Epiphytic macroinvertebrate communities on Eurasian watermilfoil (*Myriophyllum spicatum*) and native milfoils *Myriophyllum sibericum* and *Myriophyllum alterniflorum* in eastern North America

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Abstract: Aquatic macrophytes play an important role in the survival and proliferation of invertebrates in freshwater ecosystems. Epiphytic invertebrate communities may be altered through the replacement of native macrophytes by exotic macrophytes, even when the macrophytes are close relatives and have similar morphology. We sampled an invasive exotic macrophyte, Eurasian watermilfoil (*Myriophyllum spicatum*), and native milfoils *Myriophyllum sibericum* and *Myriophyllum alterniflorum* in four bodies of water in southern Quebec and upstate New York during the summer of 2005. Within each waterbody, we compared the abundance, diversity, and community composition of epiphytic macroinvertebrates on exotic and native *Myriophyllum*. In general, both *M. sibericum* and *M. alterniflorum* had higher invertebrate diversity and higher invertebrate biomass and supported more gastropods than the exotic *M. spicatum*. In late summer, invertebrate density tended to be higher on *M. sibericum* than on *M. spicatum*, but lower on *M. alterniflorum* than on *M. spicatum*. Our results demonstrate that *M. spicatum* supports macroinvertebrate communities that may differ from those on structurally similar native macrophytes, although these differences vary across sites and sampling dates. Thus, the replacement of native milfoils by *M. spicatum* may have indirect effects on aquatic food webs.

Résumé : Les macrophytes aquatiques jouent un rôle important dans la survie et la prolifération des invertébrés dans les écosystèmes d'eau douce. Les communautés d'invertébrés épiphytes peuvent être modifiées par le remplacement des macrophytes indigènes par des marcophytes exotiques, même lorsque ces macrophytes sont de proches parents et possèdent une morphologie similaire. Nous avons échantillonné un macrophyte exotique envahissant, le myriophylle à épis (*Myriophyllum spicatum*), et des myriophylles indigènes (*Myriophyllum sibericum* et *Myriophyllum alterniflorum*) dans des plans d'eau du sud du Québec et du nord de l'état de New York durant l'été 2005. Dans chaque plan d'eau, nous avons comparé l'abondance, la diversité et la composition de la communauté de macroinvertébrés épiphytes sur les *Myriophyllum* exotique et indigènes. En général, tant *M. sibericum* que *M. alterniflorum* portent une plus grande diversité et une biomasse plus importante d'invertébrés ainsi qu'un plus grand nombre de gastéropodes que le *M. spicatum* exotique. En fin d'été, la densité des invertébrés tend à être plus importante sur *M. sibericum* que sur *M. spicatum*, mais plus faible sur *M. alterniflorum* que sur *M. spicatum*. Nos résultats démontrent que *M. spicatum* porte des communautés de macroinvertébrés qui peuvent différer de celles qui se retrouvent sur les macrophytes indigènes de structure similaire, bien que ces différences puissent varier d'un site à un autre et d'une date d'échantillonnage à l'autre. Ainsi, le remplacement des myriophylles indigènes par *M. spicatum* peut avoir des effets indirects sur les réseaux alimentaires aquatiques.

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Introduction

Aquatic macrophytes play key ecological roles in lakes and rivers, primarily as a source of primary productivity and as a habitat for abundant and diverse faunal communities (Kershner and Lodge 1990; Killgore et al. 1991; Toft et al. 2003). In particular, submersed macrophyte beds support dense communities of invertebrates and thus serve as important feeding areas for fish (Rozas and Odum 1988; Strayer and Malcom 2007). Such communities are being

transformed by introductions of invasive exotic macrophytes that dominate or replace native macrophytes (Boylen et al. 1999; Myers and Bazely 2003). Exotic macrophytes can alter the physical and chemical environment, particularly when their growth form and life history traits differ from those of the native species they replace (Carpenter and Lodge 1986; Cattaneo et al. 1998; Caraco and Cole 2002). However, the effects of macrophyte species replacements on aquatic communities remain relatively unexplored (but see Keast 1984; Strayer et al. 2003; Toft et al. 2003). It is

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of interest to know if morphologically similar exotic and native macrophytes will support similar epiphytic macroinvertebrate communities.

Within a given ecosystem, native macrophytes and their associated invertebrates may have interacted over the course of their evolution. If shared evolutionary history matters, then we would expect native macrophytes to support more diverse invertebrate communities than exotic macrophytes in North American inland waters because the vast majority of freshwater invertebrate species in North America are native (Pennak 1989; Merritt and Cummins 1996). Furthermore, exotic macrophytes might facilitate the establishment and population growth of exotic invertebrates, particularly if these species have shared an evolutionary history — a prediction of the "invasional meltdown" hypothesis (Simberloff and Von Holle 1999). Exotic macrophytes might also act as a vector for the introduction of exotic invertebrates (Johnson et al. 2001; Toft et al. 2003). For these reasons, we would expect to find more exotic invertebrates living on exotic macrophytes.

Physical and chemical properties of aquatic macrophytes may influence the abundance, diversity, and community composition of epiphytic invertebrates, potentially resulting in different invertebrate communities associated with different macrophyte species (Cyr and Downing 1988; Chilton 1990; Cheruvelil et al. 2002). Structurally complex macrophytes with finely divided leaves tend to support higher densities of epiphytic invertebrates compared with those with simple leaves (Krull 1970; Cheruvelil et al. 2000, 2002). The chemicals exuded by aquatic macrophytes may also directly affect the abundance of certain invertebrates (Marko et al. 2005), whereas other exudates may influence the growth of epiphytic algae — an important invertebrate food source (Wium-Andersen et al. 1982; Cattaneo 1983; Gross et al. 1996). Therefore, it follows that even macrophytes with similar structure may support contrasting invertebrate communities.

Our objective was to determine if the invasive exotic macrophyte Eurasian watermilfoil (*Myriophyllum spicatum*) supports invertebrate communities equivalent in composition, diversity, and abundance to those on structurally similar native *Myriophyllum* species. *Myriophyllum spicatum* 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 distributed across North America, where it often outcompetes native milfoils and other aquatic macrophytes through crowding and shading (Boylen et al. 1999). Milfoils are submersed, canopy-forming macrophytes that occur either in mixed or monospecific beds in ponds, lakes, and lentic areas of large rivers (Aiken et al. 1979). Milfoils generally have finely divided, feathery leaves arranged in whorls of four around the stem. Native milfoils *Myriophyllum sibiricum* and *Myriophyllum alterniflorum* and the exotic *Myriophyllum spicatum* are very similar in their growth form and leaf morphology (Gerber and Les 1994; Crow and Hellquist 2000); *M. sibiricum* and *M. spicatum* have similar-sized leaves, whereas *M. alterniflorum* has slightly smaller leaves. If leaf structure (i.e., complex versus simple leaves) largely determines epiphytic invertebrate abundance and diversity, milfoils should support similar invertebrate communities. However, assum-

