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 macrophytes exotiques, même lorsque ces macrophytes sont de proches parents et possèdent une morphologie similaire. Nous avons échantillonné un macrophyte exotique envahissant, le myriophyliée à épis (*Myriophyllum spicatum*), et des myriophyliées 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 macroinvertebrés épiphytes sur les *Myriophyllum* exotique et indigène. 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 macroinvertebrés 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 myriophyliées indigènes par *M. spicatum* peut avoir des effets indirects sur les réseaux alimentaires aquatiques.

[Traduit par la Rédaction]

**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 (Kersher and Lodge 1990; Killgore et al. 1991; Toft et al. 2003). In particular, submerged 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...
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; Cheruvil 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; Cheruvil 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 Helquist 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, assuming 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. sibiricum, 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. sibiricum are sometimes difficult to distinguish (Crow and Helquist 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...
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 until 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.

<table>
<thead>
<tr>
<th>Site</th>
<th>Location</th>
<th>Plants sampled</th>
<th>System type</th>
<th>No. of samples (E, N)(^a)</th>
<th>Water temperature: minimum, maximum (°C)(^b)</th>
<th>pH range</th>
<th>Site depth (m)</th>
<th>Other plant species(^c)</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lac St-Louis</td>
<td>Southwest of the Island of Montreal, Quebec; part of the St. Lawrence River</td>
<td><em>M. spicatum, M. sibericum</em></td>
<td>Fluvial lake</td>
<td>7, 6 (June) 6, 6 (July) 6, 7 (August) 19, 19</td>
<td>21 (June), 27 (August)</td>
<td>7.9–9.4</td>
<td>0.5–1.0</td>
<td><em>C. demersum, E. canadensis, P. crispus, P. perfoliatus, Potamogeton sp., Ranunculus sp., V. americana</em></td>
<td>Site near boat launch against breaker; moderate to high wave action</td>
</tr>
<tr>
<td>Richelieu River</td>
<td>Central Quebec, connects Lake Champlain and the St. Lawrence River</td>
<td><em>M. spicatum, M. sibericum</em></td>
<td>River</td>
<td>10, 10 (July) 9, 9 (August) 7, 7 (September) 26, 26</td>
<td>19 (September), 24 (July and August)</td>
<td>8.2–9.1</td>
<td>1.5–2.0</td>
<td><em>C. demersum, E. canadensis, E. nuttallii, P. crispus, P. richardsonii, Potamogeton sp., Ranunculus sp., V. americana</em></td>
<td>Site near midriver, in a wetland; steady current, low wave action</td>
</tr>
<tr>
<td>Upper Saranac Lake</td>
<td>Adirondack State Park, upstate New York</td>
<td><em>M. spicatum, M. alterniflorum</em></td>
<td>Lake</td>
<td>21, 21 (July) 18, 18 (August) 39, 39</td>
<td>19 (August), 21 (July)</td>
<td>7.7–7.9</td>
<td>1.5–2.0</td>
<td><em>C. demersum, E. canadensis, P. crispus, P. richardsonii, V. americana</em></td>
<td>Site of <em>M. spicatum</em> control program; low wave action</td>
</tr>
<tr>
<td>Upper Chateaugay Lake</td>
<td>Adirondack State Park, upstate New York</td>
<td><em>M. spicatum, M. alterniflorum</em></td>
<td>Lake</td>
<td>7, 7 (July) 9, 9 (August) 16, 16</td>
<td>17 (August), 21 (July)</td>
<td>6.7–7.8</td>
<td>1.0–1.5</td>
<td><em>E. canadensis, P. richardsonii, Ranunculus sp., Utricularia sp., V. americana</em></td>
<td>Site near lake inflow and wetland, south end of lake; low wave action</td>
</tr>
</tbody>
</table>

\(^a\)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.*
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.

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 Richelieu River, the invertebrate biomass on M. sibericum was slightly lower than on M. spicatum in early summer but by late summer was 2.3 times greater than on M. spicatum. Invertebrate density was higher on M. sibericum than on M. spicatum 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-
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 diamonds, *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).

