater invertebrate biomass than *M. spicatum*. In Chateaugay Lake, native *M. alterniflorum* had higher invertebrate biomass than exotic *M. spicatum* by a factor of two in August, while at Saranac Lake both species had similar invertebrate biomass throughout the season. Overall, gastropod biomass, which constituted a substantial portion of overall invertebrate biomass, was significantly higher on native plants at Lac St-Louis, the Richelieu River, and Chateaugay Lake (ANOVA, $p < 0.05$), while in Saranac Lake *M. spicatum* and *M. alterniflorum* supported similar gastropod biomass across the season (Fig 4).

Density

Within each site, invertebrate density tended to be different on native and exotic *Myriophyllum*, especially in mid to late summer (Fig 5). Invertebrate density was generally higher on *M. sibericum* than on *M. spicatum*; however, this difference was only significant in the Richelieu River (ANOVA, $p < 0.05$). Mean invertebrate density on *M. sibericum* was higher than *M. spicatum* by a factor of 1.5 in Lac St-Louis (August), and 2.2 in the Richelieu River (September). Invertebrate density tended to be higher on exotic *M. spicatum* than on native *M. alterniflorum,* although only significantly so at Chateaugay Lake (ANOVA, $p < 0.05$). In August, average invertebrate density on *M. alterniflorum* was lower than on *M. spicatum* by a factor of 2.2 in Chateaugay Lake.

Invertebrate Diversity and Community Composition

Diversity

Invertebrate taxa richness was higher on native *M. alterniflorum* than on exotic *M. spicatum* in both Chateaugay Lake and Saranac Lake (Fig 6, Table 2, $p < 0.05$). Invertebrate taxa richness was higher on native *M. sibericum* than exotic *M. spicatum* in the Richelieu River, ($p < 0.05$) while in Lac St-Louis both plant species supported similar taxa richness (Fig 6, Table 2). Shannon-Wiener diversity followed the same pattern as taxa richness (Fig 7, Table 2), as *M. alterniflorum* supported higher invertebrate Shannon-Wiener diversity than *M. spicatum* in both Saranac Lake and Chateaugay Lake. *Myriophyllum sibericum* supported invertebrate communities of higher Shannon-Wiener diversity than *M. spicatum* in the Richelieu River ($p < 0.05$), but at Lac St-Louis Shannon-Wiener diversity was similar on both species (Fig 7, Table 2). The inverse of the Simpson index showed a similar pattern to both taxa richness and Shannon-Wiener diversity, with the exception of Saranac Lake. At this site, although *M. alterniflorum* tended to have higher inverse Simpson diversity of invertebrates than *M. spicatum,* this difference was not significant (Table 2). Thus in the Richelieu River, Saranac Lake, and Chateaugay Lake, native *M. sibericum* and *M. alterniflorum* supported more diverse invertebrate communities than exotic *M. spicatum*, while in Lac St-Louis *M. sibericum* and *M. spicatum* supported similar diversity. Taxa richness, Shannon-Wiener diversity, and the inverse Simpson diversity index showed the same general pattern across all four sites.

Invertebrate community composition

Although native and exotic *Myriophyllum* supported many of the same invertebrate species, the abundance of certain invertebrate groups was often different on each species of plant. At three out of four sites, both species of native *Myriophyllum* had higher gastropod biomass per gram of plant than *M. spicatum* (ANOVA, $p < 0.05$). The differences between invertebrate communities on *M. alterniflorum* and *M. spicatum* are well illustrated by the invertebrate community at Chateaugay Lake (Fig 8 a, b). At this site, a detrended correspondence analysis showed that samples divided along two axes, the first representing plant type, and the second representing date. Generally, exotic *M. spicatum* supported many chironomids and oligochaetes, while native *M. alterniflorum* supported many amphipods and gastropods. Invertebrate communities associated with *M. spicatum* were characterized by naidid oligochaetes, chironomids, caddisflies of the genus *Oxyethira* (Hydroptilidae), and the exotic moth *Acentria ephemerella* (Pyralidae) (Fig 8 b). Invertebrates characteristic of *M. alterniflorum* were the gastropods *Valvata sincera* (Valvatidae) and *Amnicola limosa* (Hydrobiidae), the amphipod *Hyallela azteca*, damselflies in the family Coenagrionidae, and caddisflies of the genus *Orthotricha* (Hydroptilidae). Invertebrate communities were also different in early and late summer, with more planarians on both plant species in July and more caddisflies in August (Fig 8 b). In Saranac Lake, differences in invertebrate communities were not clearly defined by either date or plant species.

Invertebrate community composition also differed between exotic *M. spicatum* and native *M. sibericum* in the Richelieu River, while at Lac St-Louis differences were less apparent. As in Chateaugay Lake, in the Richelieu River exotic *M. spicatum* supported many chironomids and oligochaetes, while native *M. sibericum* supported many amphipods and snails. Invertebrate communities characteristic of *M. spicatum* were dominated by chironomids, oligochaetes, and the caddisfly *Brachycentrus* sp. (Brachycentridae) throughout the sampling period. Invertebrate communities on *M. sibericum* were characterized by the amphipod *Hyalella azteca*, the gastropods *Physa gyrina gyrina* (Physidae), *Gyraulus circumstriatus* (Planorbidae) and *Amnicola limosa* (Hydrobiidae), the planarian

Dugesia tigrina, ostracods, and (in September) the exotic zebra mussel *Dreissena polymorpha.* Generally the invertebrate composition on *M. spicatum* did not vary throughout the season, while those on *M. sibericum* changed in each sampling period: in July, *M. sibericum* had many gastropods and amphipods; in August, invertebrates were similar to those on *M. spicatum* with many naidid oligochaetes, chironomids, and *Brachycentrus* sp.; in September, *M. sibericum* supported many zebra mussels (Fig 8 c, d). In Lac St-Louis, gastropods were significantly higher on *M. sibericum* than on *M. spicatum* (ANOVA, $p < 0.05$), but otherwise invertebrate communities were not clearly differentiated by either date or plant type.

Abundance of exotic invertebrates

Three species of exotic invertebrates were found. The exotic moth *Acentria ephemerella (nivea)* was present at all four sites, and was higher on *M. spicatum* than on the native *Myriophyllum* species at every site. In Saranac Lake there were only two individuals in one sample of *M. spicatum,* and *A. ephemerella* was not found on *M. alterniflorum*. In Chateaugay Lake, *A. ephemerella* was also not present on *M. alterniflorum*, but was found in 38% of the samples of *M. spicatum,* and thus grouped with *M. spicatum* in the DCA analysis (Fig 8 a, b). In the Richelieu River and Lac St-Louis, *A. ephemerella* found on both *M. sibericum* and *M. spicatum*; however, in the Richelieu River *A. ephemerella* grouped with samples of *M. spicatum* in the DCA analysis (Fig 8 c, d). In the Richelieu River, *A. ephemerella* was present in 38% of the *M. spicatum* samples and 27% of the *M. sibericum* samples, and in Lac St-Louis these numbers were 16% and 10%, respectively.

In Lac St-Louis, the abundance of the Eurasian snail *Bithynia tentaculata* did not differ significantly between the two plant species on any of the sampling dates (Fig 10 a). In the Richelieu River, the density of *D. polymorpha* was significantly higher on *M. sibericum* than on *M. spicatum* only in September (T-test, $p < 0.01$, Fig 10b); in July, very few zebra mussels were found on either species of plant.

DISCUSSION

To our knowledge, the current study is the first to compare invertebrate communities on native and exotic species of *Myriophyllum*. Previous studies that compared epiphytic invertebrates on *M. spicatum* to native plants have found contrasting results (Table 3), probably because each study compared *M. spicatum* to plants of differing phylogeny, structure and life-history traits.

Invertebrate Density and Biomass

The results of this study show that invertebrate community structure generally differs on exotic and native *Myriophyllum* species. However, the relationship between invertebrate abundance on exotic and native species of *Myriophyllum* varies throughout the summer, with differences in invertebrate density becoming more pronounced later in the season. As *M. spicatum* grows quickly in the spring (Grace and Wetzel 1978), it provides the first plant substrate and resources to invertebrates in some lakes. At our sampling sites, *M. spicatum* grew earlier than both species of native *Myriophyllum*, providing invertebrates with a longer period to colonize *M. spicatum* (personal observation). Because of this, we might have expected *M. spicatum* to support more invertebrates early in the summer, but instead there was generally no difference in invertebrate density. By late summer, invertebrates have had time to colonize and differentiate between plant species. It may be that the importance of subtle differences between plant species, such as plant exudates or epiphytic algal communities, have had sufficient time to affect invertebrate abundance by that late stage in the season.

Different species of aquatic plants often support epiphytic algal communities that differ in abundance and taxonomic composition (Blindow 1987, Cattaneo et al. 1998, Laugaste and Reunanen 2005). By mid June to July, algae growing on aquatic plants in the St. Lawrence River and surrounding areas approaches peak biomass (Cattaneo 1983, Gosselain et al. 2005), and so we would expect differences in the epiphytic algal communities of native and exotic *Myriophyllum* to be more apparent in mid summer. Differences in the abundance or composition of epiphytic algae on different plant species could drive dissimilarities in invertebrate communities that are structured around epiphytic algae as a food source. Cattaneo (1983) found that the abundance of invertebrate grazers – invertebrates that feed on epiphytic algae – increased substantially a short time after peak epiphyte biomass, thus illustrating that invertebrate abundance partially depends on epiphyte abundance.

In this study, gastropods, which both graze on epiphytic algae and consume plants directly (Pip and Stewart 1976, Lodge 1986, Sheldon 1987, Bronmark 1989), were significantly more abundant on both native *Myriophyllum* species at three out of the four sites. Since native *M. sibericum* and exotic *M. spicatum* are very similar in structure and have approximately equal plant surface area per gram of dry plant weight (Gerber and Les 1994), we can safely conclude that differences in gastropod abundance and biomass between the two species were not the result of differences in the area available for colonization of either gastropods or epiphytic algae. As gastropod abundance may vary with epiphytic algal biomass and community composition (Lodge et al. 1986, Bronmark et al. 1989), differences in epiphytic algae communities between native and exotic *Myriophyllum* species may be driving this result. Whatever the mechanism, it has been previously noted that some species of gastropods preferentially inhabit certain plant species, even when these plants are closely related (Pip and Stewart 1976, Sheldon 1987).

Plant structure

Submerged aquatic plants are often grouped into two main structural categories based on leaf morphology: dissected (complex) leaves or entire (simple) leaves (i.e. Krecker 1939, Cheruvelil et al. 2002). By these standards, the three species of *Myriophyllum* in the current study have very similar structure, as all three plants have dissected leaves arranged in whorls of four around the stem. On a finer scale, there are subtle structural differences between the three species. *Myriophyllum alterniflorum* tends to branch more frequently and has slightly smaller leaves than *M. spicatum* or *M. sibericum* (Fig 2). *Myriophyllum spicatum* and *M. sibericum* have very similar specific leaf area (surface area of leaf/dry weight of leaf) and leaf surface area/volume ratios, but *M. alterniflorum* has significantly higher specific leaf area and volume ratios than both other species (Gerber and Les 1994). In addition, dry leaf mass comprises ~65% of the total dry weight of leaves and shoots for both *M. spicatum* and *M. sibericum,* and ~55% for *M. alterniflorum* (Gerber and Les 1994). Hence, subtle differences in leaf morphology exist between *M. alterniflorum* and *M. spicatum*, but *M. spicatum* and *M. sibericum* have quite similar leaf morphology. The range of whole plant surface area/ g biomass ratios on *M. spicatum* and *M. sibericum* also overlap, varying between 320 and 1205 cm^2/g on *M. spicatum*, and between 534 and 761 cm^2/g on *M. sibericum* (Kowalczewski 1975, Gerrish and Bristow 1979, Sushma et al. 1995, Armstrong et al. 2003). Thus, while the dissimilarity in invertebrate communities on *M. alterniflorum* and *M. spicatum* may be partially attributed to plant structure, structural differences are less likely to cause differences in invertebrates between *M. sibericum* and *M. spicatum.*

It is likely that plant characteristics other than structure influence invertebrate abundance and diversity on these plants. Marko et al. (2005) found that the milfoil weevil, a specialist herbivore native to North America, prefers *M. spicatum* to its native host, *M. sibericum*, and this preference is driven by differences in the amount of certain chemicals exuded by these plants. Previous studies have also found that *M. spicatum* exudes chemicals that may deter the growth of certain types of epiphytic algae, and that these chemicals may differ either in the type or amount exuded relative to other species of *Myriophyllum* (Gross et al. 1996). Thus, chemical differences exist between different species of *Myriophyllum*, and these may affect both the relative palatability of these plants to herbivores, and the growth of epiphytic algae, an important invertebrate food source.

Exotic invertebrates

The invasional meltdown hypothesis postulates that previously established exotic species facilitate the invasion or proliferation of other exotic species. This may occur by different mechanisms, including co-adaptation of exotic species in their native range prior to invasion (Simberloff and Von Holle 1999). This hypothesis predicts that *M. spicatum* would support more exotic invertebrates than either *M. sibericum* or *M. alterniflorum*. However, this hypothesis is not supported by the results of our study. For example, the abundance of the exotic snail *Bithynia* *tentaculata* was not significantly different on native and exotic plants. *Bithynia tentaculata* established in the Great Lakes and St. Lawrence River area more than a century ago, several decades prior to the recorded invasion of *M. spicatum*, and therefore may have had sufficient time to adapt to native plants (Aiken et al. 1978, Mills et al. 1993). In the Richelieu River, *M. sibericum* supported more zebra mussels than *M. spicatum*; however, it is unlikely that differences in plant exudates or epiphytic algae would have driven this result, given that zebra mussels are filter feeders and use plants as a substrate on which to settle (Lewandowski 1982). The veliger larvae of zebra mussels are planktonic and eventually settle and grow on solid surfaces, and so submerged plants may become densely colonized by juvenile mussels (Lewandowski 1982). Given that larval dispersal is largely determined by vagaries of water currents (Lewandowski 1982), it is likely that small-scale differences in hydrology within a site rather than differences between plant species determine the degree to which the mussels colonize plants.

The exotic moth *A. ephemerella* was the only exotic invertebrate that appeared to preferentially colonize exotic *M. spicatum*. The density of *A. ephemerella* was slightly higher on *M. spicatum* than on either native species of *Myriophyllum* at all four sites, and in the Richelieu River and Chateaugay Lake DCA analysis showed that this moth tended to group with exotic plant samples. Not a single *A. ephemerella* was collected from samples of *M. alterniflorum* in either Chateaugay or Saranac Lake, while at both these sites *A. ephemerella* was found on *M. spicatum*, perhaps indicating that *A. ephemerella* prefers to colonize *M. spicatum*. This moth was introduced from Europe, and was first discovered in the St. Lawrence River in 1927 (Berg 1942, Sheppard 1945). *Acentria ephemerella* is a generalist herbivore that feeds on many species of plants (Buckingham and Ross 1981). It is therefore highly possible that *A. ephemerella* and *M. spicatum* could have interacted over the course of their evolution in their native range. Currently, this moth is being studied as a possible biological control agent for *M. spicatum* (Johnson et al. 2000). At our study sites, *A. ephemerella* was often found on native *M. sibericum* growing in the same area as *M. spicatum*, which suggests that in areas where native and exotic *Myriophyllum* co-occur, caution should be used before introducing this species into new regions, even though it may cause more damage to *M. spicatum* than to native plants (Johnson et al.1997).

Implications for aquatic communities:

The establishment of *M. spicatum* may reduce the density of many species of native plants, including native milfoils (Grace and Wetzel 1978, Smith and Barko 1990, Boylen et al. 1999). Since *M. spicatum* supports lower invertebrate diversity and biomass than its native congeners, the displacement of native *Myriophyllum* species by *M. spicatum* could conceivably cause habitat-wide reductions in epiphytic invertebrate diversity and biomass. In addition, the species composition of invertebrate communities may change. Such changes may have indirect impacts on vertebrate predators including amphibians, fish, and waterfowl. Invertebrate biomass on *M. alterniflorum* was greater or equivalent to invertebrate biomass on *M. spicatum,* even though invertebrate density on *M. alterniflorum* was lower than on *M. spicatum* in late summer, suggesting that the mean body size of invertebrates may be reduced by *M. spicatum* invasion. This is also reflected in the community composition of the invertebrates on these plants, as *M. alterniflorum* supported larger snails and amphipods, while *M. spicatum* was dominated by smaller annelids and chironomids. A shift to smaller, less energetically profitable invertebrates might alter food quality and accessibility for fish and waterfowl (Werner and Hall 1974, Egger 1977). Smaller size and lower diversity of benthic invertebrates can limit the body size of yellow perch (*Perca flavescens*) (Kovecses et al. 2005). *Myriophyllum spicatum* also supported fewer snails than the two native *Myriophyllum* species, reducing the food available for molluscivorous fish. Overall, these results suggest that the effects of *M. spicatum* invasion on epiphytic invertebrates may have multiple indirect effects on local and habitat-wide scales.

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Table 1: Characteristics of sites sampled, 2005.

Site	Location	Plants sampled	Water body type	No. of Samples (E,N)	Water temp min/ max (C°)	pH range	Depth at site (m)	Other plant species present	Notes
Lac St-Louis	SW of the Island of Montreal, part of St Lawrence River, Quebec	***M. spicatum,*** *M. sibericum*	Fluvial Lake	7,6 June 6,6 July 6,7 Aug **= 19, 19**	21 (Jun)/ 27 (Aug)	7.9-9.4	0.5-1.0	*C. demersum, E. canadensis,* ***P. crispus,*** *P. perfoliatus, Potamogeton* sp., *Ranuculus* sp. , *V. americana*	Site near boat launch against breaker, moderate to high wave action
Richelieu River	Central Quebec, connects Lake Champlain and the St Lawrence River	***M. spicatum,*** *M. sibericum*	River	10,10 July 9,9 Aug 7,7 Sept **= 26, 26**	19 (Sep)/ 24 (Jul and Aug)	8.2-9.1	1.5-2.0	*C. demersum, E. canadensis, E. nuttallii ,* ***P. crispus****, P. richardsonii, Potamogeton* sp., *Ranuculus* sp., *V. americana*	Site near mid river wetland, steady current, low wave action
Upper Saranac Lake	Adirondack State Park, Upstate New York	***M. spicatum*** *M. alterniflorum*	Lake	21,21 July 18,18 Aug **=39, 39**	19 (Aug)/ 21 (Jul)	7.7-7.9	1.5-2.0	*C. demersum, E. canadensis, P. crispus, P. richardsonii, V. americana*	Site of *M. spicatum* control program, low wave action
Upper Chateaugay Lake	Adirondack State Park, Upstate New York	***M. spicatum*** *M. alterniflorum*	Lake	7,7 July 9,9 Aug **=16, 16**	17(Aug)/ 21 (Jul)	6.7-7.8	1.0-1.5	*E. canadensis, P. richardsonii, Ranuculus* sp., *Utricularia* sp., *V. americana,*	Site near lake inflow and wetland, S end of lake, low wave action

Note:

Exotic plant species are in bold. Macrophyte genera are as follows: *C – Ceratophyllum, E – Elodea, P – Potamogeton, and V – Vallisneria.* Number of samples gives the number of samples of exotic and native plants on each sampling date, followed by a total in bold.