ing that biochemical or subtle physical differences between these species may provoke adaptations in epiphytic invertebrates (Gross et al. 1996; Marko et al. 2005), we hypothesized that native species of *Myriophyllum* support more abundant and diverse invertebrate communities than *M. spicatum* because of their shared evolutionary history with native invertebrates. Particular attention was given to gastropods because of their important contribution to epiphytic invertebrate biomass. We also hypothesized that *M. spicatum* supports more abundant and diverse exotic invertebrates than native species of *Myriophyllum*. We tested these hypotheses in a multisite field study in which the density, biomass, diversity, and community composition of epiphytic invertebrates on the exotic *M. spicatum* were compared with native *M. sibiricum* and *M. alterniflorum*.
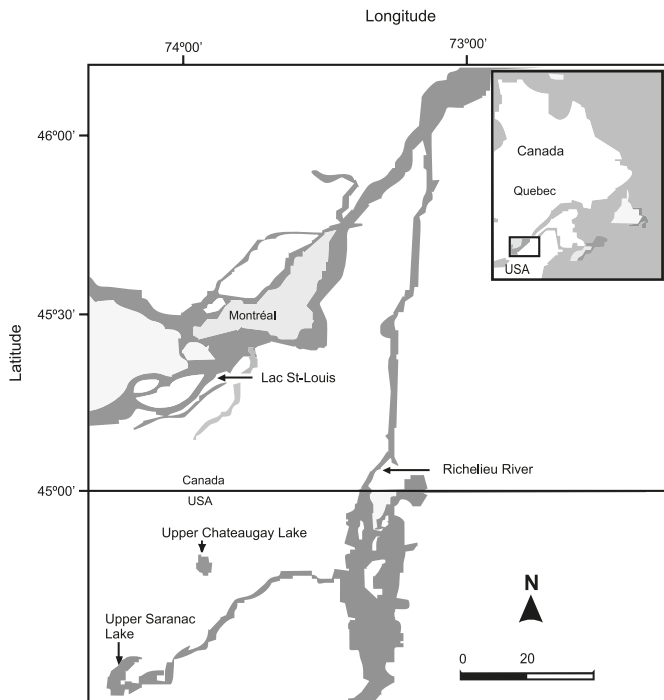
Materials and methods

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 St-Louis (a fluvial lake on the St. Lawrence River) in southern Quebec and Upper Saranac Lake and Upper Chateaugay Lake in the Adirondack State 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 visually surveyed plants in each waterbody in June or July and selected a site within each where the relative abundance (percent cover) of both native and exotic *Myriophyllum* species was approximately equal. All subsequent samples were then taken from the same site. In Lac St-Louis and the Richelieu River, we sampled *M. spicatum* and the native *M. sibericum*, whereas in Saranac Lake and Chateaugay Lake, we sampled *M. spicatum* and the native *M. alterniflorum*. Two weeks prior to sampling, Saranac Lake was undergoing a milfoil control program wherein *M. spicatum* was manually harvested at discrete periods by divers who took care to leave native macrophytes intact and minimize disturbance in the lake. 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 monthly intervals in the summer of 2005.

Epiphytic invertebrate sampling

At each site, a snorkeler or SCUBA diver collected macrophytes and epiphytic invertebrates using a modified Downing box sampler, a plexiglas box that encloses plant material and associated invertebrates in 6 L of water (Downing 1986; Rasmussen 1988). On one side of this box is a screen (0.5 mm) to drain water while keeping macroinvertebrates and macrophytes inside. Within each site, we limited the depth variation at which samples were taken to within 1 m. Macrophytes were identified in the field prior to sampling. Because *M. spicatum* and *M. sibericum* are sometimes difficult to distinguish (Crow and Hellquist 2000), we only sampled at sites where morphological differences between the two species were sufficiently pronounced to ensure correct identification. At each site, we collected 6–10 replicate samples of each macrophyte species, except at Saranac Lake where additional samples were taken because

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Fig. 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.

there were relatively few invertebrates on the macrophytes. The number of samples taken at each site depended on the density of invertebrates and the availability of macrophytes, but sampling effort was equal for both native and exotic macrophytes. Samples were taken from the interior of a mixed bed of macrophytes at sites within 20 m of the shoreline. We made an effort to collect native and exotic macrophytes 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 that were transported in a cooler to the lab within 3 h and kept refrigerated (for <48 h) until their pH was measured using a digital meter (AP63 pH meter, Accumet Portable Laboratory, Fisher Scientific, Ottawa, Ontario).

Sample processing

In the field, we placed macrophytes from each sample into plastic trays and removed loose invertebrates from both the tray and sampler using forceps. Invertebrates were immediately preserved in 70% ethanol. The macrophytes 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 h of collection. Working under a dissection microscope, we removed all of the remaining invertebrates from the macrophytes using forceps and preserved them in 70% ethanol. Macrophytes were subsequently rinsed of debris (e.g., silt and marl), blotted to remove excess water, dried in an oven at 65 °C for 16 h un-

til a stable weight was reached, and then weighed on an electronic balance (±0.01 g).

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 (±0.001 g) of invertebrates grouped according to their taxonomic order in each sample. The range of biomass was too small to be measured with any more accuracy using dry weights. Although preservation alters the wet weight of invertebrates, 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. Invertebrate grouped wet weights were measured within <10 s of their removal from ethanol after gentle blotting with tissue paper.

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 ln-transformed prior to statistical analysis to meet assumptions of normality. Homogeneity of variance across sampling groups at each site was verified using Levene's test. A repeated-measures analysis of variance (ANOVA) was used to compare the mean invertebrate density on native and exotic *Myriophyllum* at each site, with date as the within-subjects factor and plant type (native or exotic) as the between-subjects factor; the same was done for invertebrate biomass. At one site (Richelieu River), a significant interaction effect between sampling date and macrophyte species was found, which prompted us to run post hoc comparisons in each date using Bonferroni-corrected *t* tests. Densities of exotic invertebrate species on native and exotic *Myriophyllum* were compared using repeated-measures ANOVA when the abundance of an exotic invertebrate species was normally distributed across a site. Otherwise, we used two-tailed *t* tests to compare the density of an exotic invertebrate species on each sampling date that density was normally distributed — which occurred for all dates except when no exotic invertebrates were found on either native or exotic macrophytes. All statistical tests were preformed using SPSS version 14.0 for Windows (SPSS Inc., Chicago, Illinois).