![Graphs showing gastropod biomass](image)

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).

![Graphs showing invertebrate density](image)
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. 7a, 7b). 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 hydropsilid genus *Oxyethira* (Hx), and the Eurasian pyralid moth, *Acentria ephemerella* (= *Acentria nivea*) (Ac) (Fig. 7b). Invertebrates characteristic of *M. alterniflorum* were the gastropods *Valvata sincera* (Vs) and *Amnicola limosa* (Am), the amphipod *Hyallela azteca* (Hy), damselflies in the fami-

**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.

<table>
<thead>
<tr>
<th>Site</th>
<th>Taxa richness</th>
<th>$e^{H'}$</th>
<th>$1/D'$</th>
<th>Invertebrate abundance*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lac St-Louis</td>
<td>40.4</td>
<td>7.5</td>
<td>4.2</td>
<td>1050</td>
</tr>
<tr>
<td>Richelieu River</td>
<td>45.4</td>
<td>4.6</td>
<td>2.8</td>
<td>7020</td>
</tr>
<tr>
<td>Saranac Lake</td>
<td>31.5</td>
<td>6.5</td>
<td>3.6</td>
<td>580</td>
</tr>
<tr>
<td>Chateaugay Lake</td>
<td>26</td>
<td>8.3</td>
<td>6.1</td>
<td>650</td>
</tr>
</tbody>
</table>

*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 (*).

*Diversity comparisons on native and exotic macrophytes were made at the level of abundance of invertebrates on the macrophyte species with the fewest invertebrates.

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family 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. 7b). 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. 7c, 7d), while such differences were less apparent in Lac St-Louis. In the Richelieu River, 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 Hyallela azteca (Hy), the gastropods Physa gyrina gyrina (Ph), Gyrulaulus 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. 7c, 7d). 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 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. 7a, 7b). 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. 7c, 7d). 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 zebra mussel Dreissena polymorpha did not differ significantly between M. sibericum and M. spicatum on any of the sampling dates (Fig. 8a). 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. 8b).
**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 (Bliniow 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...
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 sibiricum* 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. sibiricum*. *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. sibiricum* 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. sibiricum* (Gerber and Les 1994). Hence, subtle differences in leaf morphology exist between *M. alterniflorum* and *M. spicatum*, but *M. spicatum* and *M. sibiricum* have quite similar leaf morphology. The range of whole plant surface area – biomass ratios on *M. spicatum* and *M. sibiricum* also overlap, varying between 320 and 1205 cm² g⁻¹ on *M. spicatum* (Kowalczevski 1975; Sher-Kaul et al. 1995) and between 534 and 761 cm² g⁻¹ on *M. sibiricum* (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. sibiricum* 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. sibiricum* 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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**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. sibiricum*; open triangles, *M. spicatum*; *, a significant difference in invertebrate abundance on native and exotic plants (*t* test, *p* < 0.01).
M. spicatum

The invasion 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 moth 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 multispecies 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.

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

<table>
<thead>
<tr>
<th>Study</th>
<th>Region</th>
<th>Sampling year</th>
<th>Native plants</th>
<th>Invertebrate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Keast 1984</td>
<td>Southeast Canada</td>
<td>1979</td>
<td>Potamogeton robbinsii, Vallisneria americana</td>
<td>N/A</td>
</tr>
<tr>
<td>Chilton 1990</td>
<td>Midwest US</td>
<td>1983</td>
<td>Ceratophyllum demersum</td>
<td>N/A</td>
</tr>
<tr>
<td>Cheruvellil et al. 2000</td>
<td>Midwest US</td>
<td>1998</td>
<td>Ranunculus sp., Potamogeton pectinatus</td>
<td>N/A</td>
</tr>
</tbody>
</table>

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.

<sup>a</sup>Number of invertebrates per m<sup>2</sup> of plant surface area.

<sup>b</sup>Number of invertebrates per 10 m length of plant stem.
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