Table 2: Taxa richness, Shannon-Wiener diversity, and Simpson diversity compared on native and exotic *Myriophyllum* species.

Site	Taxa Richness		Exp (Shannon-Wiener)		1/Simpson diversity		Invertebrate Abundance
	Native	Exotic	Native	Exotic	Native	Exotic	
Lac St-Louis	40.4	42	7.5	7.8	4.2	4.3	1050
Richelieu River	45.4	43	4.6	3.6	2.8	2.1	7020
Saranac Lake	31.5	22	6.5	4.8	3.6	2.8	580
Chateaugay Lake	26	18	8.3	4.3	6.1	3.1	650

Note:

The exponent of Shannon-Wiener diversity represents the number of different invertebrate species we would find if all species in the community were equally common, and thus provides a less abstract measure of diversity than the raw Shannon-Wiener values (Jost 2006). The inverse of Simpson diversity also represents the number of species that would be found if all species were equally common (Jost 2006); however, Simpson diversity is weighted more heavily on how evenly invertebrate abundance is distributed across taxa than Shannon-Wiener diversity. Diversity comparisons on native and exotic plants were made at the abundance listed, which is the abundance of invertebrates on the plant species with fewer invertebrates.

Table 3: Invertebrates on *Myriophyllum spicatum* in invaded ecosystems compared to those on native plants.

Study	Region	Sampling Year(s)	Native plants	Invertebrate	
				Taxa richness	Density
Keast 1984	SE Canada	1979	*Potamogeton robbinsii, Vallisneria americana*	N/A	E > N (47, 25)
Chilton 1990	Midwest USA	1983	***Ceratophyllum demersum***	N/A	E < N (253, 676)
Cheruvelil et al. 2000	Midwest USA	1998	***Ranuculus*** **sp.,** ***Potamogeton pectinatus***	N/A	E < N (75, 77)
Krull 1970	NE United States	1966	***Ceratophyllum demersum, Elodea canadensis, Utricularia vulgaris,*** *Potamogeton pectinatus, Lemna trisulca, Najas flexilis, N. marina, Heteranthera dubia, Rhizoclonium hieroglyphicum*	E < N (18, 33)	E < N (36, 100)
Balci and Kennedy 2003	Southwest USA	1998	*Heteranthera dubia*	E < N (21, 24)	E = N* (2276, 1888)
Krecker 1939	NE United States	1935-36	***Elodea canadensis, Potamogeton pectanus, P. compressus***	E > N (22, 14)	E > N** (1442, 535)

Note:

E = exotic plant (*M. spicatum*), N = native plant. Plants with similar structure (divided leaves) to *M. spicatum* are in bold. Density is the number of invertebrates per unit plant weight, unless otherwise indicated.

* This study looked at the number of invertebrates per m^2 plant surface area.

* *This study looked at number of invertebrates per 10m length of stem.

FIGURE CAPTIONS

Figure 1: Map of study sites in Southern Quebec and Upstate New York, 2005. In Lac St-Louis and the Richelieu River (Quebec), native *Myriophyllum sibericum* and exotic *M. spicatum* were sampled and in Upper Saranac Lake and Upper Chateaugay Lake (New York), native *M. alterniflorum* and exotic *M. spicatum* were sampled.

Figure 2: Sketches of a) *Myriophyllum sibericum*; b) *M. spicatum*; and c) *M alterniflorum.*

Figure 3: Invertebrate biomass on exotic and native *Myriophyllum* species (±1 SE). Filled circles represent native plants, open circles, exotic plants. * Indicates a significant difference in invertebrate biomass on native and exotic plants, ¶indicates a significant difference between dates, ** indicates a significant interaction between plant type and date (Two-way ANOVA, $p < 0.05$).

Figure 4: Gastropod biomass on exotic and native *Myriophyllum* species (±1 SE). Filled circles represent native plants, open circles, exotic plants. * Indicates a significant difference in gastropod biomass on native and exotic plants (Two-way ANOVA, $p < 0.05$). No interaction or date terms were significant.

Figure 5: Invertebrate density (number of invertebrates per gram of plant dry weight) on exotic and native *Myriophyllum* species (±1 SE). Filled circles represent native plants, open circles, exotic plants. * Indicates a significant difference in invertebrate density on native and exotic plants, ¶indicates a significant difference between dates, ** indicates a significant interaction between plant type and date (Two-way ANOVA, $p < 0.05$).

Figure 6: Rarefaction curves for invertebrate taxa richness on exotic and native *Myriophyllum* species. Filled circles represent native plants, open circles, exotic plants. Error bars represent standard deviation based on 50 randomized runs.
* Indicates a significant difference in invertebrate taxa richness between the two plant species ($p < 0.05$)

Figure 7: Shannon-Wiener diversity of invertebrates on exotic and native *Myriophyllum* species. Filled circles represent native plants, open circles, exotic plants. Error bars represent standard deviation based on 50 randomized runs. * Indicates a significant difference in invertebrate Shannon-Wiener diversity between the two plant species ($p < 0.05$)

Figure 8: Detrended correspondence analysis of the invertebrate communities at Chateaugay Lake and the Richelieu River. At Chateaugay Lake, numbers (a) up to 16 are from July, those greater than 16 are from August; in the Richelieu River, c) from 1-21 are from July, 22-40 are from August, and 41-55 are from September. Species codes (b, d) are as follows: *Ac = Acentria ephemerella (nivea),* Lepidoptera; *Am = Amnicola limosa,* Gastropoda; *Br = Brachycentrus sp,* Trichoptera; *Ca = Caenis* sp., Ephemeroptera; *Cd* = Cladocera; *Ce* = Ceratopogonidae, Diptera; *Ch* = Chironomidae, Diptera; *Ci = Chimarra* sp., Trichoptera; *Cl* = Cladocera; *Co* = Coenagrionidae, Odonata; *Dr = Dreissena polymorpha,* Mollusca; *Dt = Dugesia tigrina,* Tubellaria; *Du = Dugesia* sp., Tubellaria; *El* = Elmidae, Coleoptera; *En = Enallagma* sp., Odonata; *Eu =Euhrychiopsis lecontei*, Coleoptera; *Ga = Gammarus* sp., Amphipoda; *Gy = Gyraulus circumstratus,* Gastropoda; *Hd* = Hydracarina; *He = Helobdella* sp., Annelida; *Ho = Orthotrichia* sp., Trichoptera; *Hx = Oxyethira* sp., Trichoptera; *Hy = Hyalella azteca,* Amphipoda; *Is* = Isopoda; *Le* = Leptoceridae, Trichoptera; *Ll = Leptocerus* sp., Trichoptera; *Nc = Nectopsyche* sp., Trichoptera; *Ne = Nehalennia* sp., Odonata; *Ni* = Nididae, Annelida; *Os* = Ostracoda; *Pe = Promenetus exacuous exacuous,* Gastropoda; *Ph = Physa gyrina gyrina,* Gastropoda; *Pl = Platycentropus,* Trichoptera; *Po = Polycentropus* sp., Trichoptera; *Pp = Pristina* sp., Annelida; *Py* = Pyralidae, Lepidoptera; *St = Stylaria lacustris,* Annelida; *Tr = Triaenodes* sp., Trichoptera; *Vs = Valvata sincera,* Gastropoda.

Figure 9: Density of (a) zebra mussels (*Dreissena polymorpha*) in the Richelieu River (±1 SE), and (b) an exotic snail (*Bithynia tentaculata*) in Lac St-Louis (±1 SE). Filled circles represent native plants, open circles, exotic plants. * Indicates a significant difference in invertebrate biomass on native and exotic plants (T-test, $p < 0.05$).

Figure 1

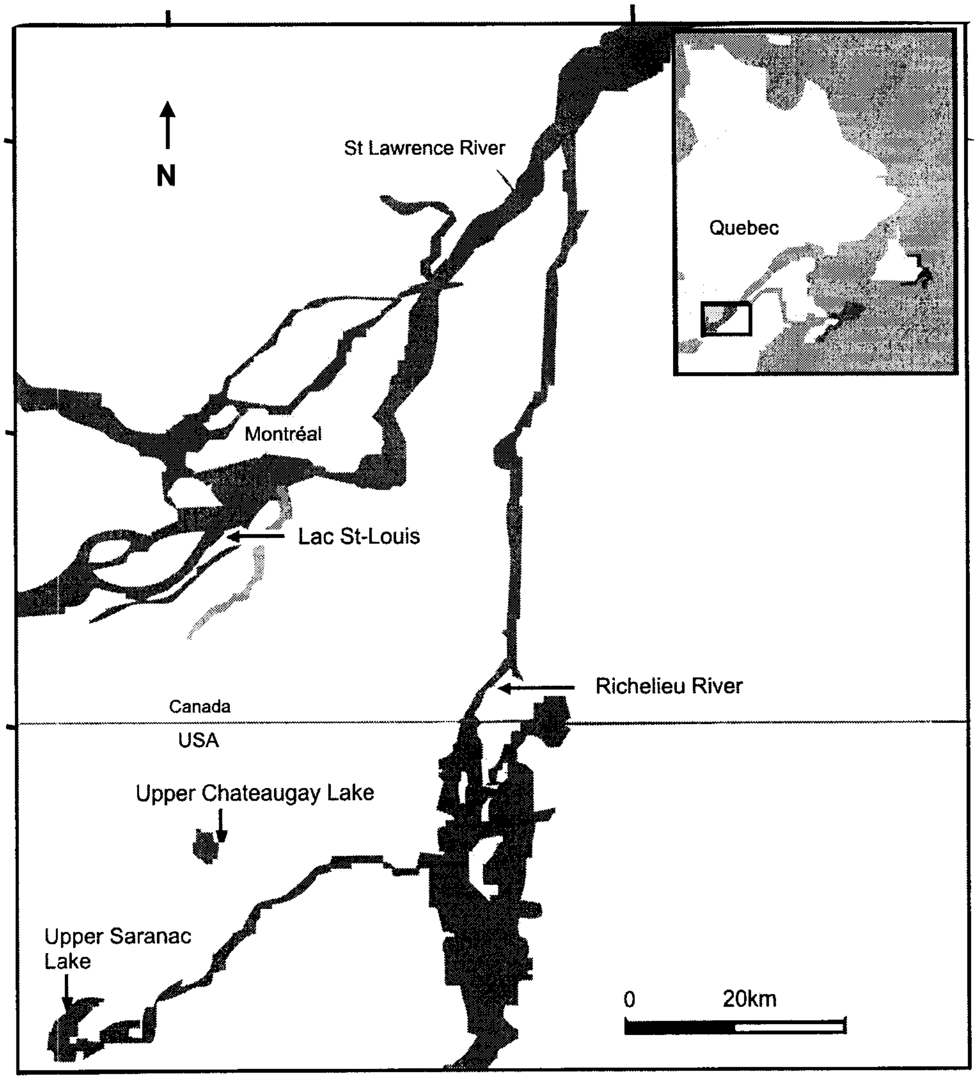

N
St Lawrence River
Quebec
Montréal
Lac St-Louis
Richelieu River
Canada
USA
Upper Chateaugay Lake
Upper Saranac Lake
0
20km

Figure 2

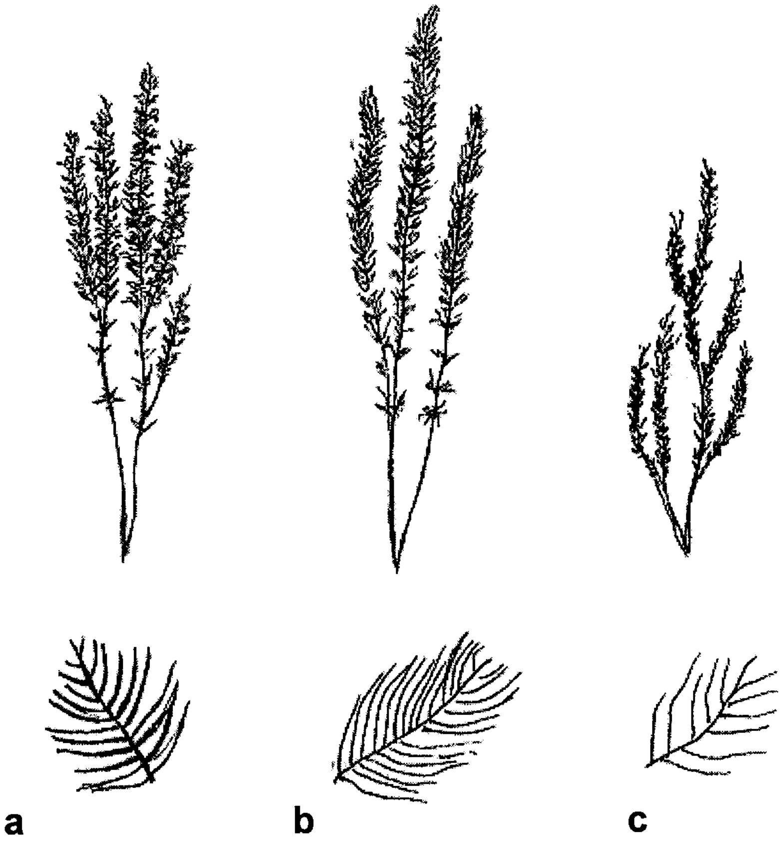


Figure 3

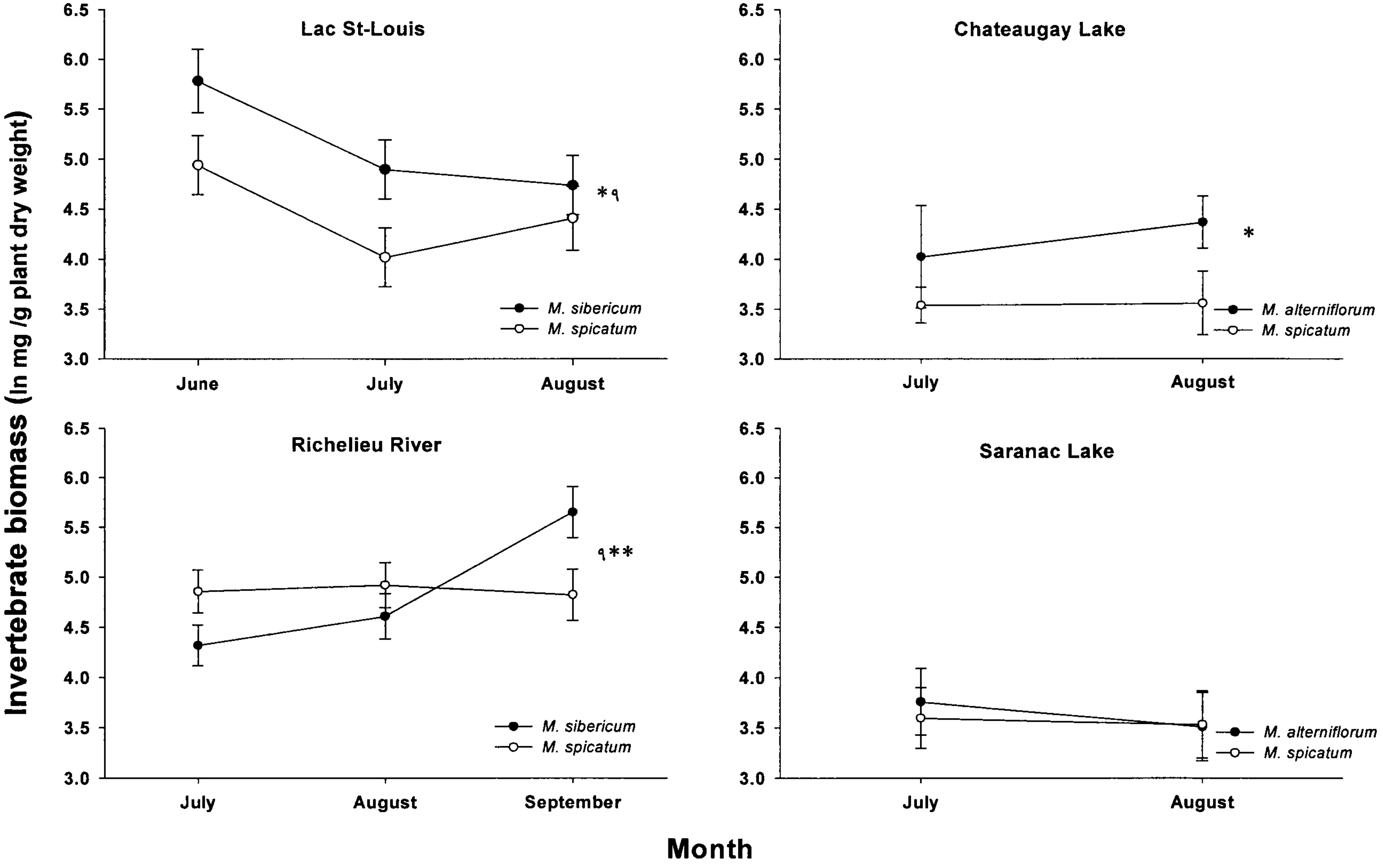

Invertebrate biomass (ln mg /g plant dry weight)
Month
Lac St-Louis
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
June
July
August
*¶
M. sibericum
M. spicatum
Chateaugay Lake
July
August
*
M. alterniflorum
M. spicatum
Richelieu River
July
August
September
¶**
M. sibericum
M. spicatum
Saranac Lake
July
August
M. alterniflorum
M. spicatum