To measure invertebrate diversity, we calculated taxa richness, the Shannon–Wiener index, and the inverted Simpson index. The latter indices are calculated based on both taxa richness and evenness, but the Shannon–Wiener index is influenced more by taxa richness than by 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 macrophytes at each site and were used to compare invertebrate diversity on two species of macrophytes while controlling for differences in the total abundance of invertebrates on the different macrophyte species. Shannon–Wiener diversity and inverse Simpson diversity were calculated based on 50 randomizations sampled with replacement to generate error bars (Colwell 2005). We also ran a detrended correspondence analysis (DCA) to reveal trends in inverte-
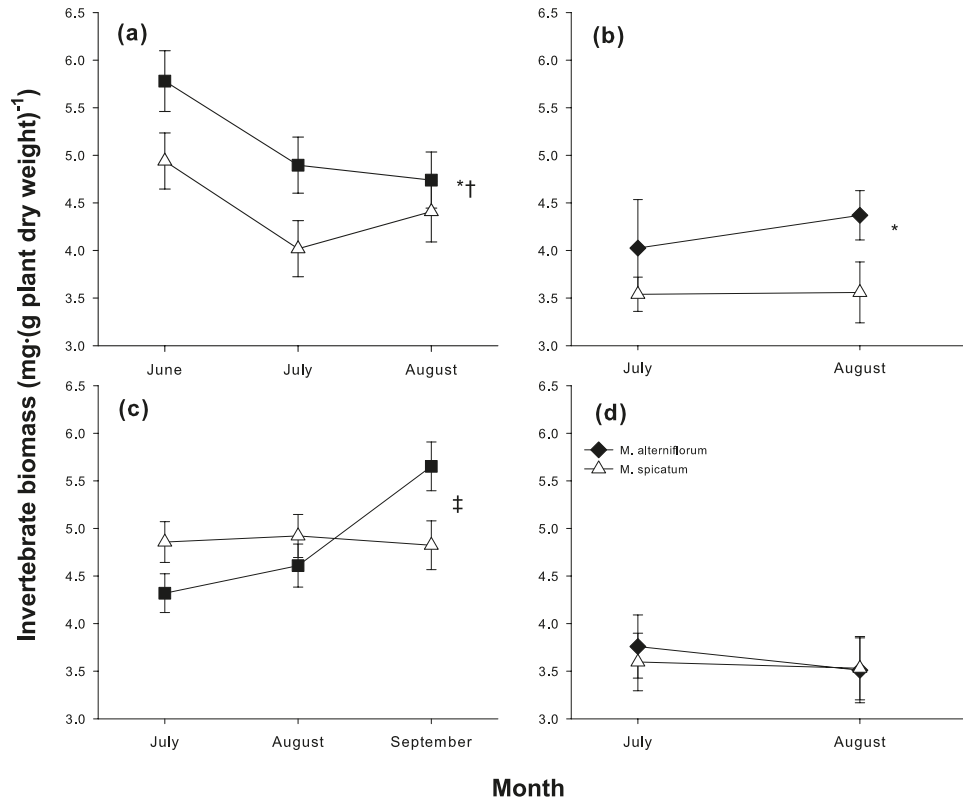
Table 1. Characteristics of sampling sites in 2005.

Site	Location	Plants sampled	System type	No. of samples (E, N)[a]	Water temperature: minimum, maximum (°C)[b]	pH range	Site depth (m)	Other plant species[c]	Notes
Lac St-Louis	Southwest of the Island of Montreal, Quebec; part of the St. Lawrence River	*M. spicatum, M. sibericum*	Fluvial lake	7, 6 (June) 6, 6 (July) 6, 7 (August) **19, 19**	21 (June), 27 (August)	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 (August) 7, 7 (September) **26, 26**	19 (September), 24 (July and August)	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 midriver, in a 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 (August) **39, 39**	19 (August), 21 (July)	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 (August) **16, 16**	17 (August), 21 (July)	6.7–7.8	1.0–1.5	*E. canadensis, P. richardsonii, Ranuculus* sp., *Utricularia* sp., *V. americana*	Site near lake inflow and wetland, south end of lake; low wave action

[a]Number of samples of exotic (E) and native (N) macrophytes (month sampled is indicated in parentheses); the total number for each is in bold.

[b]Month sampled is indicated in parentheses.

[c]Exotic macrophyte species are in bold. Macrophyte genera: *C, Ceratophyllum; E, Elodea; P, Potamogeton; V, Vallisneria.*

Fig. 2. Invertebrate biomass (milligrams wet weight per gram of plant dry weight) on exotic and native *Myriophyllum* species (±1 standard error, SE) in (*a*) Lac St-Louis, (*b*) Chateaugay Lake, (*c*) Richelieu River, and (*d*) Saranac Lake: solid squares, *M. sibericum*; solid diamonds, *M. alterniflorum*; open triangles, *M. spicatum*; *, a significant difference in invertebrate biomass on native and exotic plants; †, a significant difference between dates; ‡, a significant interaction between plant type and date (repeated-measures analysis of variance, $p < 0.05$).

Results

Invertebrate abundance

At three of the four sites, invertebrate biomass was significantly higher on native *Myriophyllum* species than on *M. spicatum* during at least one sampling period in the summer (ANOVA, $p < 0.05$; Fig. 2). In early to mid-summer, invertebrate biomass was higher on native *M. sibericum* than on *M. spicatum* in Lac St-Louis by a factor of 2.2, whereas from June to August, total invertebrate biomass declined on both macrophyte species. In the Riche-lieu River, the invertebrate biomass on *M. sibiricum* was slightly lower than on *M. spicatum* in early summer but by late summer was 2.3 times greater than on *M. spicatum*. In Chateaugay Lake, *M. alterniflorum* had twice as much invertebrate biomass than *M. spicatum* during August, whereas at Saranac Lake, both species had similar invertebrate biomass throughout the season. Gastropod biomass, which constituted a substantial portion (>60% at three sites) of the total invertebrate biomass, was also significantly higher on native macrophytes at Lac St-Louis, Chateaugay Lake, and Richelieu River sites (ANOVA, $p < 0.05$). In Saranac Lake,

M. spicatum and *M. alterniflorum* supported similar gastropod biomass (Fig. 3).

Within each site, invertebrate density tended to differ on native and exotic *Myriophyllum*, especially in mid- to late summer (Fig. 4). Invertebrate density was higher on *M. sibericum* than on *M. spicatum* (ANOVA, $p < 0.05$). Mean invertebrate density on *M. sibericum* was higher than on *M. spicatum* by a factor of 1.5 in Lac St-Louis (August) and by a factor of 2.2 in the Richelieu River (September). Invertebrate density tended to be higher on *M. spicatum* than on *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 and by a factor of 1.8 in Saranac Lake. The mean body size (estimated from the ratio of biomass to density) of invertebrates on *M. spicatum* was generally lower than on *M. alterniflorum* (Figs. 2 and 4).

Invertebrate diversity and community composition

In general, the two native species of *Myriophyllum* supported either equivalent or greater invertebrate diversity than *M. spicatum*. Invertebrate taxa richness was consistently higher on *M. alterniflorum* than on *M. spicatum* ($p < 0.05$; Fig. 5; Table 2). Invertebrate taxa richness was also higher on *M. sibericum* than on *M. spicatum* in the Richelieu River ($p < 0.05$), whereas in Lac St-Louis, both macrophytes species supported similar taxa richness. Shannon–

brate community composition at each site, using CANOCO version 4.5 (Biometris, Wageningen). Before running a DCA, we excluded rare taxa, which were defined as those species present in less than three replicate samples at a site throughout the season.