Figure 4

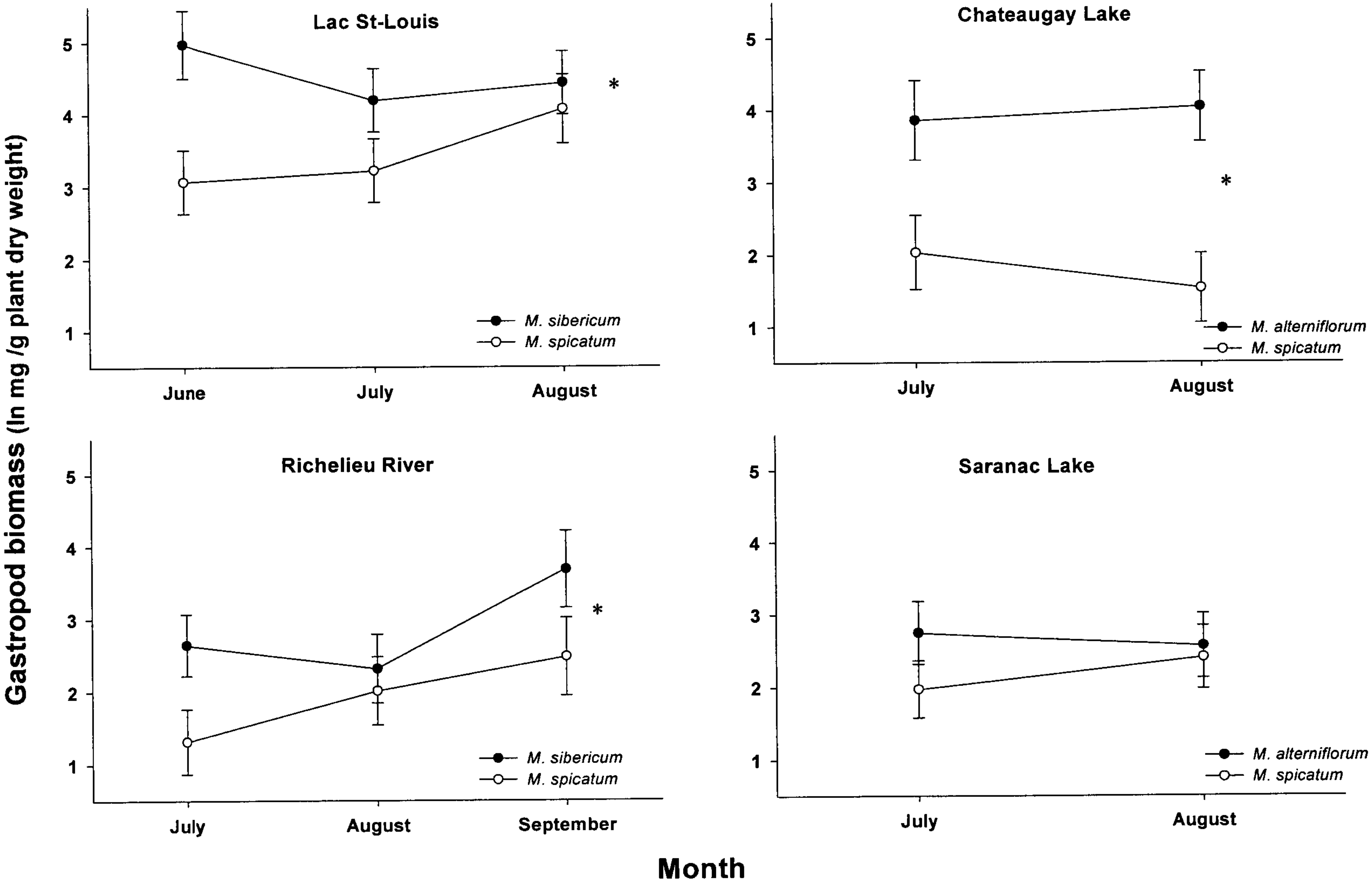

Lac St-Louis
Chateaugay Lake
Richelieu River
Saranac Lake
Gastropod biomass (ln mg /g plant dry weight)
1
2
3
4
5
June
July
August
September
*
M. sibericum
M. spicatum
M. alterniflorum
Month

Figure 5

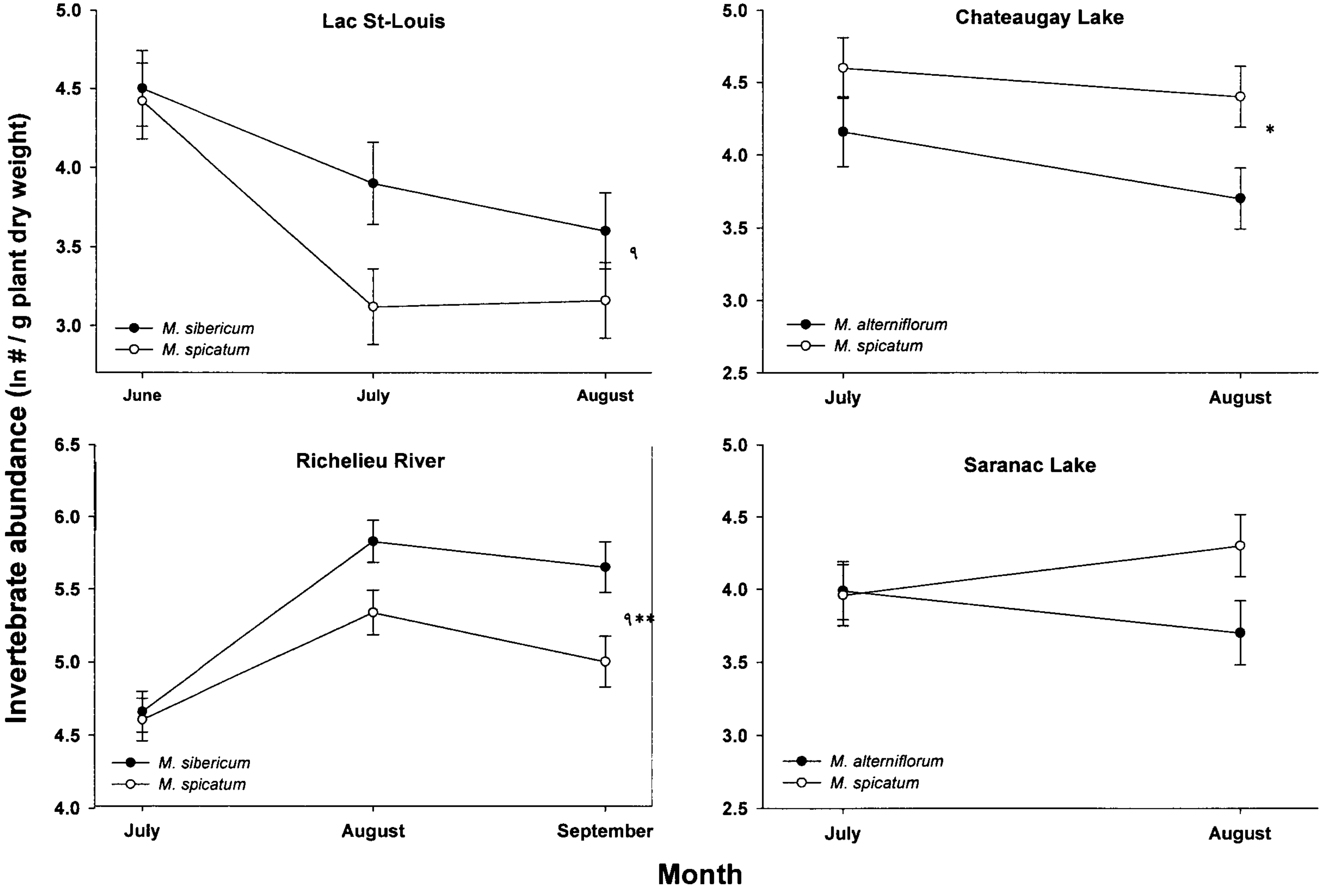

Lac St-Louis
5.0
4.5
4.0
3.5
3.0
June
July
August
٩
M. sibericum
M. spicatum
Chateaugay Lake
5.0
4.5
4.0
3.5
3.0
2.5
July
August
*
M. alterniflorum
M. spicatum
Richelieu River
6.5
6.0
5.5
5.0
4.5
4.0
July
August
September
٩**
M. sibericum
M. spicatum
Saranac Lake
5.0
4.5
4.0
3.5
3.0
2.5
July
August
M. alterniflorum
M. spicatum
Invertebrate abundance (ln # / g plant dry weight)
Month

Figure 6

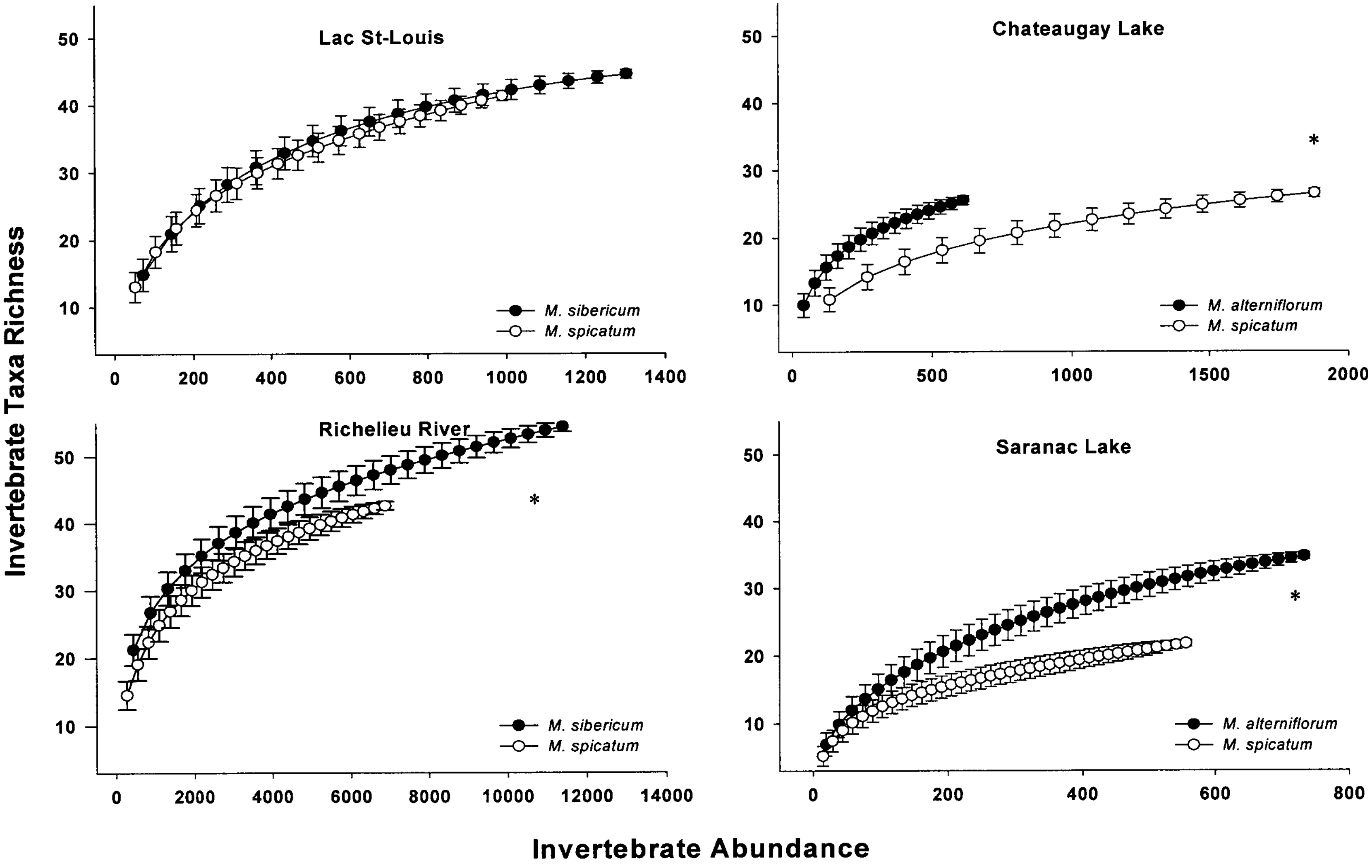
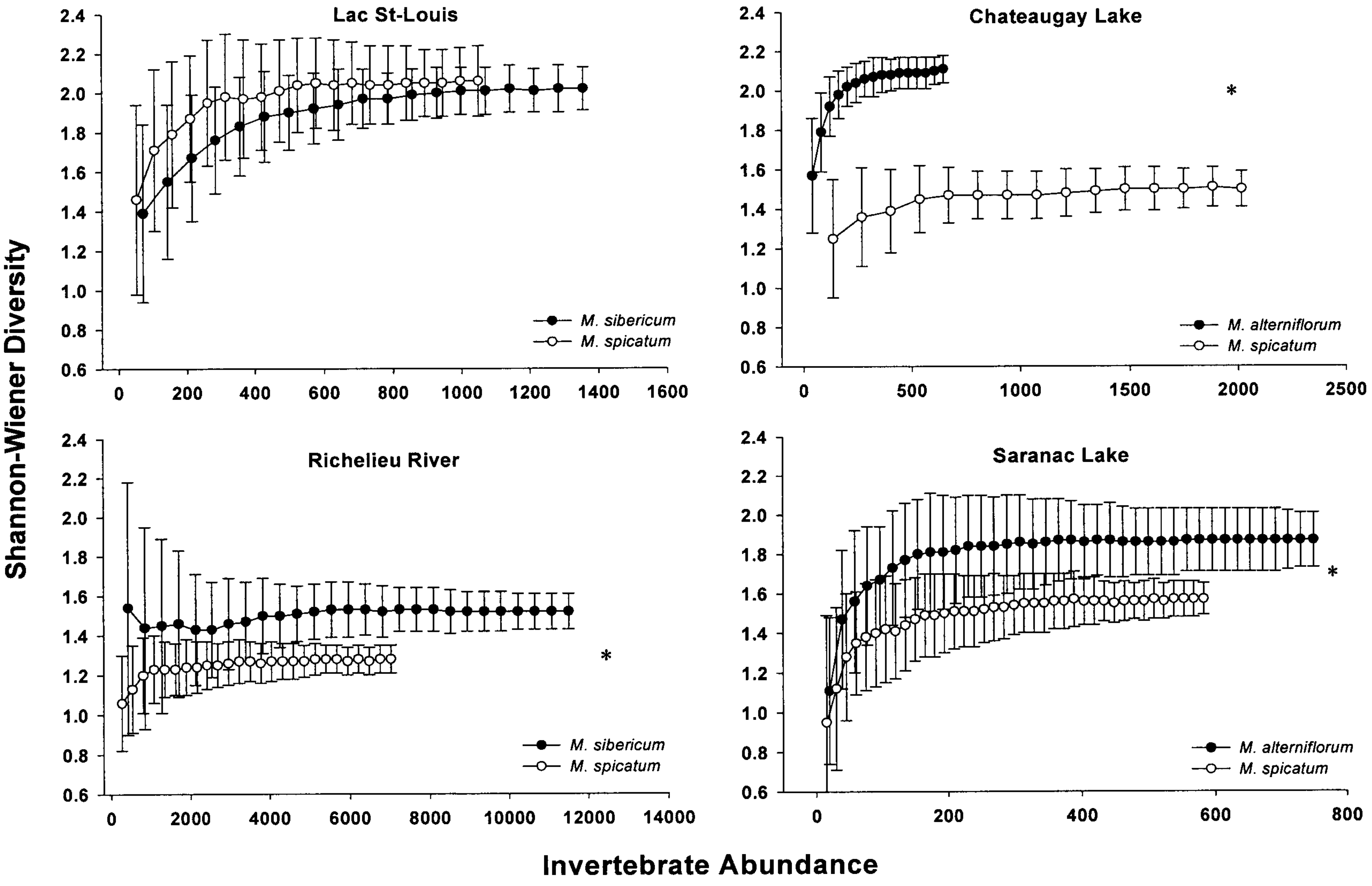

Lac St-Louis
Chateaugay Lake
Richelieu River
Saranac Lake
M. sibericum
M. spicatum
M. alterniflorum
M. spicatum
*
Invertebrate Taxa Richness
Invertebrate Abundance
10
20
30
40
50
0
200
400
600
800
1000
1200
1400
500
1000
1500
2000
2000
4000
6000
8000
10000
12000
14000

Figure 7



Lac St-Louis
Chateaugay Lake
Richelieu River
Saranac Lake
Shannon-Wiener Diversity
Invertebrate Abundance
M. sibericum
M. spicatum
M. alterniflorum
*
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0
200
400
600
800
1000
1200
1400
1600
500
1500
2000
2500
2000
4000
6000
8000
10000
12000
14000

Figure 8

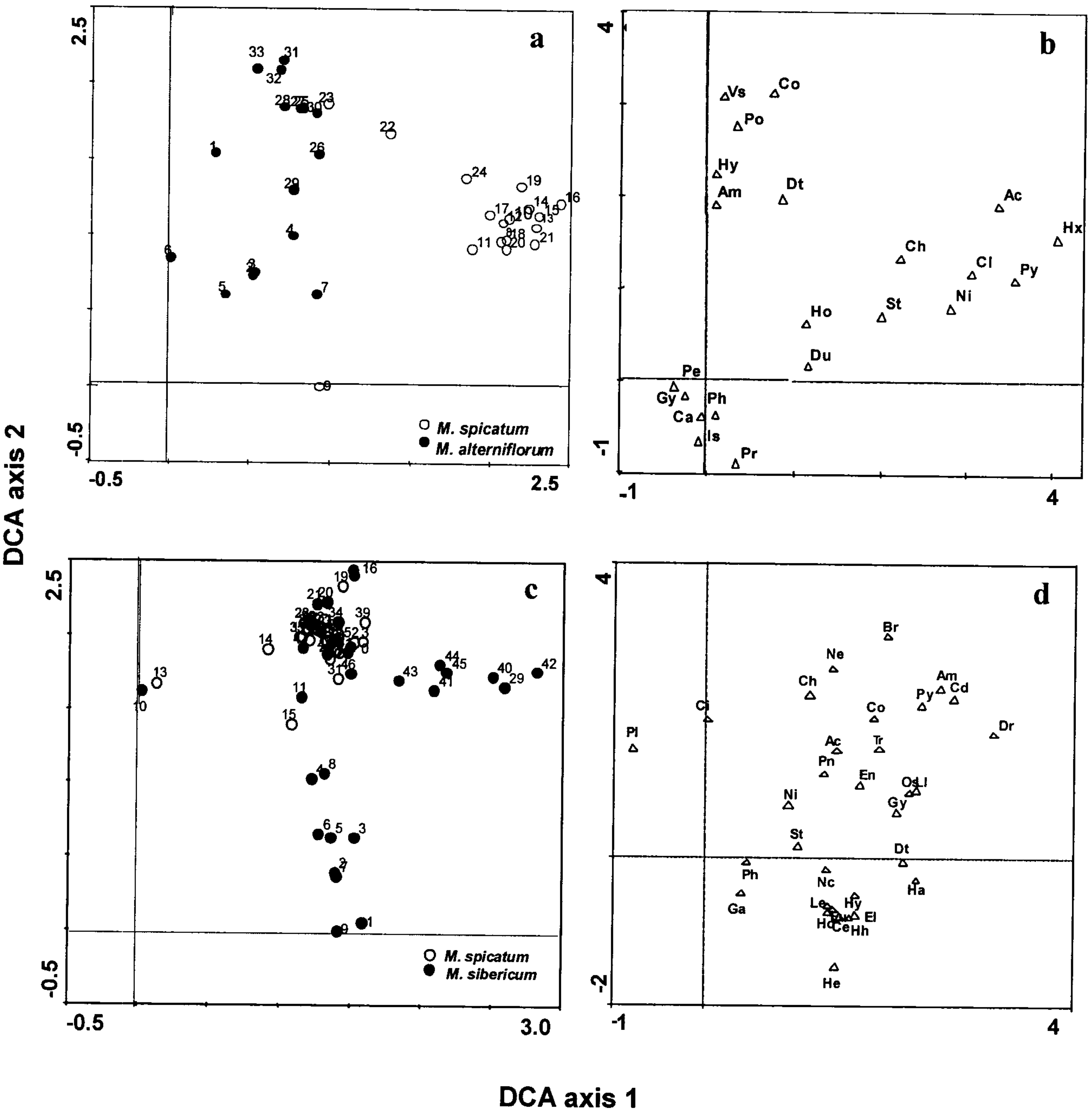
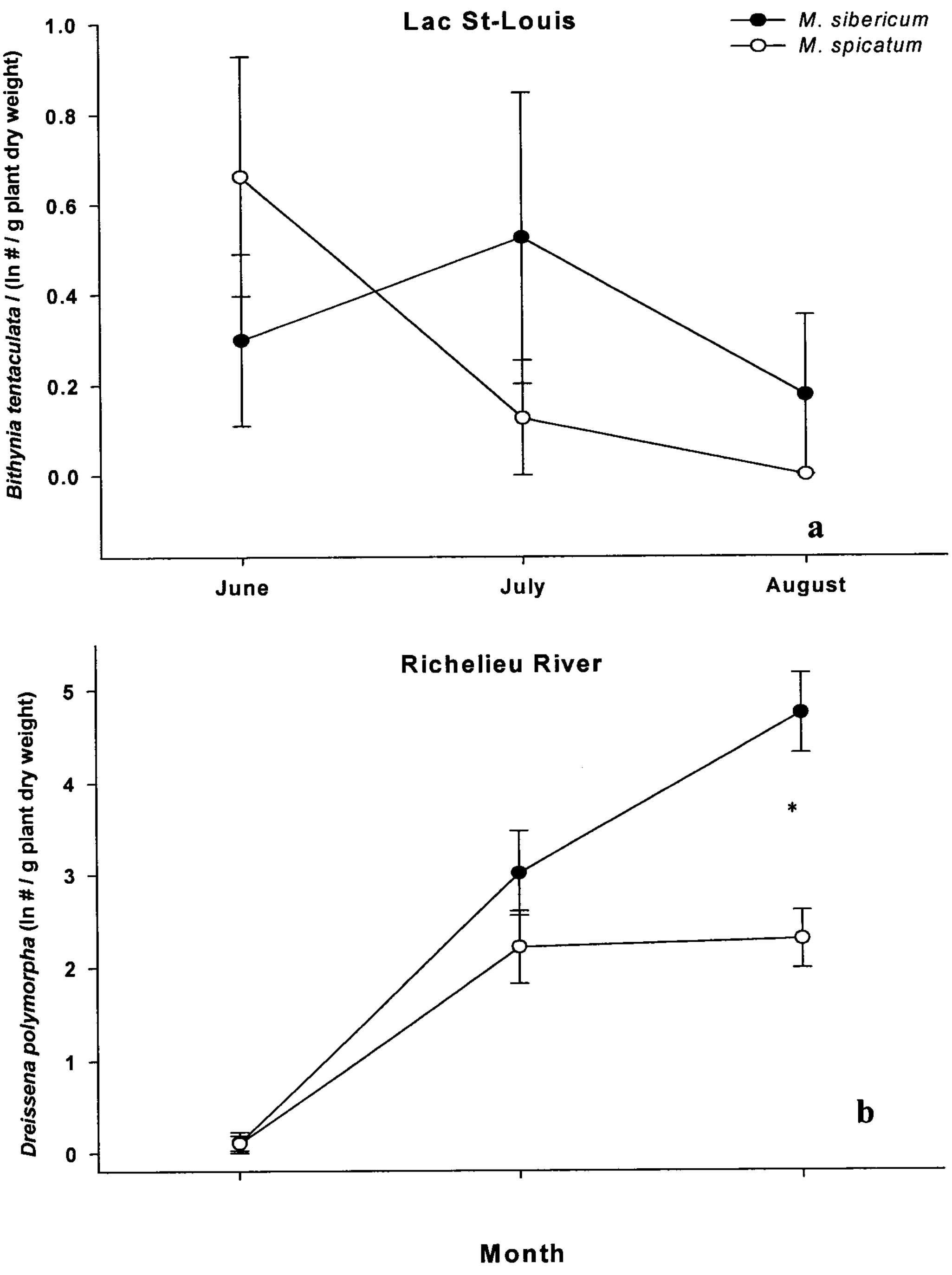

a
b
c
d
DCA axis 2
DCA axis 1
2.5
-0.5
-0.5
2.5
4
-1
-1
4
2.5
-0.5
-0.5
3.0
4
-2
-1
4
M. spicatum
M. alterniflorum
M. spicatum
M. sibericum
Vs
Co
Po
Hy
Am
Dt
Ac
Hx
Ch
Cl
Py
Ni
St
Ho
Du
Pe
Gy
Ph
Ca
Is
Pr
Br
Ne
Am
Ch
Py
Cd
Ci
Co
Pl
Dr
Ac
Tr
Pn
En
Os
Li
Ni
Gy
St
Dt
Ph
Nc
Ha
Ga
Le
Hy
Hc
Ce
El
Hh
He

Figure 9


Lac St-Louis
M. sibericum
M. spicatum
Bithynia tentaculata / (ln # / g plant dry weight)
1.0
0.8
0.6
0.4
0.2
0.0
a
June
July
August
Richelieu River
Dreissena polymorpha (ln # / g plant dry weight)
5
4
3
2
1
0
*
b
Month

CONNECTING STATEMENT

From chapter 1, it is clear that *Myriophyllum spicatum* supports different invertebrate communities than do its structurally similar, native congeners. Invertebrate biomass, density, and diversity differed between native and exotic *Myriophyllum*, as did the types of invertebrates that these plants supported. However, I do not know if my findings for *Myriophyllum* can be generalized to other invasive plants.

The exotic *Potamogeton crispus* may also co-occur with or replace its native congeners in North America. *Potamogeton crispus* and *M. spicatum* are similar in that they are both submerged aquatic plants, introduced into North America from Eurasia. However, *P. crispus* and *M. spicatum* have different invasion histories – *P. crispus* was found in North America several decades before *M. spicatum*; they also have different morphologies – *P. crispus* has broad curly leaves while *M. spicatum* has finely divided ones. Thus, the differences in invertebrate communities between exotic and native *Potamogeton* may or may not resemble those between exotic and native *Myriophyllum*.

In the next chapter, I investigate this question by comparing invertebrate communities on exotic and native species of *Potamogeton*. I also compare epiphytic algal biomass on exotic and native *Potamogeton*, and examine the relationship between invertebrate biomass and epiphytic algal biomass.

Epiphytic macroinvertebrates and algae on the exotic freshwater plant *Potamogeton crispus* and its native congeners

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ABSTRACT

Aquatic plants are an important component of aquatic ecosystems, both as a major source of primary productivity and as substrate for epiphytic algae and invertebrates. Currently, exotic aquatic plant invasions are increasing on a global scale, but the effects of these plants on epiphytic invertebrate communities are still largely unknown. The objective of this study was to determine if closely related exotic and native plants support similar invertebrate abundance, diversity, and community composition, and also to examine the role of epiphytic algae in this relationship. To address this, we compared epiphytic invertebrate communities and epiphytic algal biomass on the exotic *Potamogeton crispus* to those on the native *P. perfoliatus* and *P. richardsonii*. We sampled plants and invertebrates from four lakes and rivers in southern Quebec during the spring and early summer of 2006. Exotic *P. crispus* tended to support greater invertebrate density than either species of native *Potamogeton*, while at three out of four sites native *Potamogeton* species had higher invertebrate taxa richness than exotic *P. crispus*. Epiphytic algal biomass was negatively correlated with invertebrate grazer biomass. Native and exotic *Potamogeton* supported different epiphyte biomass, but the direction of this difference varied across sites. Thus *P. crispus* supports an invertebrate community that differs in some aspects from those of its native congeners, but these differences are not strongly linked to epiphytic algal biomass.

INTRODUCTION

The effects of freshwater plant invasions on chemical and physical aspects of the environment have been well studied (Carpenter and Lodge 1986, Madsen 1997, Cattaneo et al. 1998, Caraco and Cole 2002), but relatively few studies have examined the effect of these invasions on plant-associated invertebrate communities (but see Keast 1984, Strayer et al. 2003, Toft et al. 2003). In particular, it is currently unknown whether exotic plants support similar invertebrate communities to closely related and morphologically similar native plants. Within a given region, interactions between freshwater native plants and invertebrates may have led to coadapted relationships. Given these potential affinities, and as the majority of freshwater invertebrates in North American systems are native (Pennak 1989, Merritt and Cummins 1996), we might expect native plants to support more invertebrates than exotic plants. Similarly, exotic plants may support more exotic invertebrates, especially if these species have a shared evolutionary history (Simberloff and Von Holle 1999, Toft et al. 2003).

Different species of aquatic plants often support epiphytic invertebrate communities that differ in density, biomass, diversity, and species composition (Krecker 1939, Chilton 1990, Cheruvelil et al. 2002). Two major factors that can affect the abundance or community composition of epiphytic invertebrates are a plant's structure (growth form and leaf morphology), and the substances (exudates) it secretes (Cheruvelil et al. 2002, Marko et al. 2005). In general, structurally complex plants with finely divided leaves support higher densities of epiphytic invertebrates than do plants with simple, undivided leaves (Krecker 1939, Cheruvelil et al. 2000, Cheruvelil et al. 2002). In addition, some plants exude chemicals, which can influence the abundance of invertebrates that feed on their tissues (Marko et al 2005). Epiphytic algal biomass and diversity also often differ between species of aquatic plants (Blindow 1987, Cattaneo et al. 1998), perhaps because aquatic plants exude biochemicals and nutrients (McRoy and Goering 1974, Carignan and Kalff 1982, Wium-Andersen et al. 1982, Pip 1992, Gross et al. 1996) that may influence the growth of epiphytic algae (Bronmark 1989, Gross et al. 1996). Thus if an exotic plant exudes chemicals that are different from those exuded by native plants, this could lead to differences in the epiphytic algal communities. As many invertebrates, known as grazers, feed on epiphytic algae, differences in epiphytic algae could lead to differences in grazer communities (Cattaneo 1983, Lodge 1986). Grazers often make up the majority of invertebrates on aquatic plants (Cattaneo 1983, Keast 1984); therefore, changes in grazer abundance could cause changes to the abundance or composition of the invertebrate community as a whole.

The overall objective of this study was to determine if *P. crispus* supports invertebrate communities similar to those on its native congeners, and the role of epiphyte biomass, if any, in this relationship. To achieve this goal, we compared invertebrate abundance, diversity, and community composition on an invasive exotic plant, *Potamogeton crispus*, and two of its common native congeners, *P. richardsonii* and *P. perfoliatus*. We also examined the relationship between invertebrate grazer biomass and epiphytic algal biomass on these plants. *Potamogeton crispus* is an ideal model organism for this study, as it was introduced into North America from Eurasia in the 1840s (Stuckey 1979) and is now established in a broad range of freshwater ecosystems across North America, where it sometimes dominates aquatic plant communities (Tobiessen et al. 1992). Both native *Potamogeton* species in this study are also widespread in North America (Crow and Hellquist 2000). Because the three *Potamogeton* species in this study have fairly similar leaf morphology (Fig 1), we might expect all three species to support similar invertebrate communities. Alternatively, because of potential coadaptation between native aquatic plants and invertebrates, we might expect that native species of *Potamogeton* would support more abundant and diverse aquatic invertebrate communities than the exotic *P. crispus*. Therefore, we tested the following hypotheses: (1) invertebrates are more abundant and diverse on native *Potamogeton* than on exotic *P. crispus*; (2) the exotic *P. crispus* supports more abundant exotic invertebrates than native *Potamogeton*; (3) invertebrate grazer abundance is positively related to epiphytic algal biomass, and (4) epiphytic algal biomass is higher on native plants.

METHODS

Field sites

We sampled exotic and native *Potamogeton* and associated invertebrates from four bodies of water in southern Quebec, located within a 120 km radius of the Island of Montreal (Fig 2). These sites include both lakes and rivers, and represent a range of environmental conditions in which exotic and native *Potamogeton* co-occur (Table 1). In each lake or river, we visually surveyed macrophytes prior to sampling, and selected one site within each waterbody where native and exotic *Potamogeton* were present in roughly equal abundance in a stand of mixed macrophytes. Because no sites were found that contained all three plant species, we chose sites that had the exotic *P. crispus* and either native *P. perfoliatus* or *P. richardsonii*. We then collected all subsequent samples from this same site in each waterbody; however, samples were collected from different individual plants each time. In Lac-St Louis and Lac Memphremagog, we sampled the native *P. perfoliatus* and the exotic *P. crispus*, and in Ile Charron and the Richelieu River, we sampled the native *P. richardsonii* and the exotic *P. crispus*. Because *P. crispus* senesces by mid summer, at each site we sampled once in late spring (late May/early June) and once in early summer (Late June/early July) of 2006, at one-month intervals. Due to extreme spring flooding in Lac Memphremagog and the Richelieu River, we were unable to sample at these two sites as early as at Lac-St Louis and Ile Charron in the St. Lawrence River.

Plant, epiphytic algae, and invertebrate sampling

Plants and epiphytic invertebrates were sampled as in Chapter 1. In addition, we also collected epiphytic algae from the plants in each sample, taking care not to dislodge epiphytes while harvesting the plants. We took seven to eight samples of each plant species at each site, and measured water temperature, pH, depth and other macrophyte species as in Chapter 1.

Sample processing

In the field, we sealed plants from each sample in plastic bags and stored them in a dark cooler. We removed loose invertebrates from the sampler using forceps and preserved them in 70% ethanol. We then transported plant samples to the lab where they were kept in a dark refrigerator and processed within 24 hours of collection. The remaining invertebrates were removed from the plants using forceps and preserved in 70% ethanol. To remove epiphytic algae, we placed each plant sample in a one-litre jar, added 150mL of water, and rapidly shook samples at a controlled rate for 90 seconds. We drained the water into a 500mL jar and repeated the process by rinsing the plants with an additional 100mL of water and shaking for another 60 seconds. For consistency, the same person processed all epiphytic algae samples. This method has been used by others and has been shown to effectively remove the bulk of the epiphytes on aquatic plants (Carignan and Kalff 1982, Cattaneo et al. 1998, Jones et al. 2000). After processing, plants appeared free of epiphytes and virtually all of the macrophyte leaves remained intact. We then blotted the plants dry, dried them at 65°C for 16 hours until a stable dry weight was reached, and weighed them using a digital scale to determine dry weight (± 0.01g). Epiphytic algae was filtered through a Whatman filter (GF, 48mm) in a Buchner funnel at low suction. Filters were stored in the freezer for two to three weeks, and the amount of chlorophyll *a* was determined using a spectrophotometer (Milton Roy Spectronic 401, Spectronic Instruments, USA) following the procedure of Bergman and Peters (1980).

We identified the preserved invertebrates to the lowest taxonomic level possible under a dissection microscope and used a digital scale to measure the wet weight of each order of invertebrates in each sample (± 0.001g). We weighed invertebrate order rather than species or genus, because the weight of specific taxa was often too small to be measured accurately. Although preservation alters the wet weight of invertebrates, for each date at each site all samples were stored in the same conditions (i.e. temperature and light) and weighed within the same week to minimize error due to desiccation in alcohol.

Statistical analysis

We calculated (1) the invertebrate density (number of invertebrates per gram plant dry weight), (2) invertebrate biomass (gram invertebrate wet weight per gram plant dry weight), (3) exotic invertebrate density (number of exotic invertebrates per gram plant dry weight), and (4) epiphytic algal biomass (μg chlorophyll *a* per gram dry plant weight) in each sample. These three measurements were log transformed prior to statistical analysis to meet assumptions of normality. At each site, we used two-way analysis of variance (ANOVA) with the factors plant type (native and exotic) and date (early and mid summer) to test for variation in (1) invertebrate density; (2) invertebrate biomass; (3) exotic invertebrate density; and (4) epiphytic algal biomass due to sampling date and plant type. All of the aforementioned tests were done using SPSS version 14.0 for Windows (SPSS Inc., Chicago, Illinois).

At each site we created individual-based Coleman rarefaction curves for taxa richness and accumulation curves for Shannon-Wiener diversity and inverse Simpson diversity on native and exotic *Potamogeton* (Colwell 2005). Shannon-Wiener and inverse Simpson diversity curves were calculated using 50 randomizations, sampled with replacement. This produces error bars that can be used for statistical comparison (Colwell 2005). These curves estimate the relationship between invertebrate diversity and invertebrate abundance for each plant species, which allows us to compare invertebrate diversity on native and exotic plants while controlling for differences in invertebrate abundance (Magurran 2004). To examine invertebrate community composition, at each site we ran a detrended correspondence analysis (DCA) using CANOCO version 4.5 (Biometris, Wageningen). Before running a DCA, we eliminated rare taxa, i.e., those present in fewer than three replicate samples at a site throughout the season. We calculated the density and biomass of invertebrate grazers, defined as those invertebrates that feed on epiphytic algae (Merritt and Cummins 1996, Barbour et al. 1999). Using regression analysis, we tested the relationship between invertebrate grazer biomass (biomass of grazers per gram dry plant weight) and epiphytic algal biomass (the residuals of a regression between chlorophyll *a* and plant dry weight. We then tested for differences in the relationship between grazer biomass and epiphyte biomass on native and exotic plants, using analysis of covariance (ANCOVA). We repeated the analysis using grazer density instead of grazer biomass. The above analyses were preformed using SPSS version 14.0 (SPSS 14.0, Chicago, Illinois).

RESULTS

Invertebrate Abundance

Invertebrate density was significantly higher on exotic *P. crispus* than on native *P. richardsonii* in both the Richelieu River and Ile Charron (ANOVA, $p < 0.05$). In Lac-St Louis and Lac Memphremagog, invertebrate density was not significantly different between exotic *P. crispus* and native *P. perfoliatus*; however, *P. crispus* tended to have higher invertebrate density than *P. perfoliatus* at both sites (Fig 3). Invertebrate density did not change significantly from early June to early July in the Richelieu River or in Lac Memphremagog, while at both of the St. Lawrence sites (Ile Charron and Lac-St Louis), invertebrate density changed from late May to late June (ANOVA, $p < 0.05$, Fig 3).

Invertebrate biomass was different on *P. crispus* and *P. richardsonii* at both sites where *P. richardsonii* was sampled: in the Richelieu River, *P. crispus* had higher invertebrate biomass than *P. richardsonii*, while at Ile Charron the reverse was found (Fig 4). At these two sites invertebrate biomass increased over the summer (ANOVA, $p < 0.05$). Overall, there was no significant difference in invertebrate biomass between *P. crispus* and *P. perfoliatus* at either site (ANOVA, $p < 0.05$), although in Lac-St Louis biomass tended to be higher on *P. perfoliatus* in May (Fig 4).

Exotic Invertebrates

Only one exotic invertebrate species, the larva of the aquatic moth *Acentria ephemerella* (=*nivea*), was found at any of the sites. *Acentria ephemerella* was present at every site, and was common on both native and exotic plants except at Lac-St Louis, where only three individuals were found; therefore, we did not run an ANOVA at this site. The density of *A. ephemerella* was not significantly different on exotic and native *Potamogeton* at any of the other three sites (ANOVA, $p > 0.05$).