Fig. 3. Gastropod biomass (milligrams wet weight per gram of plant dry weight) on exotic and native *Myriophyllum* species (±1 standard error, SE) in (*a*) Lac St-Louis, (*b*) Chateaugay Lake, (*c*) Richelieu River, and (*d*) Saranac Lake: solid squares, *M. sibericum*; solid diamods, *M. alterniflorum*; open triangles, *M. spicatum*; *, a significant difference in gastropod biomass on native and exotic plants; †, a significant interaction between plant type and date (repeated-measures analysis of variance, *p* < 0.05).
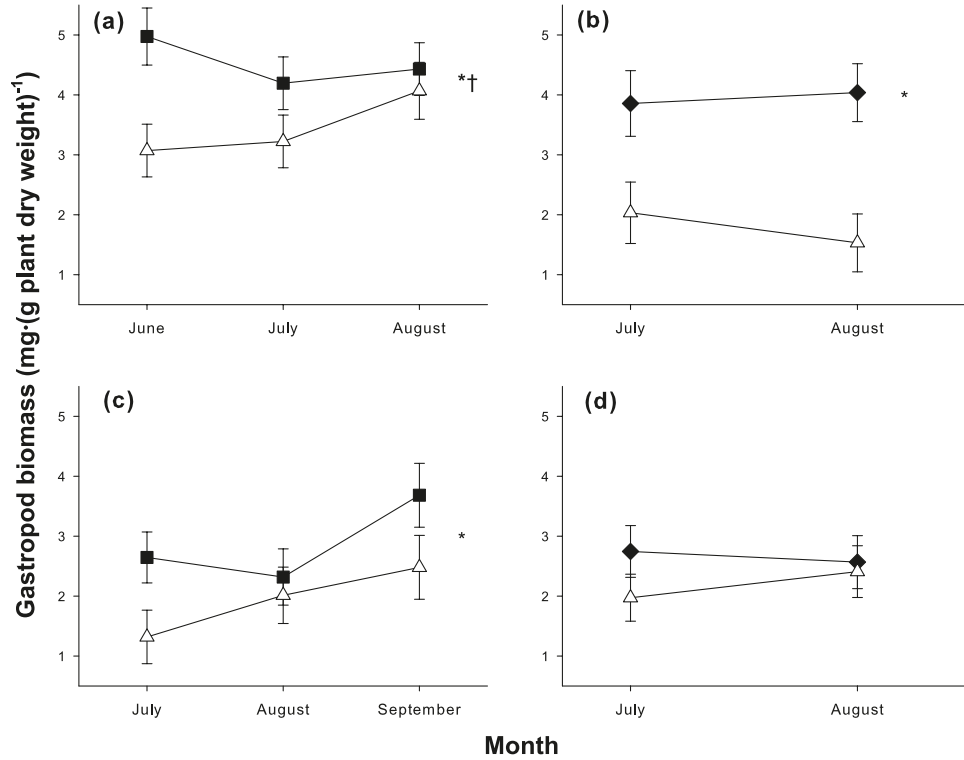

Fig. 4. Invertebrate density (number of invertebrates per gram of plant dry weight) on exotic and native *Myriophyllum* species (±1 standard error, SE) in (*a*) Lac St-Louis, (*b*) Chateaugay Lake, (*c*) Richelieu River, and (*d*) Saranac Lake: solid squares, *M. sibericum*; solid diamonds, *M. alterniflorum*; open triangles, *M. spicatum*; *, a significant difference in invertebrate density on native and exotic plants; †, a significant difference between dates (repeated-measures analysis of variance, *p* < 0.05).
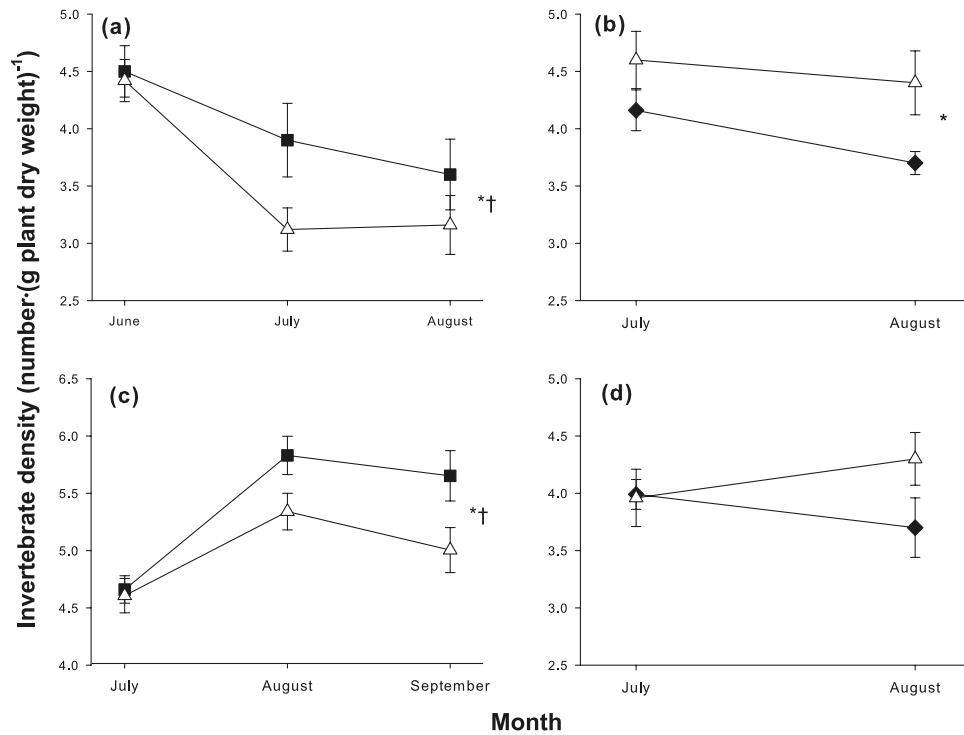
Fig. 5. Rarefaction curves for invertebrate taxa richness on exotic and native *Myriophyllum* species in (*a*) Lac St-Louis, (*b*) Chateaugay Lake, (*c*) Richelieu River, and (*d*) Saranac Lake: solid squares, *M. sibericum*; solid diamonds, *M. alterniflorum*; open triangles, *M. spicatum*; *, a significant difference in invertebrate taxa richness between the two plant species ($p < 0.05$). Error bars represent standard deviation based on 50 randomized runs.
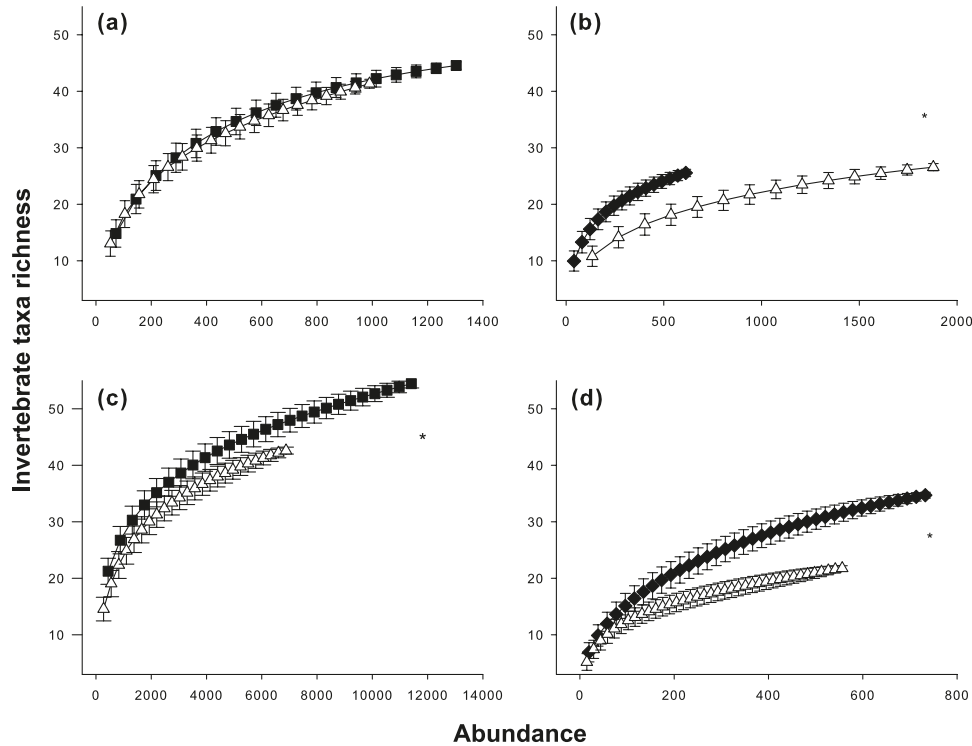