Invertebrate diversity and community composition

Invertebrate taxa richness was higher on native *Potamogeton* at three sites ($p < 0.05$), while at the fourth site, Lac-St Louis, taxa richness was similar on native *P. perfoliatus* and exotic *P. crispus* (Fig 5). There was no difference in inverse Simpson diversity between exotic and native *Potamogeton* except at Lac-St Louis, where inverse Simpson diversity was significantly greater on *P. perfoliatus* than on *P. crispus* (Fig 6). Shannon-Wiener diversity was not significantly different for native and exotic *Potamogeton* at any of the sites (Table 2).

At each site, grazer invertebrates made up 65% to 95% of the total invertebrate abundance, and 60% to 98% of the total invertebrate biomass. Grazer abundance tended to be higher on *P. perfoliatus* than on *P. crispus*, and higher on *P. crispus* than on *P. richardsonii*; however, grazers clearly accounted for the majority of both invertebrate abundance and biomass on all three species of plants at each site. The detrended correspondence analysis (DCA) for each site showed that samples separated along the first axis based on sampling date, while the second axis was difficult to interpret. Samples did not separate by plant species at any of the sites.

Epiphytic algae and grazers

Epiphytic algal (epiphyte) biomass did not follow a consistent trend across sites when compared on exotic and native *Potamogeton*. In the Richelieu River, epiphyte biomass was significantly higher on *P. crispus* than on *P. richardsonii* (ANOVA, $p < 0.05$), but at Ile Charron epiphyte biomass tended to be lower on *P. crispus* than on *P. richardsonii* in May (Fig 7). Epiphyte biomass was significantly different on *P. crispus* and *P. perfoliatus* in both Lac Memphremagog and at Lac-St Louis: In Lac Memphremagog, *P. perfoliatus* had higher epiphyte biomass than *P. crispus*, and at Lac-St Louis *P. crispus* had higher biomass than *P. perfoliatus* (ANOVA, $p < 0.05$). At three sites epiphyte biomass decreased from early to late summer (ANOVA, $p < 0.05$), but it did not decrease at Lac Memphremagog (Fig 7). There was a significant negative correlation between grazer biomass and epiphyte biomass (Fig 8); and this relationship was not significantly different for native and exotic *Potamogeton* as neither the slopes nor intercepts differed significantly (ANCOVA, $p > 0.05$). The correlation between grazer density and epiphyte biomass was not significant.

DISCUSSION

Our results show that there are significant differences in invertebrate density and taxa richness supported by exotic and native *Potamogeton*; however, no consistent patterns were detected in invertebrate community composition and biomass. Although epiphytic algal biomass was different on exotic and native plants, the direction of this difference varied between sites, and thus general trends were not apparent.

Potamogeton crispus has been established in North America since as early as 1841 (Stuckey 1979), and specimens of *P. crispus* from 1932 are reported from Ile Sainte-Thérèse in the St. Lawrence River, located just NW of the Ile Charron site in our study; therefore, it is likely that *P. crispus* has been established in the St. Lawrence sites for at least 70 years (Herbier Marie-Victorin, Montreal, Quebec). Given the length of time that *P. crispus* has been established at these sites, it may be that native invertebrates have had time to adapt to this plant, which could explain why we do not see major differences between the invertebrate communities on native and exotic *Potamogeton* species.

Plant Morphology

We hypothesized that invertebrate abundance would be higher on native *Potamogeton* due to coadaptation with native invertebrates. Our results did not support this hypothesis: *P. crispus* generally supported greater invertebrate density than either species of native *Potamogeton*. Similarly, Krecker (1939) found that *P. crispus* supported higher numbers of invertebrates per length of plant stem than either the native *P. pectinatus* or *P. compressus*; however, in this study the native plants were structurally distinct from *P. crispus*. Aquatic plants of different structure may support invertebrate communities that differ in density (Keast 1984, Cheruvelil et al. 2002), even when such plants are phylogenetically similar (Krecker 1939).

Submerged aquatic plants are often classified as having either dissected leaves (complex structure) or entire leaves (simple structure) (Cheruvelil et al. 2000, Cheruvelil et al. 2002). Under this broad classification, all three *Potamogeton* species in our study would be classified into the same structural group (simple) as they all have broad, elongated, unstalked leaves (Fig 1). In addition, all three species have similar specific leaf area (leaf surface area per dry weight $cm^2 g^{-1}$, Table 3); therefore, per gram of dry weight, each plant should on average provide the same amount of surface area available for colonization by invertebrates and algae. However, on a finer scale, these *Potamogeton* species have subtle differences in leaf morphology. In North America, *P. crispus* is the only species of *Potamogeton* that has leaves with a serrated edge (Crow and Hellquist 2000). The leaves of this plant are also more rigid and curly than the leaves of either of the native *Potamogeton* species in this study. *Potamogeton perfoliatus* also has curly leaves, which appeared similar in size to those of *P. crispus* at our sites, but the leaves are less rigid and the leaf curls are not as dense as those of *P. crispus* (Fig 1). *Potamogeton richardsonii* has broad, curly leaves that are larger than *P. crispus* and *P. perfoliatus*. The tight curls and serrated edge of *P. crispus* may provide more refugia and a greater variety of textural surfaces for invertebrates, and might explain why invertebrate density is greater on *P. crispus* than on native *Potamogeton* species. Furthermore, the leaves of *P. perfoliatus* and *P. crispus* are closer in size to one another and are thus slightly more similar than the leaves of *P. crispus* and *P. richardsonii*, even though all three plants have similar specific leaf area (Table 3). This structural difference could perhaps explain why invertebrate density and biomass are more similar on *P. crispus* and *P. perfoliatus* than on *P. crispus* and *P. richardsonii*. However, leaf morphology cannot explain all the differences in invertebrate abundance between native and exotic *Potamogeton*; for example, when *P. crispus* was compared to *P. richardsonii*, invertebrate biomass was higher on exotic *P. crispus* than on native *P. richardsonii* at one site, while at the other site the invertebrate biomass was higher on *P. richardsonii* than on *P. crispus*.

Epiphytic algae and aquatic plants

The relationship between epiphytic algae (epiphytes) and aquatic plants is complex, and there is debate in the literature as to whether epiphytes and plants are mutualists, or if epiphytes are actually detrimental to aquatic plants (Bronmark 1989). If mutualists, one would expect plants and epiphytes to exchange nutrients or minerals; conversely, if epiphytes are detrimental, one would expect native plants to contain chemicals to deter epiphytes (Bronmark 1989). However, in this study we did not find any evidence of coadaptation between epiphytes and plants, as differences in epiphytic algal biomass on native and exotic plants did not follow a consistent pattern. This suggests that whether *P. crispus* supports more or fewer epiphytes than the native *Potamogeton* species depends more on the abiotic and biotic site conditions, rather than on a physiological or morphological difference between exotic and native plant species. For example, invertebrates that feed on epiphytes may affect epiphyte abundance (Cattaneo 1983, Jones et al 2000). Since the species composition of aquatic invertebrates at each site was slightly different, this could drive differences in epiphyte abundance on exotic and native species of *Potamogeton* at different sites.

Epiphytic algae and invertebrates

Epiphytic algae are an important food source for many invertebrate grazers (Bronmark 1989, Cattaneo 1983), and grazers comprised the majority of the invertebrates at all four sites in our study. In southern Quebec, the initial increase of epiphyte biomass in the spring is soon followed by an increase in grazer biomass and a subsequent decline in epiphyte biomass (Cattaneo 1983). The negative correlation we found between grazer biomass and epiphyte biomass may indicate a negative effect of grazing pressure on epiphytes.

Our initial hypothesis predicted that at sites where epiphytic algal biomass was higher on one plant species, invertebrate abundance would also be higher on that plant species. This pattern was observed between *P. crispus* and *P. richardsonii,* as at Ile Charron *P. crispus* had both higher epiphyte biomass and invertebrate biomass, and at the Richelieu River the reverse was true. However, this pattern did not occur between *P. crispus* and *P. perfoliatus*. Thus neither exotic nor native *Potamogeton* species systematically supported greater epiphytic algal biomass, and invertebrate abundance was not consistently linked to epiphytic algal biomass. Clearly, factors other than epiphytic algal biomass influence differences in the density and biomass of invertebrates on native and exotic *Potamogeton* species.

Exotic Invertebrates

We hypothesized that *P. crispus* would support more exotic invertebrates than would native *Potamogeton* species. Our results do not support this hypothesis, as *A. ephemerella,* the one exotic invertebrate we found, was generally present in similar numbers on the exotic *P. crispus* and native *Potamogeton* at each site. *Acentria ephemerella* is a generalist herbivore, introduced in the 1920s from Europe, where it is widespread and feeds directly on the tissues of several aquatic plant species (Berg 1942, Sheppard 1945, Buckingham and Ross 1981). Thus *A. ephemerella* and *P. crispus* may have interacted in their native range prior to their introduction to North America, as they have overlapping native ranges in Europe (Berg 1942, Bolduan et al. 1994). Despite this, *A. ephemerella* was not more abundant on *P. crispus* than on native *Potamogeton.*

Implications for aquatic ecosystems

Consistent with our initial hypothesis, native *Potamogeton* species supported higher invertebrate taxa richness than *P. crispus* at three out of four sites. At three sites, inverse Simpson diversity also tended to be higher on both species of native *Potamogeton,* but the difference was significant only at one site. Thus when *P. crispus* invades a lake, it could reduce invertebrate biodiversity by supporting lower invertebrate biodiversity than some of the native plants it replaces. Conversely, *P. crispus* generally supported greater invertebrate density than native *Potamogeton,* particularly in comparison to *P. richardsonii.* However, at two sites native *Potamogeton* tended to support greater invertebrate biomass, suggesting a greater mean body size of invertebrates on native *Potamogeton* than on *P. crispus* at these sites. As reduced prey diversity and size may be less energetically efficient for fish

(Eggers 1977) and limit the body size of benthivorous fish such as yellow perch (Kovecses et al. 2005), the replacement of native *Potamogeton* by *P. crispus* in some habitats may have indirect effects on fish growth. In general, the results from this study suggest that the replacement of native pondweeds by *P. crispus* in lakes may result in significant changes to epiphytic invertebrate communities, but these changes are highly variable from site to site.

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Table 1. Characteristics of sites sampled 2006.

Site	General Location	Plants sampled	Water body type	No. of samples (E,N)	Water temp min/ max (C°)	pH range	Depth at site (m)	Other plant species present	Notes
Lac-St Louis	SW of the Island of Montreal, part of St Lawrence River, Quebec	***P. crispus,*** *P. perfoliatus*	Fluvial Lake	(7,7) May (7,7) June **=14, 14**	17 (May) /22 (June)	7.1-9.0	0.5 - 1	*C. demersum, E. canadensis, M. sibericum,* ***M. spicatum,*** *Potamogeton* sp., *Ranuculus* sp., *V. americana*	Site near boat launch against breaker, moderate to high wave action
Ile Charron	NE of the Island of Montreal in the St Lawrence River, Quebec	***P. crispus,*** *P. richardsonii*	River	(7,7) May (7,7) June **=14, 14**	19 (May)/ 25(June)	7.1-8.3	0.5 - 1.5	*C. demersum, E. canadensis, M. spicatum, Potamogeton* sp., *V. americana,*	Site near boat launch in man-made harbour. Gentle current, low wave action
Lac Memphremagog	Eastern Townships of Quebec, crosses US boarder into Vermont	***P. crispus,*** *P. perfoliatus*	Lake	(7,7) June (8,8) July **=15, 15**	15 (June)/ 23 (Jul)	6.7-8.2	0.5 - 1	*C. demersum, E. canadensis, V. americana*	Site near stream inflow, middle of the eastern side of lake (Quebec). Low wave action
Richelieu River	Central Quebec, connects Lake Champlain and the St. Lawrence River	***P. crispus,*** *P. richardsonii*	Lake	(8,8) June (7,7) July **=15, 15**	17 (June) 27 (Jul)	6.7-7.8	1.5 - 2.0	*C. demersum, E. canadensis, E. nuttallii M. sibericum,* ***M. spicatum,*** *Potamogeton* sp., *Ranuculus* sp., *V. americana*	Site near mid river wetland, steady current, low wave action. Extreme flooding and current in spring 2006

Note:

Exotic plant species are in bold. Plant genera are as follows: *C – Ceratophyllum, E – Elodea, M – Myriophyllum, and V – Vallisneria.*

Number of samples gives the number of samples of exotic and native plants on each sampling date, followed by the total.

Table 2: Taxa Richness, Shannon-Wiener diversity, and Simpson diversity compared on native and exotic *Potamogeton* species.

Site	Taxa Richness		Exp (Shannon-Wiener)		1/Simpson diversity		Invertebrate Abundance
	Native	Exotic	Native	Exotic	Native	Exotic	
Lac-St Louis	30	30	12.2	9.0	8.77	4.8*	1050
Ile Charron	24	21*	5.0	5.7	2.9	3.2	7020
Lac Memphremagog	15	13*	4.5	4.0	3.2	3.3	580
Richelieu River	31	23*	10.0	8.2	6.5	5.6	650

Note:

The exponent of Shannon-Wiener diversity represents the number of different invertebrate species we would find if all species in the community were equally common, and thus provides a less abstract measure of diversity than do the raw Shannon-Wiener values (Jost 2006). The inverse of Simpson diversity also represents the number of species that would be found if all species were equally common (Jost 2006); however, Simpson diversity is weighted more heavily on how evenly invertebrate abundance is distributed across taxa than Shannon-Wiener diversity is. Diversity comparisons on native and exotic plants were made at the abundance listed, which is the abundance of invertebrates on the plant species with lower invertebrate abundance.

* Indicates a significant difference between native and exotic *Potamogeton* species.

Table 3: Specific leaf area (SLA) for *Potamogeton crispus*, *P. perfoliatus*, and *P. richardsonii*.

Study	*P. crispus* ± SE	*P. perfoliatus* ± SE	*P. richardsonii* ± SE
Spence et al. 1973	677 ± 140 *	750 ± 140 *	
Nicholson and Best 1974			625 ± 224
Sushma et al. 1995		762 **	
Maberly and Madsen 1998	707 ± 140		
Armstrong et al. 2003			799 ± 59

Note:

Units are leaf area per plant dry weight ($cm^2 g^{-1}$).

*SLA was averaged across measurements from plants at different depths.

** No standard error was given in this study.

Figure Captions

Figure 1: Sketches of a) *Potamogeton crispus* b) *P. perfoliatus* and c) *P. richardsonii.*

Figure 2: Map of study sites. In Lac-St Louis and Lac Memphremagog, *Potamogeton crispus* and *P. perfoliatus* were sampled, and in the Richelieu River and at Ile Charron, *P. crispus* and *P. richardsonii* were sampled.

Figure 3: Invertebrate density on exotic and native *Potamogeton* species. Filled circles represent native plants, open circles, exotic plants. Sampling periods are in either late May/early June, and then again in late June/early July. * Indicates a significant difference in invertebrate density between the two plant species. ¶Indicates a significant difference in invertebrate density between dates (ANOVA, $p < 0.05$). Interaction terms were not significant at any site.

Figure 4: Invertebrate biomass on exotic and native *Potamogeton* species. Filled circles represent native plants, open circles, exotic plants. Sampling periods are in either late May/early June, and then again in late June/early July. * Indicates a significant difference in invertebrate density between the two plant species. ¶Indicates a significant difference in invertebrate density between dates. ** Indicates a significant interaction effect between date and plant type. (ANOVA, $p < 0.05$).

Figure 5: Invertebrate taxa richness on exotic and native *Potamogeton* species. Filled circles represent native plants, open circles, exotic plants. Error bars represent standard deviation based on 50 randomized runs. * Indicates a significant difference in invertebrate taxa richness between the two plant species ($p < 0.05$).

Figure 6: Simpson diversity of epiphytic invertebrate communities on exotic and native *Potamogeton* species. Filled circles represent native plants, open circles, exotic plants. Error bars represent standard deviation based on 50 randomized runs,

sampled with replacement. * Indicates a significant difference in invertebrate Simpson diversity between the two plant species ($p < 0.05$).

Figure 7: Epiphytic algal biomass, as estimated by chlorophyll *a*, on exotic and native *Potamogeton* species. Filled circles represent native plants, open circles, exotic plants. Sampling periods are in either late May/early June, and then again in late June/early July. * Indicates a significant difference in invertebrate density between the two plant species. ٩Indicates a significant difference in invertebrate density between dates. ** Indicates a significant interaction effect. (ANOVA, $p < 0.05$).

Fig 8: Regression between grazer biomass and epiphytic algal biomass, as estimated by chlorophyll *a*. The y-axis contains the residuals from a regression between chlorophyll *a* (μg) and plant dry weight (g).

Figure 1

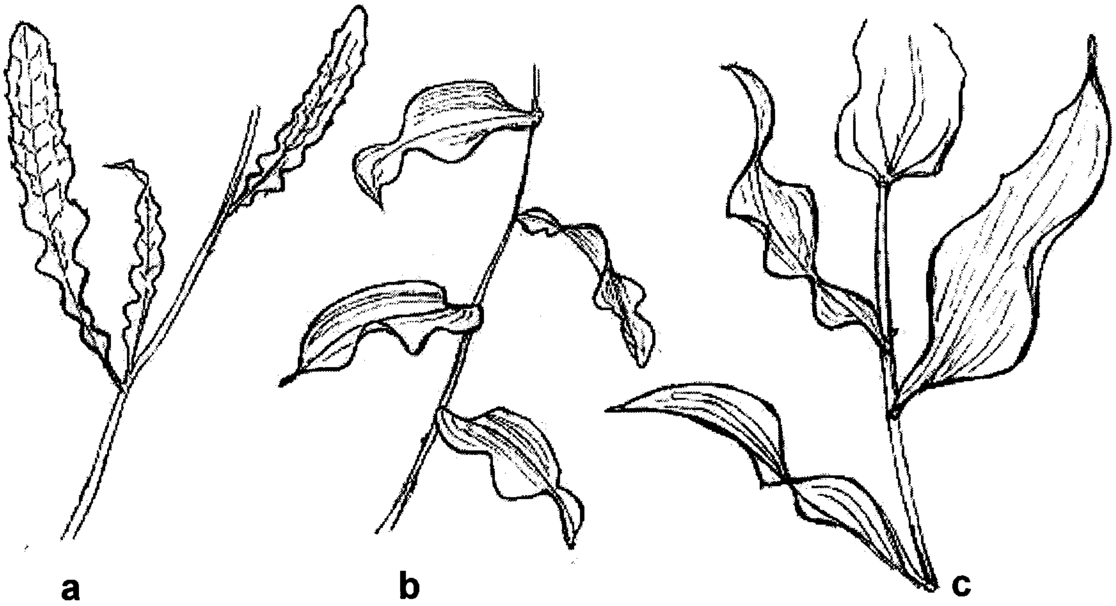


Figure 2

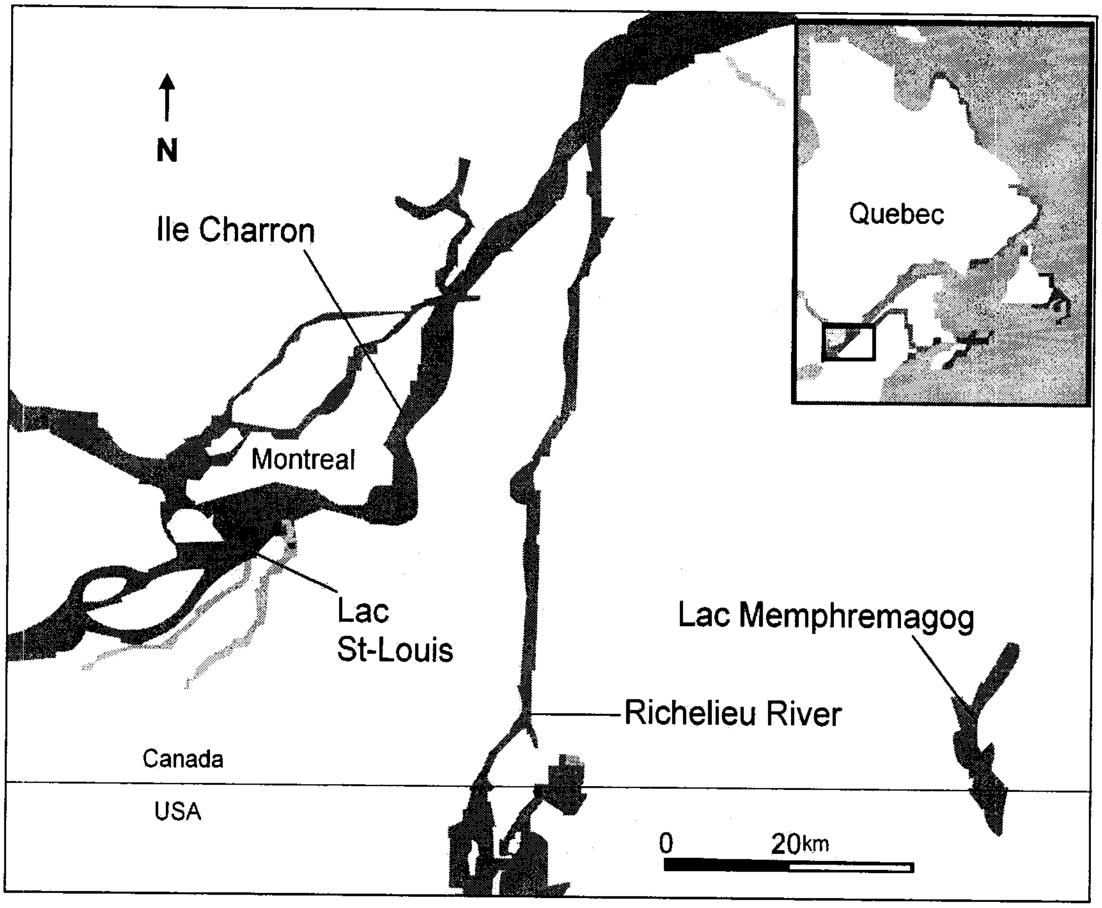

N
Ile Charron
Quebec
Montreal
Lac
St-Louis
Lac Memphremagog
Richelieu River
Canada
USA
0
20km

Figure 3

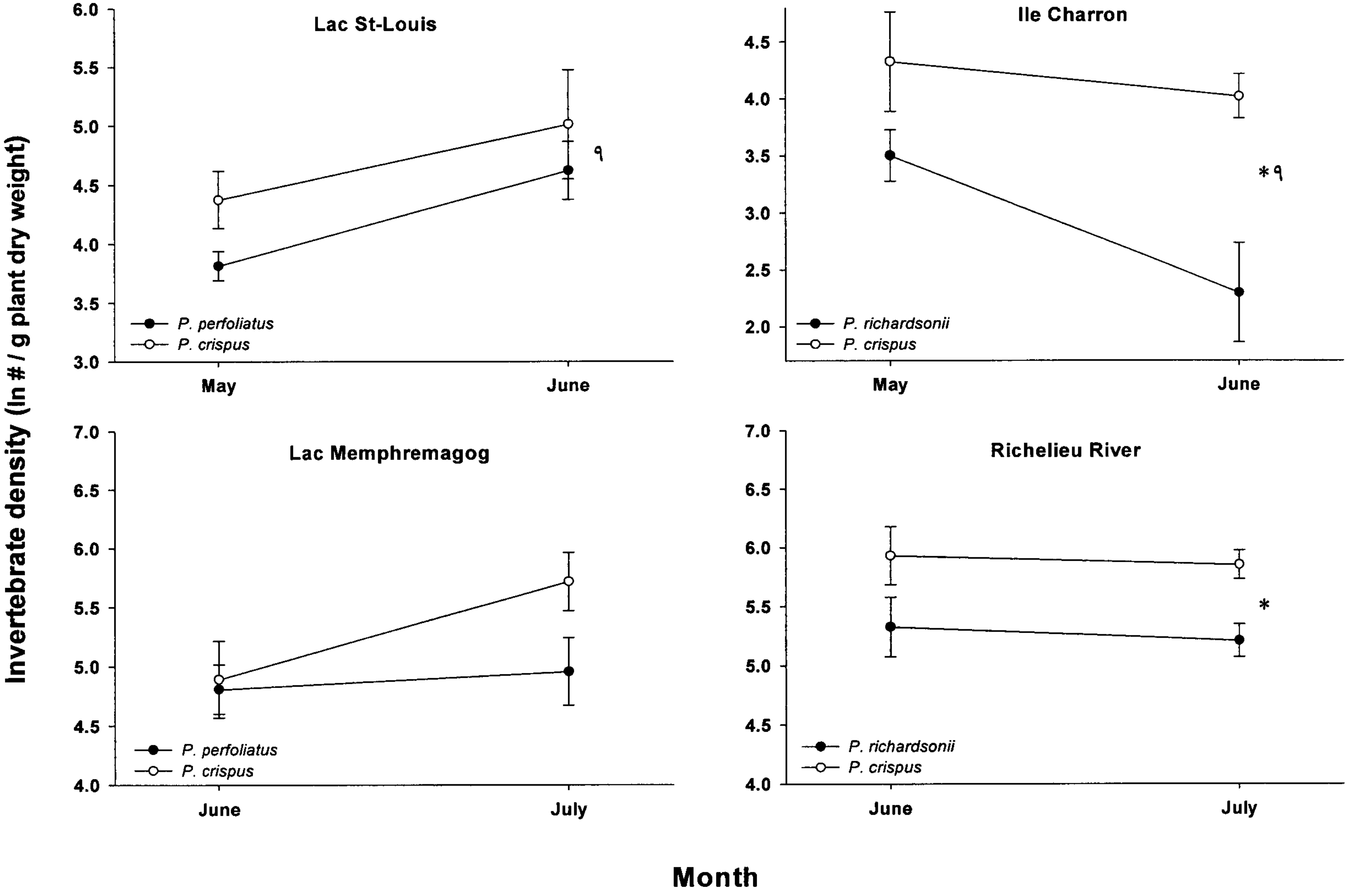

Lac St-Louis
Ile Charron
Lac Memphremagog
Richelieu River
Invertebrate density (ln # / g plant dry weight)
Month
6.0
5.5
5.0
4.5
4.0
3.5
3.0
4.5
4.0
3.5
3.0
2.5
2.0
7.0
6.5
6.0
5.5
5.0
4.5
4.0
May
June
July
P. perfoliatus
P. crispus
P. richardsonii
*
*

Figure 4

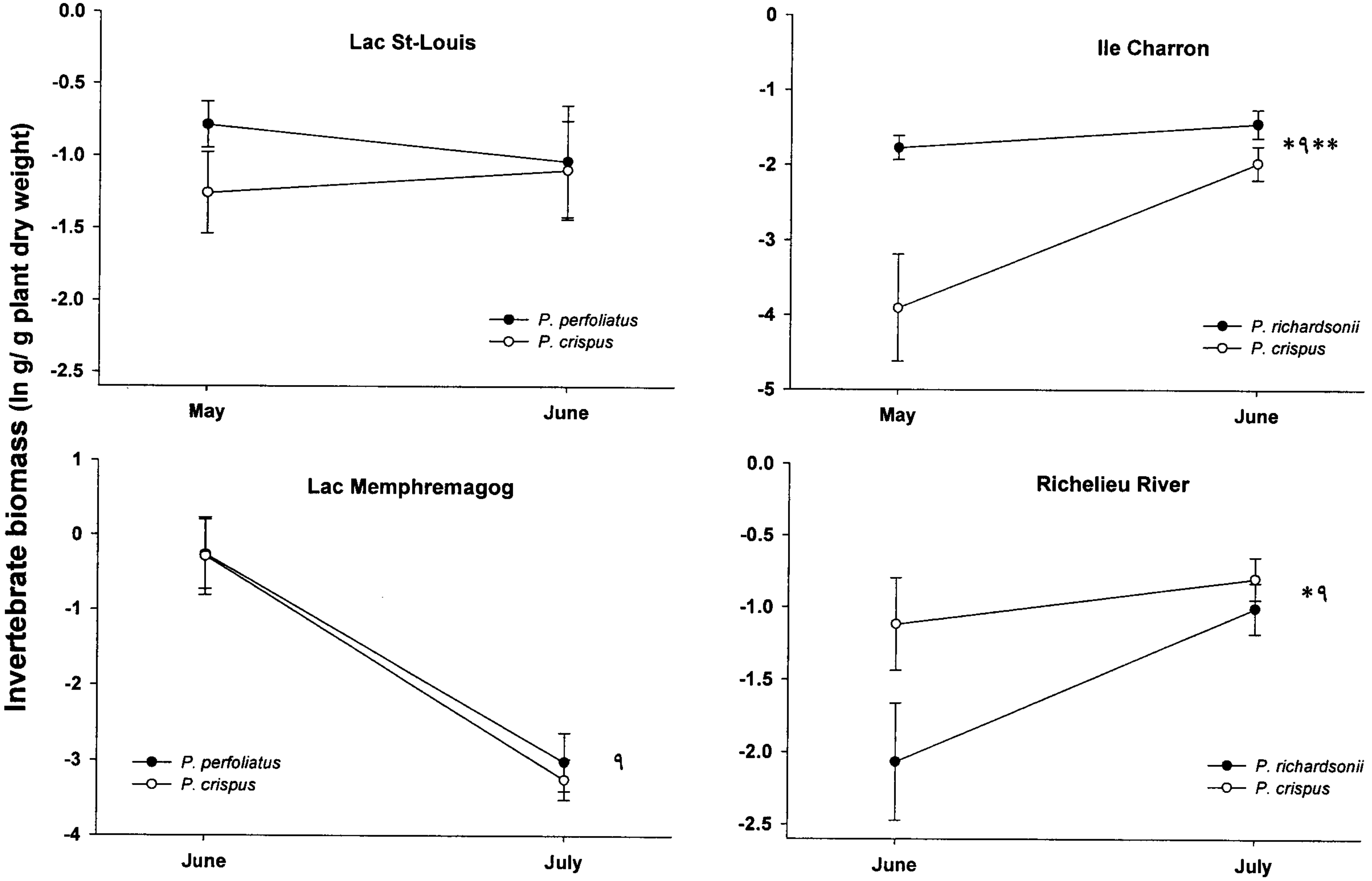

Invertebrate biomass (ln g/ g plant dry weight)
Lac St-Louis
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
May
June
P. perfoliatus
P. crispus
Ile Charron
0
-1
-2
-3
-4
-5
May
June
*¶**
P. richardsonii
P. crispus
Lac Memphremagog
1
0
-1
-2
-3
-4
June
July
¶
P. perfoliatus
P. crispus
Richelieu River
0.0
-0.5
-1.0
-1.5
-2.0
-2.5
June
July
*¶
P. richardsonii
P. crispus

Figure 5

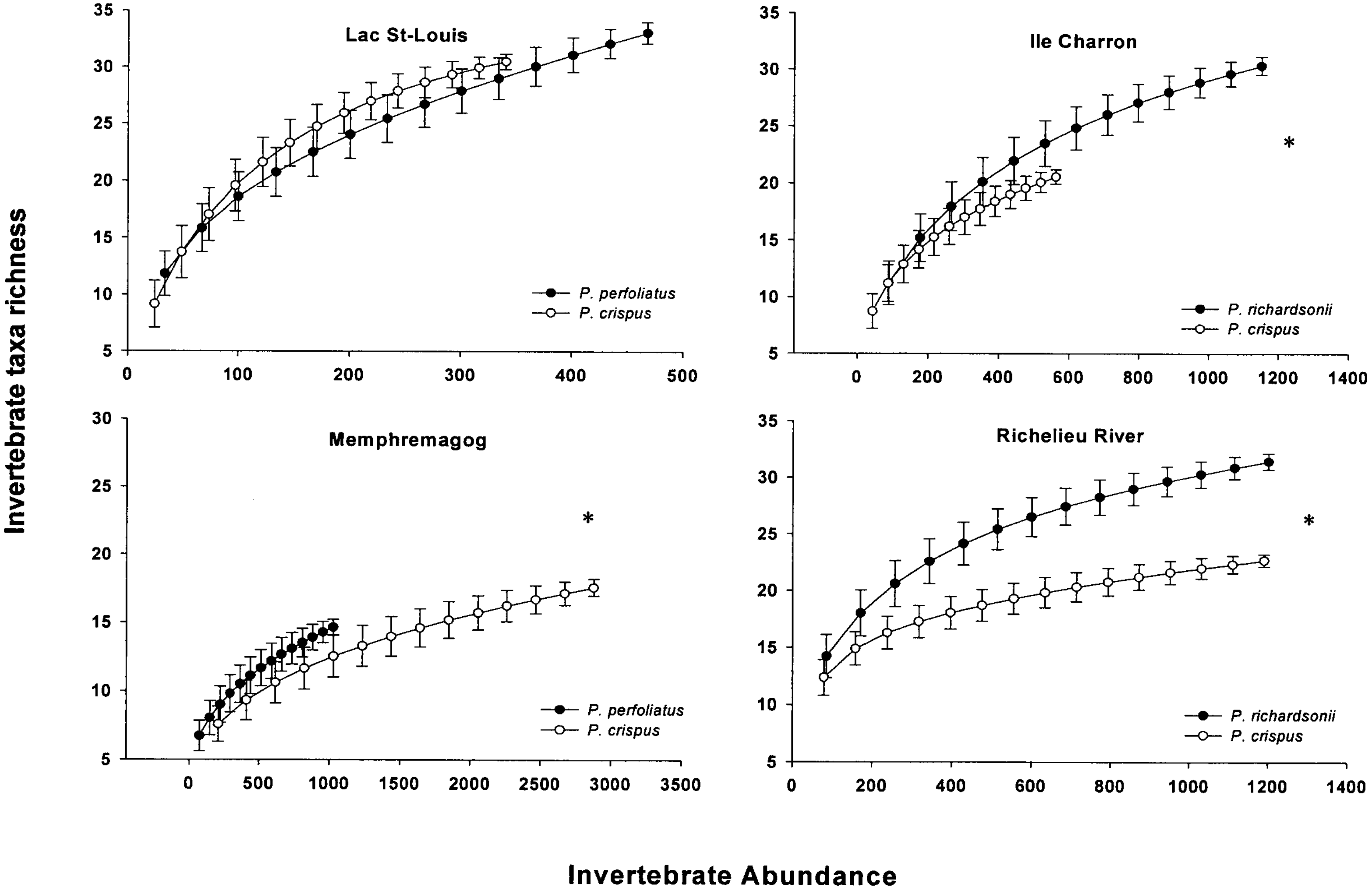

Lac St-Louis
Ile Charron
Memphremagog
Richelieu River
P. perfoliatus
P. crispus
P. richardsonii
*
Invertebrate taxa richness
Invertebrate Abundance
0
100
200
300
400
500
600
800
1000
1200
1400
1500
2000
2500
3000
3500
5
10
15
20
25
30
35

Figure 6

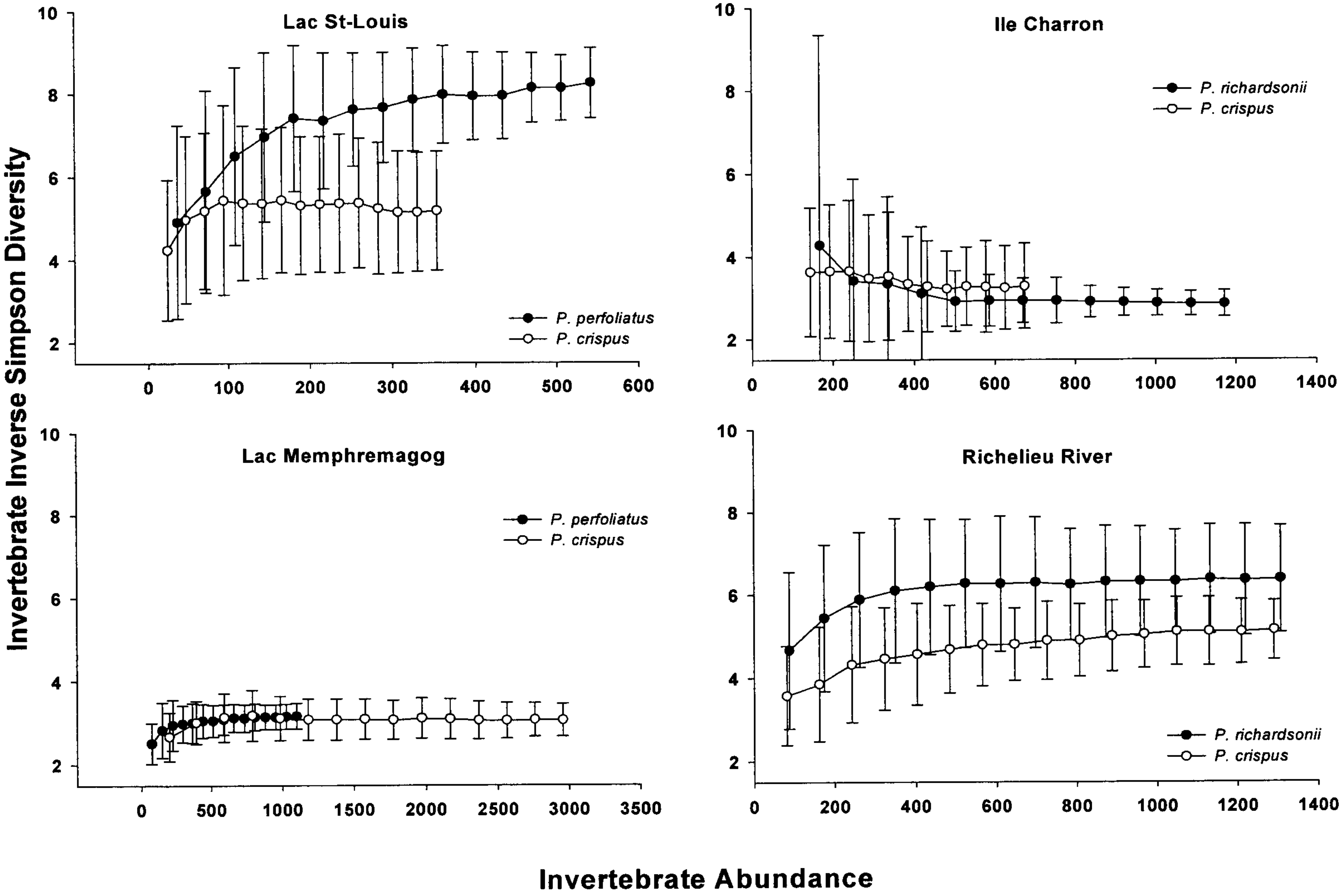

Lac St-Louis
P. perfoliatus
P. crispus
Ile Charron
P. richardsonii
P. crispus
Lac Memphremagog
P. perfoliatus
P. crispus
Richelieu River
P. richardsonii
P. crispus
Invertebrate Inverse Simpson Diversity
Invertebrate Abundance
10
8
6
4
2
0
100
200
300
400
500
600
1000
1200
1400
1500
2000
2500
3000
3500