Table 2. Taxa richness, the exponent of Shannon–Wiener diversity ($e^{H'}$), and the inverse Simpson diversity ($1/D'$) compared on native and exotic *Myriophyllum* species.

	Taxa richness		$e^{H'}$		$1/D'$		
Site	Native	Exotic	Native	Exotic	Native	Exotic	Invertebrate abundance[a]
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: Both the exponent of Shannon-Wiener diversity and the inverse Simpson diversity indices represent the number of different species that we would find if all species in the community were equally common (Jost 2006); however, the inverse Simpson index is more sensitive to how evenly invertebrate abundance is distributed across taxa. Significantly different values ($p < 0.05$) are indicated by an asterisk (*).
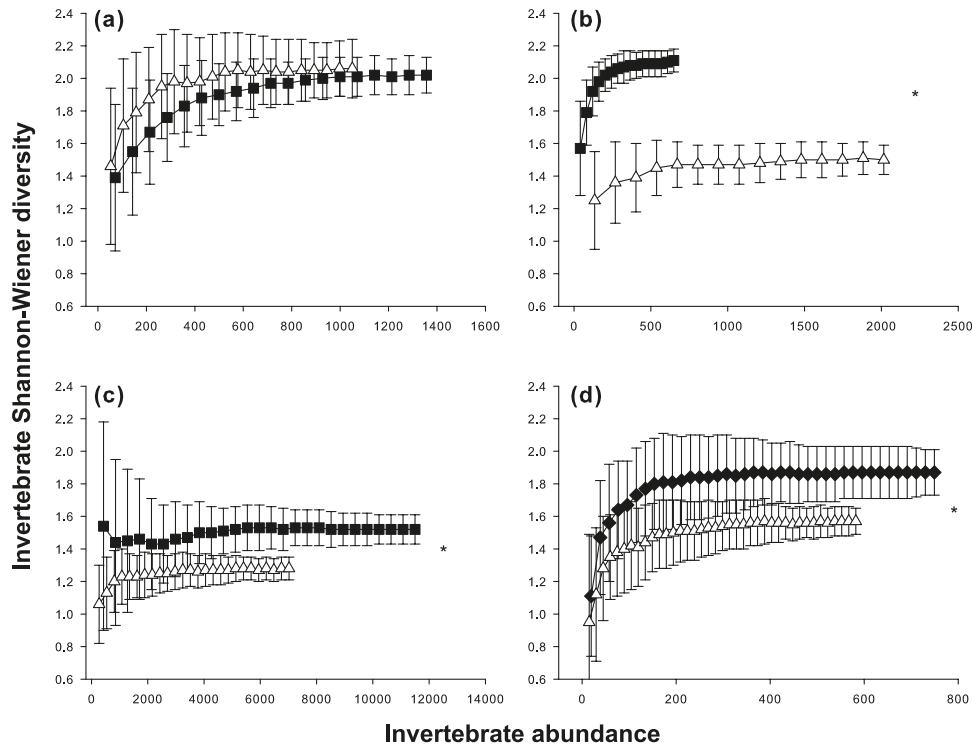
[a]Diversity comparisons on native and exotic macrophytes were made at the level of abundance of invertebrates on the macrophyte species with the fewest invertebrates.

Wiener diversity followed the same pattern as taxa richness (Fig. 6; Table 2). The inverse Simpson index showed a similar pattern, with the exception of Saranac Lake; at this site, *M. alterniflorum* tended to have higher inverse Simpson diversity of invertebrates than *M. spicatum*, but the difference was not significant (Table 2). Thus, across all sites, taxa richness, Shannon–Wiener diversity, and the inverse Simpson diversity index of invertebrates on native milfoils were equal to or significantly higher than on *M. spicatum* (Table 2).