Figure 7

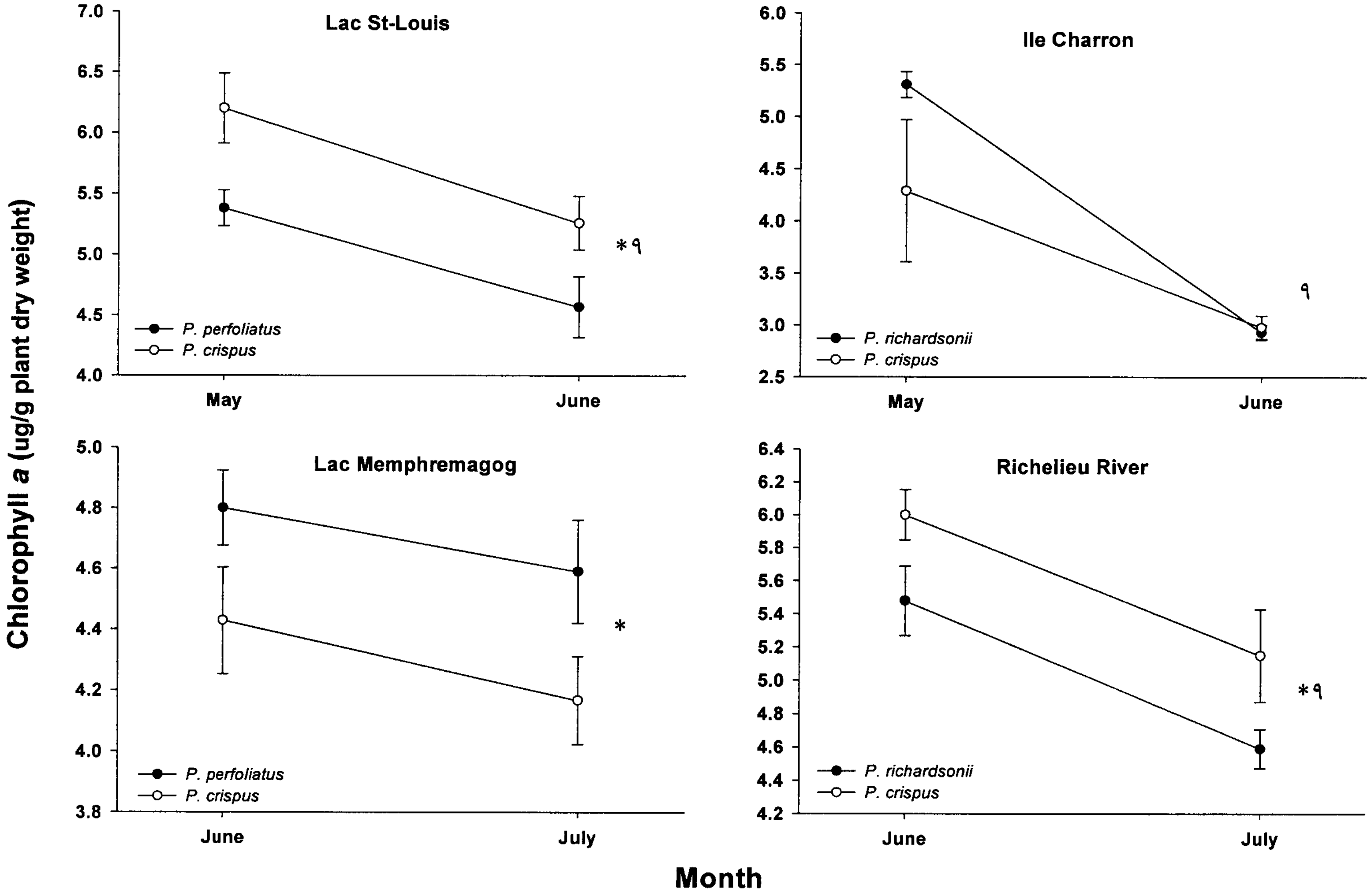
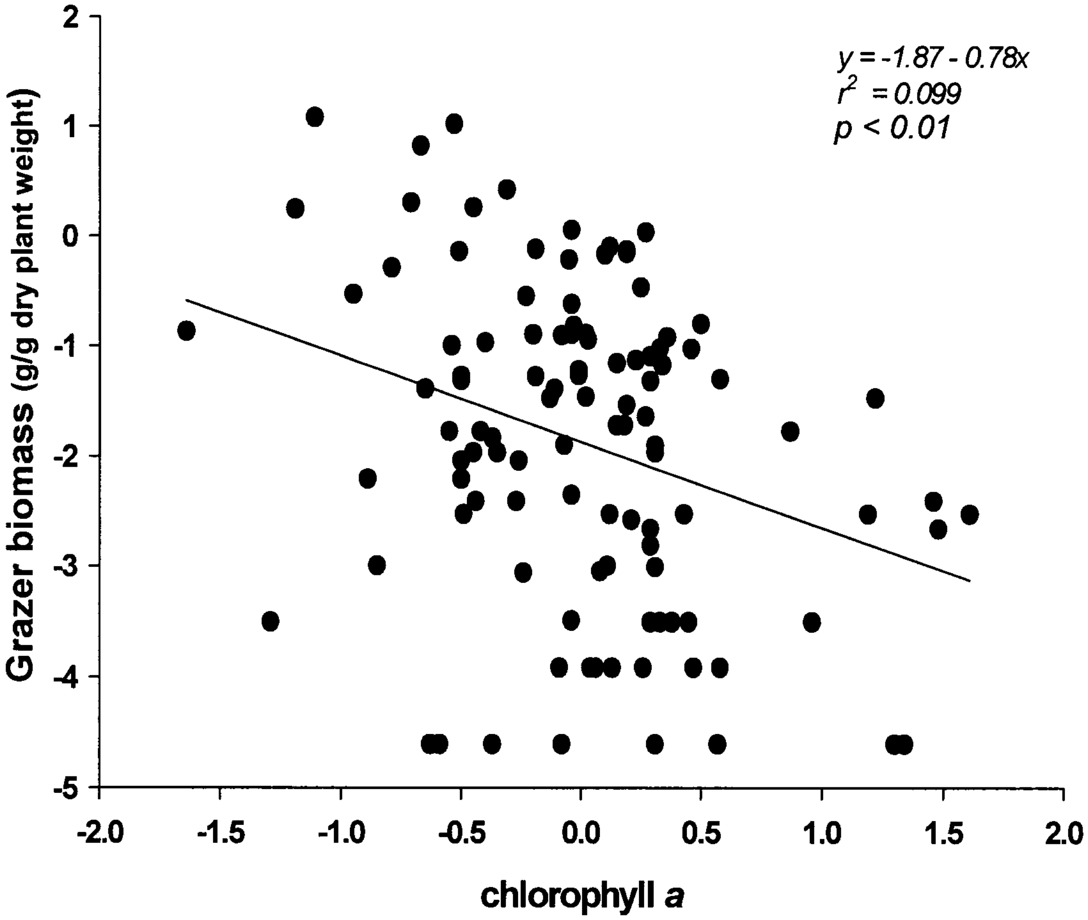

Lac St-Louis
7.0
6.5
6.0
5.5
5.0
4.5
4.0
May
June
*٩
P. perfoliatus
P. crispus
Ile Charron
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
May
June
٩
P. richardsonii
P. crispus
Lac Memphremagog
5.0
4.8
4.6
4.4
4.2
4.0
3.8
June
July
*
P. perfoliatus
P. crispus
Richelieu River
6.4
6.2
6.0
5.8
5.6
5.4
5.2
5.0
4.8
4.6
4.4
4.2
June
July
*٩
P. richardsonii
P. crispus
Chlorophyll a (ug/g plant dry weight)
Month

Figure 8


$y = -1.87 - 0.78x$
$r^2 = 0.099$
$p < 0.01$
Grazer biomass (g/g dry plant weight)
2
1
0
-1
-2
-3
-4
-5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
chlorophyll *a*

General Conclusions

The results of this study clearly show that invertebrate communities on native and exotic plants are not equivalent, even when these plants are similar in structure. Thus when exotic plants replace native plants, it is likely that epiphytic invertebrate communities will also be transformed. Through meta-analysis, I demonstrated that exotic plants appear to support lower invertebrate density than native plants in the same waterbody. Although differences in invertebrate communities on native and exotic plants vary from site to site and study to study, general trends are still apparent. These trends were investigated further through field studies in Chapters 1 and 2.

In Chapter 1, I found that invertebrate communities on native and exotic *Myriophyllum* differ significantly: at three out of four sites, native *Myriophyllum* species had greater invertebrate diversity and supported greater invertebrate biomass than did exotic *M. spicatum*. In addition, both species of native *Myriophyllum* supported more snails than did *M. spicatum*. This study revealed that even very structurally similar congeneric plants do not necessarily provide equivalent habitat for invertebrates, and that invertebrate communities as a whole are sensitive to subtle differences between plant species.

In Chapter 2, I found that differences in invertebrates on native and exotic species of *Potamogeton* varied across sites and season, more so than on *Myriophyllum*. Even so, some general trends were apparent. While the community composition of invertebrates was very similar on native and exotic *Potamogeton* species: invertebrate taxa richness tended to be lower on exotic *P. crispus* than native *Potamogeton* species – at three out of four sites, *P. crispus* supported lower invertebrate taxa richness than native *Potamogeton*. In contrast to the results of the meta-analysis, exotic *P. crispus* supported higher invertebrate densities than both species of native *Potamogeton*. Furthermore, although invertebrate grazer biomass and epiphytic algae biomass were correlated, patterns in the relative abundance of invertebrates on native and exotic *Potamogeton* were not consistent with patterns in the relative biomass of epiphytic algae on these plants, and neither native nor exotic *Potamogeton* consistently supported greater epiphytic algal biomass.

Therefore, the replacement of native plants by exotic plants – even those very similar in structure – has the potential to alter aquatic invertebrate density, biomass, diversity, and community composition on a system-wide scale. In particular, field studies suggest that invertebrate diversity may be reduced, while meta-analysis suggests that invertebrate density may also decline as exotic plants become increasingly dominant in inland waters.

Future study directions

The physical and biochemical factors that structure invertebrate communities on native and exotic plants remain to be determined. I found several differences in invertebrate communities on exotic and native *Myriophyllum* species, but can only speculate on the mechanism behind these results. Researchers have now identified at least two chemical differences between native and exotic *Myriophyllum* species that affect the abundance of the specialist milfoil weevil, *E. lecontei* (Marko 2005). Future studies could further examine the interactions between aquatic invertebrates and plant exudates, and also the interactions between plant exudates and epiphytic algae communities, on native and exotic *Myriophyllum*. These studies could help to explain the differences in invertebrate communities between *M. spicatum* and its native congeners.

To further investigate the interactions between exotic invertebrates and exotic plants, the abundance of exotic invertebrates on native and exotic plants could be compared through meta-analysis. Meta-analysis might reveal general trends not apparent in individual field studies, as often only a few exotic invertebrate species may be recovered at a site (Toft et al 2003, Chapters 1 and 2) making it difficult to distinguish trends from a single field study alone. In addition, incorporating the time since invasion into a meta-analysis of invertebrates on native and exotic plants could help to explain why differences in invertebrate communities on native and exotic plants vary from system to system. Such an analysis could also help us predict the long-term versus short-term impacts of plant invasions.

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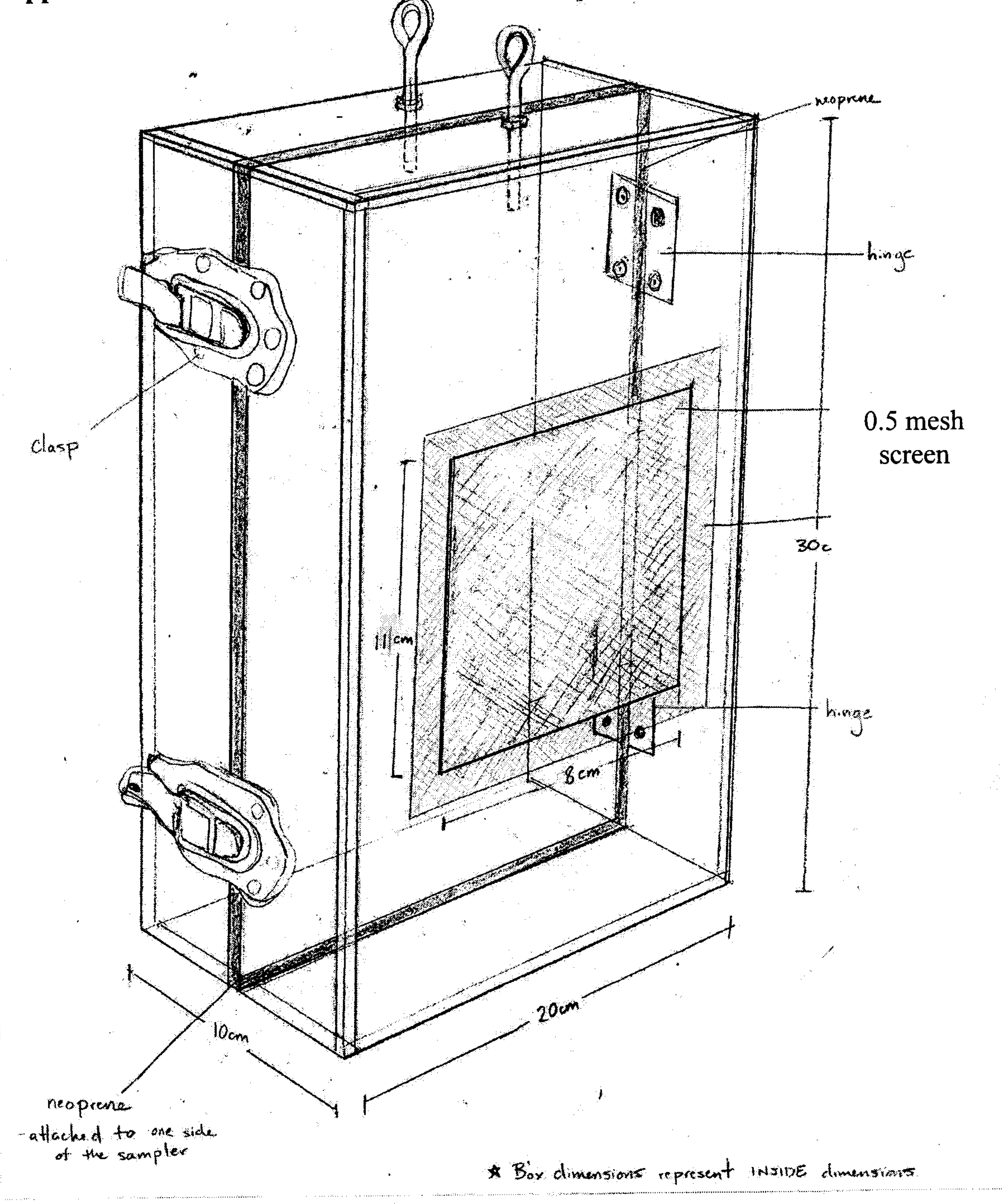
Toft, J.D., C.A. Simenstad, J.R. Cordell, and L.F. Grimaldo. 2003. The effect of introduced water hyacinth on habitat structure, invertebrate assemblages, and fish diets. Estuaries. **26:** 746-758.

Appendix A



Modified Downing box sampler: Operates by opening the box, gently placing it around an individual or stand of macrophytes, and closing the latches. Water drains out through the screen when the box is lifted from the water, leaving macrophytes and associated epiphytic invertebrates inside. Basal surface area = 200cm^2, volume = 6 L.

Appendix B: Invertebrates on *Myriophyllum spicatum, M. sibericum*, and *M. alterniflorum;* and *Potamogeton crispus, P. perfoliatus*, and *P. richardsonii*. The average invertebrate density (number of individuals/ gram plant dry weight) is given for each species at each site, ± standard error.