Although native and exotic *Myriophyllum* supported many of the same invertebrate species, the abundance of certain invertebrate groups (e.g., gastropods) was often different on each milfoil species. At three of our four sites, both species of native *Myriophyllum* had higher gastropod biomass per gram of plant dry weight than *M. spicatum* (ANOVA, $p <$

0.05). The differences between invertebrate community composition on *M. alterniflorum* and *M. spicatum* were particularly distinct in Chateaugay Lake. At this site, detrended correspondence analysis showed that samples divided along two axes: the first representing plant type, and the second representing sampling date (Figs. 7*a*, 7*b*). Generally, *M. spicatum* supported many chironomids and oligochaetes, whereas *M. alterniflorum* supported many amphipods and gastropods. Invertebrate communities associated with *M. spicatum* were characterized by an abundance of naidid oligochaetes (Ni), chironomids (Ch), caddisflies of the hydroptilid genus *Oxyethira* (Hx), and the Eurasian pyralid moth, *Acentria ephemerella* (= *Acentria nivea*) (Ac) (Fig. 7*b*). Invertebrates characteristic of *M. alterniflorum* were the gastropods *Valvata sincera* (Vs) and *Amnicola limosa* (Am), the amphipod *Hyallela azteca* (Hy), damselflies in the fam-

Fig. 6. Shannon–Wiener diversity of invertebrates on exotic and native *Myriophyllum* species in (*a*) Lac St-Louis, (*b*) Chateaugay Lake, (*c*) Richelieu River, and (*d*) Saranac Lake: solid squares, *M. sibericum*; solid diamonds, *M. alterniflorum*; open triangles, *M. spicatum*; *, a significant difference in invertebrate Shannon–Wiener diversity between the two plant species ($p < 0.05$). Error bars represent standard deviation based on 50 randomized runs.

ily Coenagrionidae (Co), and caddisflies of the genus *Orthotricha* (Ho). Invertebrate communities were also different in early and late summer, with more planarians on both macrophyte species in July and more caddisflies in August (Fig. 7*b*). In Saranac Lake, differences in invertebrate communities were not clearly defined by either date or macrophyte species.

Invertebrate community composition also differed between *M. spicatum* and *M. sibericum* in the Richelieu River (Figs. 7*c*, 7*d*), while such differences were less apparent in Lac St-Louis. In the Richelieu River, as in Chateaugay Lake, *M. spicatum* supported many chironomids and oligochaetes, whereas *M. sibericum* supported many amphipods and snails. Invertebrate communities characteristic of *M. spicatum* were dominated by chironomids (Ch), oligochaetes (Ni, St), and the caddisfly *Brachycentrus* sp. (Br) throughout the sampling period. Invertebrate communities on *M. sibericum* were characterized by the amphipod *Hyalella azteca* (Hy), the gastropods *Physa gyrina gyrina* (Ph), *Gyraulus circumstriatus* (Gy), and *Amnicola limosa* (Am), the planarian *Dugesia tigrina* (Du), ostracods (Os), and in September, the Eurasian zebra mussel, *Dreissena polymorpha* (Dr). Generally, the invertebrate composition on *M. spicatum* did not vary throughout the season, whereas 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 (Ni), chironomids (Ch), and *Brachycentrus* sp. (Br); in September, *M. sibericum* supported many zebra mussels (Figs. 7*c*, 7*d*). In Lac St-Louis, gastro-
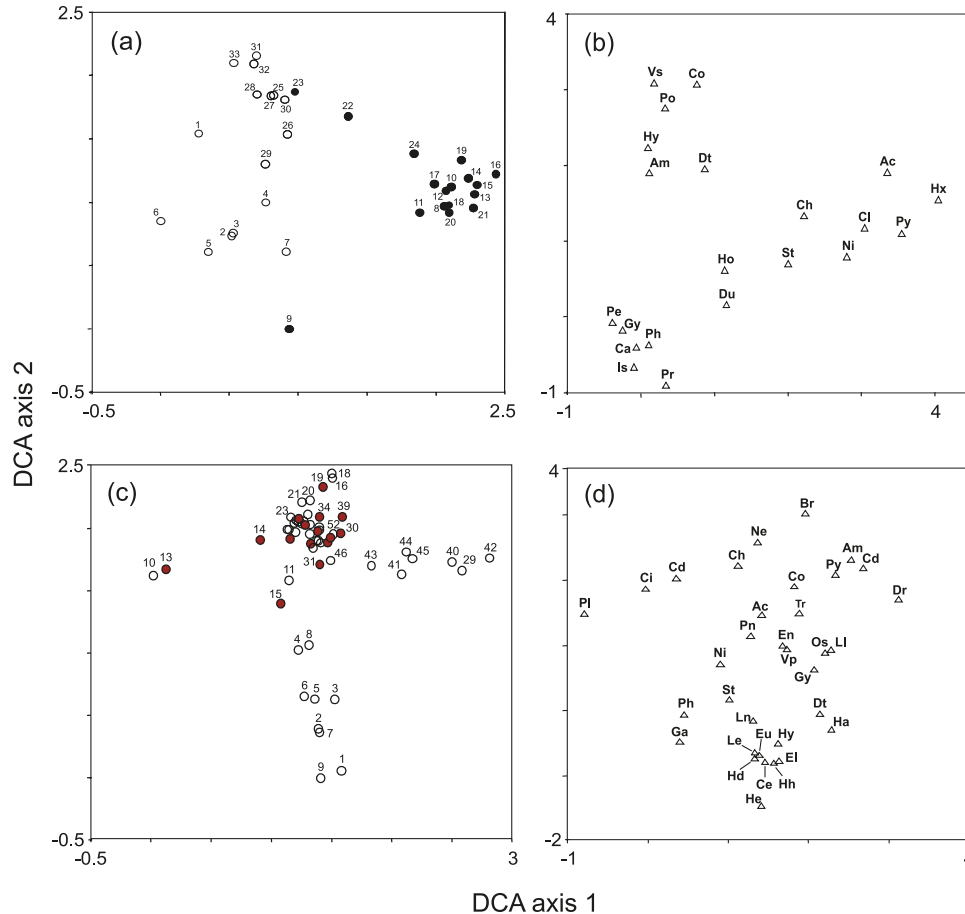
pods were significantly higher on *M. sibericum* than on *M. spicatum* (ANOVA, $p < 0.05$), but otherwise invertebrate communities were not clearly differentiated by either date or macrophyte species.

Exotic invertebrates

Three species of exotic invertebrates were found. The Eurasian moth *Acentria ephemerella* was present at all four sites and was higher on *M. spicatum* than on the native *Myriophyllum* species at every site. In Saranac Lake, we found only two specimens of *A. ephemerella* in one sample of *M. spicatum* and none on *M. alterniflorum*. In Chateaugay Lake, *A. ephemerella* again was not found on *M. alterniflorum* but was present in 38% of the samples of *M. spicatum* and thus was grouped with *M. spicatum* in the DCA analysis (Figs. 7*a*, 7*b*). In the Richelieu River and Lac St-Louis, *A. ephemerella* occurred on both *M. sibericum* and *M. spicatum* but was more likely to group with the Eurasian milfoil in the Richelieu River (Figs. 7*c*, 7*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 frequencies were 16% and 10%, respectively.

In Lac St-Louis, the abundance of the Eurasian snail *Bithynia tentaculata* did not differ significantly between *M. sibericum* and *M. spicatum* on any of the sampling dates (Fig. 8*a*). In the Richelieu River, the density of *Dreissena polymorpha* was significantly higher on *M. sibericum* than on *M. spicatum* in September after the peak period of zebra mussel settlement (*t* test, $p < 0.01$; Fig. 8*b*).

Fig. 7. Detrended correspondence analysis of the invertebrate communities at (*a*, *b*) Chateaugay Lake and (*c*, *d*) the Richelieu River. At Chateaugay Lake (*a*), numbers up to 16 are from July, those greater than 16 are from August; in the Richelieu River (*c*), numbers from 1 to 21 are from July, 22 to 40 are from August, and 41 to 55 are from September. Open circles in (*a*) and (*c*) represent *Myriophyllum spicatum*. Solid circles in (*a*) and (*c*) represent the native species *M. alterniflorum* and *M. sibericum*, respectively. 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*, Turbellaria; du, *Dugesia tigrina*, Turbellaria; El, Elmidae, Coleoptera; En, *Enallagma* sp., Odonata; Eu, *Euhrychiopsis lecontei*, Coleoptera; Ga, *Gammarus* sp., Amphipoda; Gy, *Gyraulus circumstriatus*, Gastropoda; Hd, Hydracarina; He, *Helobdella* sp., Annelida; Ho, *Orthotrichia* sp., Trichoptera; Hx, *Oxyethira* sp., Trichoptera; Hy, *Hyalella azteca*, Amphipoda; Is, Isopoda; Le, Leptoceridae, Trichoptera; Li, *Leptocerus* sp., Trichoptera; Nc, *Nectopsyche* sp., Trichoptera; Ne, *Nehalennia* sp., Odonata; Ni, Naididae, 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.
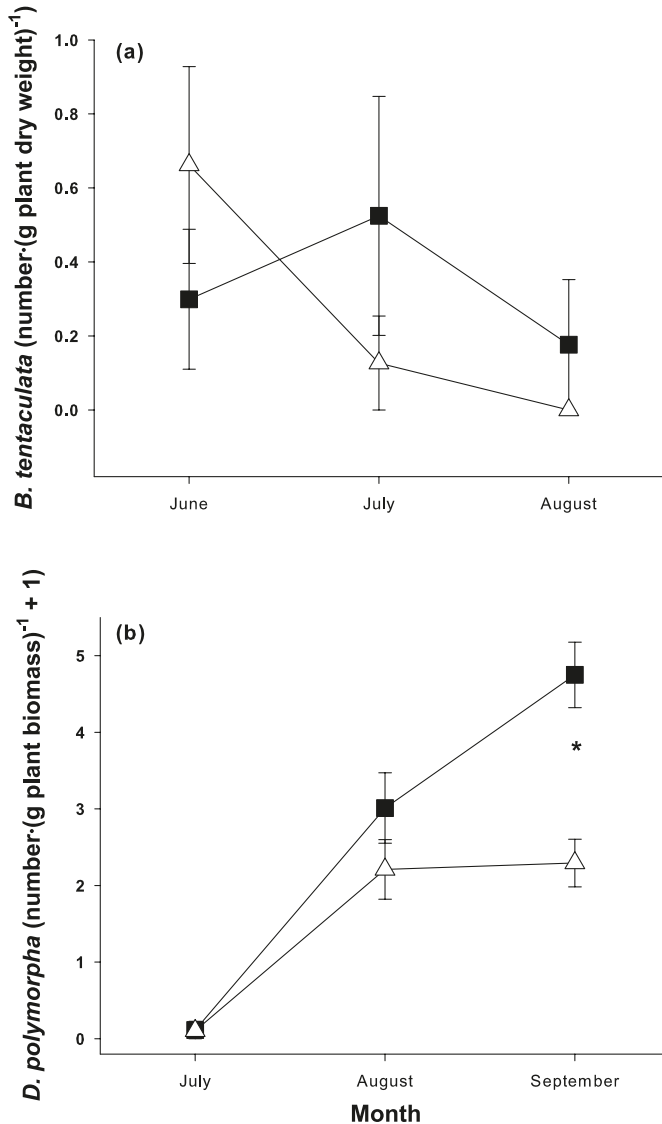

Discussion

Invertebrate abundance and body size

Our results show that invertebrate community structure can differ substantially on exotic and native milfoils of similar morphology. However, the relationship between invertebrate abundance on these macrophytes varies throughout the summer, with differences in invertebrate density becoming more pronounced later in the season. Given that *M. spicatum* grows rapidly in the spring (Grace and Wetzel 1978), it may be the first macrophyte species to provide substrate and resources to colonizing invertebrates. Indeed, at our sampling sites, *M. spicatum* grew earlier than both species of native *Myriophyllum*, but contrary to the expectation that *M. spicatum* would support more invertebrates early in the summer, there was generally no difference in invertebrate density at

that time. Invertebrates may require a few months to differentially colonize macrophyte species, and it may be that subtle differences among macrophytes (e.g., involving chemical exudates or epiphytic algal communities; Balci and Kennedy 2003; Marko et al. 2005) have significant effects on invertebrate abundance only by late summer.

Different species of aquatic macrophytes support epiphytic algal communities that may differ greatly in abundance and taxonomic composition (Blindow 1987; Cattaneo et al. 1998; Laugaste and Reunanen 2005). Algae growing on macrophytes in the St. Lawrence River and surrounding areas reach peak biomass by mid-June or July (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 midsummer. Contrasting abundances or composition of epiphytic algae

Fig. 8. Density of exotic molluscs: (*a*) the faucet snail *Bithynia tentaculata* in Lac St-Louis (±1 standard error, SE), and (*b*) the zebra mussel *Dreissena polymorpha* in the Richelieu River (±1 SE): solid squares, *M. sibericum*; open triangles, *M. spicatum*; *, a significant difference in invertebrate abundance on native and exotic plants (*t* test, *p* < 0.01).

on macrophyte species could drive dissimilarities in epiphytic invertebrate communities that are structured around algae as a food source; for example, Cattaneo (1983) found that the abundance of invertebrate grazers increased substantially a short time after peak epiphyte biomass.

Our study examined gastropod biomass in particular, because gastropods graze on epiphytic algae and consume macrophytes directly (Lodge 1986; Sheldon 1987; Brönmark 1989) and also they comprised a substantial proportion of invertebrate biomass in our samples. They had significantly higher biomass on native *Myriophyllum* species at three of the four sites. *Myriophyllum sibericum* and *M. spicatum* have very similar structure and approximately equal plant surface area per gram of dry plant weight (Gerber and Les 1994), so differences in gastropod biomass between the two

species cannot be attributed to the area available for colonization by gastropods or epiphytic algae. Given that gastropod abundance may vary with epiphytic algal biomass and composition (Lodge 1986; Brönmark 1989), differences in the epiphytes themselves on native and exotic milfoils may be driving this result. Whatever the mechanism, gastropods have been found to preferentially inhabit certain macrophyte species over others, even when these macrophytes are closely related (Pip and Stewart 1976; Sheldon 1987).

The mean body size of invertebrates was also lower on *M. spicatum* than on *M. alterniflorum*, as indicated by an equal or higher invertebrate biomass combined with a lower invertebrate density on *M. alterniflorum*. This result may reflect differences in invertebrate community composition, as *M. alterniflorum* supported larger snails and amphipods, whereas *M. spicatum* was dominated by smaller annelids and chironomids.