ORDER OR CLASS	SPECIES	Lac St-Louis				Richelieu River				Saranac Lake				Chateaugay Lake			
		M. sibericum		*M. spicatum*		*M. sibericum*		*M. spicatum*		*M. alterniflorum*		*M. spicatum*		*M. alterniflorum*		*M. spicatum*	
Diptera	Chironomidae	28.76	1.80	27.79	2.25	122.99	5.31	108.60	2.85	8.14	0.29	13.68	0.71	6.88	0.36	51.16	2.58
Diptera	Tipulidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.01
Diptera	Ceratopogonidae	0.34	0.04	0.37	0.04	1.10	0.08	0.00	0.00	0.89	0.06	1.59	0.20	0.00	0.00	0.20	0.03
Diptera	Empididae	0.00	0.00	0.00	0.00	0.13	0.03	0.00	0.00	0.13	0.02	0.00	0.00	0.00	0.00	0.00	0.00
Odonata	*Enallagma signatum*	0.72	0.08	0.45	0.05	0.28	0.03	0.26	0.03	0.76	0.08	0.43	0.07	0.00	0.00	0.00	0.00
Odonata	*Enallagma exsulans*	0.13	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Odonata	*Enallagma clausum*	0.09	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Odonata	*Enallagma vesperum*	0.02	0.00	0.08	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Odonata	*Enallagma antennatum*	0.13	0.02	0.20	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Odonata	*Nehalennia* sp.	0.00	0.00	0.00	0.00	0.09	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Odonata	*Neurocordulia* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.02	0.26	0.04	0.00	0.00	0.00	0.00
Odonata	Corduliidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Odonata	*Ischnura* sp. 1	0.25	0.03	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Odonata	*Ischnura* sp. 2	0.00	0.00	0.08	0.02	0.01	0.00	0.00	0.00	1.36	0.22	0.18	0.02	0.00	0.00	0.04	0.01
Odonata	Coenagrionidae	0.14	0.02	0.41	0.05	0.13	0.02	0.21	0.03	0.34	0.04	1.74	0.16	0.49	0.06	0.32	0.04
Ephemeroptera	*Procloeon* sp.	0.07	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ephemeroptera	*Cloeon* sp.	0.19	0.04	0.00	0.00	0.01	0.00	0.03	0.01	0.00	0.00	0.00	0.00	0.08	0.02	0.00	0.00
Ephemeroptera	*Caenis diminuta*	0.13	0.02	0.49	0.04	0.20	0.03	0.00	0.00	0.21	0.04	0.00	0.00	0.28	0.04	0.02	0.00
Copepoda		2.63	0.46	1.02	0.16	0.00	0.00	0.07	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hirudinae	*Erpobdella*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.02
Hirudina	*Helobdella elongata*	0.04	0.01	0.00	0.00	0.68	0.14	0.03	0.01	0.08	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Hirudinae	*Helobdella papillata*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.07	0.27	0.00	0.00
Hirudina	*Glossiphonia complanata*	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.01	0.00	0.00	0.80	0.10	0.00	0.00	0.00	0.00
Hirudina	*Helobdella triserialis*	0.00	0.00	0.00	0.00	0.40	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.02
Annelida	*Pristina sp.*	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.37	0.04	0.80	0.10	1.15	0.13	0.92	0.16
Annelida	Naididae	0.54	0.05	2.54	0.56	8.70	0.31	13.63	0.94	4.99	0.26	7.83	0.50	0.77	0.12	11.78	1.03
Annelida	*Stylaria lacustris*	0.00	0.00	0.00	0.00	6.23	0.34	3.16	0.24	40.12	1.45	46.54	1.85	6.33	0.37	38.70	2.76
Tubellaria	*Dugesia tigrina*	1.40	0.17	0.38	0.03	2.75	0.15	0.19	0.02	0.57	0.04	1.15	0.14	1.11	0.11	1.51	0.10
Trichoptera	pupated	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.03	0.93	0.10	0.05	0.01	0.00	0.00

Trichoptera	*Nectopsyche* sp.	0.36	0.04	0.37	0.06	0.31	0.05	0.00	0.00	0.76	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera	*Oecetis* sp.	0.05	0.01	0.12	0.02	0.12	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera	*Triaenodes* sp.	0.09	0.02	0.22	0.03	0.52	0.03	1.12	0.07	0.62	0.06	0.06	0.01	0.00	0.00	0.00	0.00
Trichoptera	*Leptocerus* sp.	0.64	0.07	0.04	0.01	0.53	0.04	0.41	0.02	0.45	0.08	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera	*Ceraclea* sp.	0.65	0.05	0.15	0.02	0.26	0.03	0.02	0.00	0.66	0.09	0.00	0.00	0.00	0.00	0.02	0.01
Trichoptera	*Mystacides* sp.	0.00	0.00	0.00	0.00	0.06	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera	*Cheumatopsyche* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera	*Hydroptila* sp.	0.37	0.05	1.13	0.21	1.41	0.15	0.00	0.00	0.21	0.04	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera	*Oxyethira* sp.	0.00	0.00	0.00	0.00	0.01	0.00	0.11	0.02	1.31	0.06	2.33	0.15	0.00	0.00	0.55	0.10
Trichoptera	*Phryganea* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.03	0.00	0.00
Trichoptera	*Agraylea* sp.	1.49	0.18	0.56	0.10	3.27	0.21	0.09	0.01	0.21	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera	*Orthotricnia* sp.	0.00	0.00	0.00	0.00	0.03	0.01	0.02	0.00	0.16	0.02	0.00	0.00	0.09	0.02	0.16	0.03
Isopoda	*Caecidotea* sp.	0.04	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.02	0.59	0.08	0.07	0.01
Trichoptera	*Platycentropus* sp.	0.02	0.00	0.02	0.00	3.26	0.70	3.88	0.78	0.35	0.04	0.13	0.02	0.27	0.04	0.02	0.01
Trichoptera	*Neureclipsis* sp.	0.00	0.00	0.00	0.00	0.06	0.01	0.15	0.02	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera	*Brachycentrus* sp.	0.00	0.00	0.14	0.03	3.79	0.28	12.06	0.54	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera	*Chimarra* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.01	0.66	0.06	0.00	0.00	0.00	0.00	0.02	0.01
Trichoptera	*Polycentropus* sp.	0.09	0.02	0.05	0.01	0.06	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera	Philopotamidae	0.00	0.00	0.00	0.00	0.09	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trichoptera	*Potamyia* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Amphipoda	*Gammarus* sp.	3.47	0.34	4.28	0.35	0.55	0.05	0.07	0.01	0.00	0.00	0.00	0.00	0.23	0.04	0.00	0.00
Amphipoda	*Hyallela azteca*	0.19	0.03	0.00	0.00	1.81	0.14	0.18	0.02	3.11	0.13	0.00	0.00	7.57	0.55	1.41	0.09
Coleoptera	Species 1	0.04	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera	Species 2	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.74	0.11	2.28	0.19	0.00	0.00	0.00	0.00
Coleoptera	*Euhrychiopsis lecontei*	0.21	0.02	0.13	0.03	0.50	0.05	0.00	0.00	0.00	0.00	0.05	0.01	0.00	0.00	0.06	0.02
Coleoptera	*Dineutus* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01
Coleoptera	*Scirtes* sp.	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera	*Ordobrevia* sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.01	0.08	0.01	0.16	0.03	0.00	0.00	0.00	0.00
Coleoptera	*Stenelmis* sp.	0.00	0.00	0.02	0.01	0.21	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera	*Dubiraphia* sp.	0.17	0.02	0.77	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera	*Ancyronyx* sp.	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera	Carabidae	0.00	0.00	0.00	0.00	0.04	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Coleoptera	*Gyrinus* sp.	0.07	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera	Dytiscidae	0.00	0.00	0.00	0.00	0.06	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera	Haplidae	0.00	0.00	0.00	0.00	0.06	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Colenterata	*Hydra* sp.	0.00	0.00	0.00	0.00	0.06	0.01	0.00	0.00	0.75	0.13	0.12	0.01	0.06	0.01	0.25	0.06
Lepidoptera	Pyralidae species 1	0.00	0.00	0.00	0.00	0.03	0.01	0.03	0.01	0.04	0.01	0.00	0.00	0.00	0.00	0.12	0.02
Lepidoptera	*Parapoynx* sp.	0.06	0.01	0.00	0.00	0.03	0.01	0.00	0.00	0.74	0.11	1.84	0.19	0.00	0.00	0.13	0.02
Lepidoptera	Nepticulidae species 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Lepidoptera	*Acentria epherella*	0.03	0.01	0.12	0.02	0.21	0.02	0.36	0.02	0.00	0.00	0.32	0.06	0.00	0.00	0.63	0.09
Hemiptera	*Neoplea* sp.	0.00	0.00	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hemiptera	*Plea* sp.	0.02	0.00	0.02	0.00	0.61	0.10	0.43	0.06	0.35	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Ostracoda		0.17	0.03	0.15	0.02	5.92	0.32	1.78	0.10	0.74	0.11	2.28	0.19	0.02	0.01	0.07	0.02
Pelecypoda		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.32	0.06	0.00	0.00	0.00	0.00
Cladocera		0.00	0.00	0.00	0.00	0.94	0.07	0.35	0.03	0.85	0.11	2.28	0.19	0.33	0.04	5.76	0.56
Copepoda		1.39	0.32	0.00	0.02	0.00	0.00	0.07	0.01	0.00	0.00	0.32	0.06	0.02	0.01	0.00	0.00
Hydracarina		0.11	0.02	0.04	0.01	0.23	0.03	0.00	0.00	0.35	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	*Dreissena polymorpha*	0.00	0.00	0.00	0.00	73.18	6.64	7.96	0.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mollusca	Ancylidae	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	*Bithynia tentaculata*	0.83	0.11	0.57	0.07	0.09	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	*Physa gyrina gyrina*	11.97	0.81	6.35	0.33	3.34	0.16	0.41	0.03	0.07	0.01	0.13	0.02	0.67	0.14	0.13	0.03
Gastropoda	*Helisoma* sp	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.31	0.04	0.42	0.05	0.00	0.00	0.00	0.00
Gastropoda	*Gyraulus circumstriatus*	4.35	0.37	1.24	0.10	9.90	0.45	3.32	0.20	5.34	0.31	2.95	0.25	10.69	0.71	1.05	0.12
Gastropoda	*Planorbula armigera*	0.00	0.00	0.09	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	*Valvata sincera sincera*	0.00	0.00	0.03	0.01	0.25	0.04	0.00	0.00	0.78	0.07	0.64	0.11	6.74	0.35	2.26	0.29
Gastropoda	*Amnicola limosa*	5.14	0.29	2.62	0.36	1.67	0.18	0.27	0.03	10.63	0.47	11.09	0.49	8.87	0.37	2.88	0.27
Gastropoda	*Valvata tricarinata*	2.16	0.22	1.03	0.11	0.07	0.01	0.00	0.00	2.76	0.15	1.08	0.07	0.00	0.00	0.00	0.00
Gastropoda	*Elimia livescens*	0.00	0.00	0.00	0.00	0.23	0.04	0.08	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	*Ferrisia fragilis*	0.00	0.00	0.00	0.00	0.09	0.01	0.10	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	*Stagnicola elodes*	0.04	0.01	0.10	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gastropoda	*Promenetus exacuous exacuous*	0.00	0.00	0.00	0.00	0.00	0.00	00.00	00.00	0.00	0.00	0.00	0.00	0.98	0.14	0.00	0.00

ORDER OR CLASS		Lac St-Louis				Lac Memphremagog				Ile Charron				Richelieu River			
		P. perfoliatus		*P. crispus*		*P. perfolatis*		*P. crispus*		*P. richardsonii*		*P. crispus*		*P. richardsonii*		*P. crispus*	
Diptera	Chironomidae	1.302	0.216	9.514	1.759	0.000	0.000	0.000	0.000	1.204	0.080	2.028	0.279	0.000	0.000	0.000	0.000
Diptera	pupating	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.514	0.244	0.092	0.025	0.256	0.066	0.000	0.000
Diptera	Ceraptopogonidae	0.000	0.000	0.529	0.141	0.000	0.000	0.267	0.069	0.376	0.100	0.000	0.000	0.000	0.000	0.391	0.104
Odonata	*Lestidae* sp.	0.000	0.000	1.190	0.318	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Odonata	*Coenagrion* sp.	0.000	0.000	1.020	0.273	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Odonata	*Enallagma* sp.1	1.383	0.202	2.439	0.220	0.490	0.112	0.918	0.139	0.000	0.000	0.589	0.085	0.000	0.000	0.000	0.000
Odonata	*Enallagma* sp. 2	0.159	0.042	0.893	0.239	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Odonata	*Enallagma exsulans*	0.595	0.159	0.000	0.000	0.000	0.000	0.000	0.000	1.161	0.204	0.000	0.000	0.000	0.000	0.000	0.000
Odonata	*Enallagma vesperum*	0.000	0.000	0.000	0.000	0.000	0.000	0.180	0.047	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Odonata	*Enallagma signatum*	0.000	0.000	1.554	0.256	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Odonata	*Telebasis* sp.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.230	0.062	0.000	0.000	0.000	0.000
Odonata	*Ishnura* sp.	0.097	0.026	0.000	0.000	0.000	0.000	0.068	0.018	0.000	0.000	0.680	0.082	0.000	0.000	0.000	0.000
Anisoptera	*Anax* sp.	0.154	0.041	0.000	0.000	0.000	0.000	0.000	0.000	3.119	0.472	0.000	0.000	0.000	0.000	0.000	0.000
Hirudinea	*Helobdella triserialis*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.123	0.032	0.000	0.000
Annelida	Naididae	10.106	1.103	36.839	4.228	37.437	4.455	61.438	4.987	0.000	0.000	0.841	0.115	24.972	1.355	43.477	4.788
Annelida	*Stylaria lacustris*	0.135	0.036	2.693	0.487	1.014	0.205	0.949	0.112	3.007	0.406	0.097	0.026	14.708	1.640	32.131	2.478
Tubellaria	Unknown species 1	1.234	0.296	0.893	0.239	0.123	0.036	0.000	0.000	1.529	0.401	0.000	0.000	0.272	0.048	0.914	0.170
Tubellaria	*Dugesia tigrina*	2.207	0.295	3.214	0.588	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.611	0.120	1.875	0.218
Amphipoda	Unknown species 1	0.452	0.090	0.348	0.093	0.000	0.000	0.000	0.000	0.752	0.137	0.073	0.013	1.081	0.279	4.991	1.148
Amphipoda	*Hyallela azteca*	2.411	0.252	2.064	0.276	0.000	0.000	0.000	0.000	1.252	0.173	3.143	0.296	0.210	0.040	0.000	0.000
Amphipoda	*Gammarus* sp.	7.538	0.499	5.299	0.743	0.000	0.000	0.000	0.000	7.485	1.159	3.652	0.441	19.817	1.484	30.867	3.278
Trichoptera	Unknown	0.077	0.021	0.817	0.148	0.000	0.000	0.000	0.000	27.532	3.959	0.032	0.009	1.173	0.197	8.718	1.191
Trichoptera	Polycentropodidae species unknown	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.036	0.010	0.000	0.000	0.123	0.032	0.000	0.000
Trichoptera	*Psychomyia* sp.	0.077	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Trichoptera	*Triaenodes* sp.	0.000	0.000	0.000	0.000	0.391	0.115	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Trichoptera	Philopotamidae unknown species	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.376	0.100	0.000	0.000	0.000	0.000	0.000	0.000
Trichoptera	*Neureclipsis* sp.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.446	0.119	0.000	0.000	0.589	0.099	0.295	0.056
Trichoptera	*Oecetis* sp.	0.502	0.077	0.893	0.239	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Trichoptera	*Brachycentrus* sp.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.034	0.276	68.568	5.553	139.403	8.931
Trichoptera	*Cheumatopsyche* sp.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.456	0.083

Trichoptera	*Leptocerus* sp.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.384	0.357	0.000	0.000
Trichoptera	Leptoceridae species unknown	0.595	0.159	0.420	0.112	0.000	0.000	0.667	0.172	0.000	0.000	0.000	0.000	0.000	0.000	0.240	0.064
Trichoptera	*Triaenodes* sp.	0.166	0.044	0.174	0.047	0.000	0.000	0.000	0.000	0.027	0.007	0.000	0.000	0.000	0.000	0.000	0.000
Trichoptera	*Hydroptila* sp.	3.466	0.550	0.893	0.239	0.000	0.000	0.000	0.000	0.445	0.100	0.000	0.000	0.000	0.000	0.000	0.000
Trichoptera	*Agraylea* sp.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.271	0.032	0.000	0.000
Coleoptera	*Dubiraphia* sp.	0.154	0.041	4.185	0.463	0.000	0.000	0.000	0.000	0.000	0.000	0.332	0.089	0.000	0.000	0.000	0.000
Coleoptera	*Dineutus* sp.	0.000	0.000	0.000	0.000	0.123	0.036	0.000	0.000	0.397	0.106	0.113	0.030	0.000	0.000	0.000	0.000
Hemiptera	Corixidae	0.000	0.000	0.893	0.239	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Lepidoptera	*Acentria ephemerella*	0.000	0.000	1.583	0.280	1.727	0.178	1.509	0.157	2.586	0.394	1.016	0.121	3.560	0.335	4.726	0.473
Lepidoptera	*Paraponyx* sp.	0.159	0.042	0.000	0.000	0.000	0.000	0.000	0.000	4.952	0.521	0.000	0.000	0.000	0.000	0.000	0.000
Isopoda	*Lirceus* sp.	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.376	0.100	0.044	0.012	0.000	0.000	0.000	0.000
Isopoda	Caecidotea	0.000	0.000	3.750	0.782	0.000	0.000	0.000	0.000	0.777	0.136	0.000	0.000	0.000	0.000	0.000	0.000
Coelenterata	*Hydra* sp.	0.000	0.000	0.000	0.000	0.000	0.466	0.775	0.111	0.376	0.100	0.000	0.069	25.837	4.104	56.308	4.123
Hydracarina		3.683	0.293	9.370	1.542	0.000	0.000	0.159	0.029	0.000	0.000	0.166	0.044	0.846	0.128	0.156	0.042
Copepoda	Harpacticoida	0.741	0.141	2.619	0.424	0.000	0.000	0.000	0.000	0.340	0.091	0.000	0.000	0.000	0.000	0.000	0.000
Gastropoda	unknown	0.684	0.110	1.488	0.276	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.481	0.128
Gastropoda	Amnicola limnosa	17.779	1.073	7.231	0.717	28.002	3.315	32.038	3.514	4.611	1.007	0.664	0.178	0.148	0.038	0.000	0.000
Gastropoda	*Fossaria* sp.	0.000	0.000	0.000	0.000	0.000	0.000	0.267	0.069	0.351	0.080	0.000	0.000	0.000	0.000	0.481	0.128
Gastropoda	*Physia* sp.	0.265	0.071	2.296	0.486	0.000	0.000	0.000	0.000	0.027	0.007	0.000	0.000	0.208	0.054	0.000	0.000
Gastropoda	*Physia gyrina gyrina*	3.178	0.410	3.623	0.493	0.000	0.000	0.000	0.000	0.000	0.000	2.124	0.296	5.755	0.766	3.339	0.717
Gastropoda	*Gyraulus circumstriatus*	7.373	1.271	4.597	0.730	0.000	0.000	0.000	0.000	12.243	1.814	14.426	1.771	2.486	0.385	0.962	0.256
Gastropoda	*Stagnicola catascopium*	0.159	0.042	0.000	0.000	0.000	0.000	0.000	0.000	85.287	12.036	0.000	0.000	0.000	0.000	0.000	0.000
Gastropoda	*Valvata tricarinata*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.123	0.032	0.000	0.000
Gastropoda	*Valvata sincera sincera*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.580	0.100	0.000	0.000
Gastropods	juvenile planorbula	0.000	0.000	0.000	0.000	0.000	0.000	0.095	0.025	0.000	0.000	0.000	0.000	0.946	0.135	0.000	0.000
Gastropoda	ferrissia fragiliis	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.123	0.032	0.000	0.000
Gastropoda	Lymnaeinae	0.123	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Gastropoda	*Helisoma* sp	1.028	0.167	0.265	0.071	13.034	1.182	23.983	3.236	0.401	0.100	0.000	0.000	0.000	0.000	0.000	0.000
Cladocera		0.000	0.000	0.000	0.000	11.659	2.269	62.475	8.625	0.000	0.000	0.000	0.000	3.080	0.430	7.039	1.657
Copepoda		0.343	0.069	0.893	0.239	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.494	0.128	0.000	0.000
Ostracoda		0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.752	0.201	0.000	0.000	0.790	0.110	0.864	0.168
Astacidae		0.097	0.026	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000