Macrophyte structure

Submersed aquatic macrophytes are often grouped into two main structural categories based on leaf morphology: dissected (complex) leaves or entire (simple) leaves (Krecker 1939; Cheruvelil et al. 2002). By these standards, the three species of *Myriophyllum* in our study are similar in structure as all have dissected leaves arranged in whorls of four around the stem. On a finer scale, however, there are structural differences among species. *Myriophyllum alterniflorum* tends to branch more frequently and has slightly smaller leaves than either *M. spicatum* or *M. sibericum*. *Myriophyllum alterniflorum* also has significantly higher specific leaf area (surface area of leaf per dry weight of leaf) and surface area to volume ratios than the other species, whereas *M. spicatum* and *M. sibericum* have very similar specific leaf area and leaf surface area to volume ratios (Gerber and Les 1994). In addition, dry leaf mass comprises ~55% of the total dry weight of leaves and shoots of *M. alterniflorum* and ~65% for both *M. spicatum* and *M. sibericum* (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 – biomass ratios on *M. spicatum* and *M. sibericum* also overlap, varying between 320 and 1205 $cm^2 \cdot g^{-1}$ on *M. spicatum* (Kowalczewski 1975; Sher-Kaul et al. 1995) and between 534 and 761 $cm^2 \cdot g^{-1}$ on *M. sibericum* (Gerrish and Bristow 1979; Armstrong et al. 2003). Thus, although subtle structural differences may account for the dissimilarity in invertebrate communities on *M. alterniflorum* and *M. spicatum*, they are less likely to be responsible for differences in invertebrates on *M. sibericum* and *M. spicatum*.

It seems probable that characteristics other than plant structure influence invertebrate abundance and diversity on these macrophytes. Chemical exudates may affect the relative palatability of exotic and native milfoils to herbivores and the growth of epiphytic algae. 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* because of differences in the amount of glycerol and uracil exuded by the two species. Previous studies have also found that *M. spicatum* releases chemicals that deter the growth of certain types of epiphytes and that these chemicals may dif-

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Table 3. Studies examining comparing invertebrates on *Myriophyllum spicatum* to those on native macrophytes in invaded regions.

Study	Region	Sampling year	Native plants	Invertebrate	
				Taxa richness	Density
Keast 1984	Southeast Canada	1979	*Potamogeton robbinsii, Vallisneria americana*	N/A	E > N (47, 25)
Chilton 1990	Midwest US	1983	**Ceratophyllum demersum**	N/A	E < N (253, 676)
Cheruvelil et al. 2000	Midwest US	1998	**Ranuculus** sp., *Potamogeton pectinatus*	N/A	E < N (75, 77)
Krull 1970	Northeast US	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 US	1998	*Heteranthera dubia*	E < N (21, 24)	E > N[a] (2276, 1888)
Krecker 1939	Northeast US	1935–1936	**Elodea canadensis**, *Potamogeton pectanus, P. compressus*	E > N (22, 14)	E > N[b] (1442, 535)

Note: E, exotic macrophyte (*M. spicatum*); N, native macrophyte(s). Plants with similar structure (divided leaves) to *M. spicatum* are indicated in bold. Density is the number of invertebrates per unit plant weight, unless otherwise indicated. N/A, not available.

[a]Number of invertebrates per m^2 of plant surface area.

[b]Number of invertebrates per 10 m length of plant stem.

fer in either the type or the amount exuded relative to other species of *Myriophyllum* (Gross et al. 1996).

Exotic invertebrates

The invasional meltdown hypothesis postulates that previously established exotic species facilitate the invasion or proliferation of other exotic species (Simberloff and Von Holle 1999) and thus predicts that *M. spicatum* would support more exotic invertebrates than either *M. sibericum* or *M. alterniflorum*. However, this prediction is not supported by the results of our study. The abundance of the Eurasian snail *Bithynia tentaculata* was not significantly different on native and exotic macrophytes. *Bithynia tentaculata* established in the Great Lakes and St. Lawrence River basin more than a century ago, several decades prior to the invasion of *M. spicatum* (Aiken et al. 1979; Mills et al. 1993), and therefore may have had sufficient time to adapt to native macrophytes. In the Richelieu River, the native *M. sibericum* supported more zebra mussels than *M. spicatum*. It seems unlikely that differences in plant exudates or epiphytic algae would have caused this result, as zebra mussels are filter feeders with larvae that are planktonic and eventually settle on solid surfaces, including submersed macrophytes. Given that larval dispersal is largely determined by vagaries of water currents (Lewandowski 1982), it is likely that small-scale variation in hydrology within a site determines the degree to which the mussels colonize macrophytes.

The Eurasian moth *A. ephemerella* was the only exotic invertebrate that appeared to preferentially colonize *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 DCA analysis showed that this moth tended to group with *M. spicatum* in the Richelieu River and Chateaugay Lake. Not a single *A. ephemerella* was collected from samples of *M. alterniflorum* in either Chateaugay Lake or Saranac Lake, whereas at both of these sites,

A. ephemerella was found on *M. spicatum*, perhaps indicating that *A. ephemerella* prefers to colonize the exotic milfoil. This moth was introduced from Europe and was first discovered in the St. Lawrence River in 1927 (Berg 1942; Sheppard 1945). It is a generalist herbivore that feeds on many species of macrophytes (Buckingham and Ross 1981) but has been considered as a possible biological control agent for *M. spicatum* as it may cause less damage to native macrophytes (Johnson et al. 1997).

Implications for aquatic communities

To our knowledge, this is the first study to compare multi-species invertebrate assemblages on native and exotic species of *Myriophyllum*. Previous studies that examined differences between epiphytic invertebrates on *M. spicatum* and native macrophytes found conflicting results (Table 3), perhaps because each compared *M. spicatum* with macrophytes of differing phylogeny, structure, and life history traits.

The establishment of *M. spicatum* can reduce the density of many other species of macrophytes, including native milfoils (Grace and Wetzel 1978; Smith and Barko 1990; Boylen et al. 1999). In situations where *M. spicatum* supports lower invertebrate diversity and biomass than its congeners, the displacement of native macrophytes by *M. spicatum* could conceivably cause habitat-wide alterations in epiphytic invertebrate communities that have consequences for higher trophic levels. Reductions in the diversity, biomass, and mean body size of epiphytic invertebrates may impact fish and other vertebrate predators by lowering the quality and accessibility of prey (Werner and Hall 1974; Eggers 1977; Kovecses et al. 2005). Overall, these results suggest that the impacts of *M. spicatum* invasion on epiphytic invertebrates may have multiple indirect effects at local and habitat-wide scales. Structurally similar, even congeneric, macrophytes do not necessarily provide equivalent habitat for invertebrate communities, which appear to be sensitive to subtle differences between macrophyte species.

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