

Comparative feeding selectivity of herbivorous insects on water lilies: aquatic vs. semi-terrestrial insects and submersed vs. floating leaves

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SUMMARY

1. The rate of grazing damage experienced by submersed and floating leaves of water lilies (*Nuphar variegata* and *Nymphaea odorata*) was monitored in lakes in the Upper Peninsula of Michigan, U.S.A. Herbivores damaged 0.2–1.7% of the leaf surface of water lilies per day. These grazing rates differed between plant species, between submersed and floating leaves, and between lakes. Some leaves had more than 60% of their surface damaged and an overall mean of 16% damage occurred during the 2–3 week monitoring period of this study.

2. Snapshot measurements of grazing damage on randomly collected submersed and floating leaves of *Nuphar* showed that submersed leaves were more damaged ($11.0 \pm 1.6\%$, $n = 84$) than floating leaves ($3.8 \pm 0.6\%$, $n = 92$). Overall, these 176 *Nuphar* leaves had 7.2% of their area damaged.

3. Five species of herbivorous insects were commonly found on water lilies (Nymphaeacea). One primarily aquatic insect (*sensu* Newman, 1991), a caddisfly larva (Trichoptera: Limniphilidae), had a generalized diet of water lilies, other macrophytes, algae, and detritus. Four of the five insects were from primarily terrestrial insect groups (Coleoptera and Diptera; 'secondary invaders', *sensu* Newman, 1991) and consumed only water lilies in food preference experiments.

4. The feeding preferences of the generalist trichopteran were altered when the macrophytes were freeze-dried, ground into a powder, and reconstituted in an alginate gel. This suggests that plant structure may be an important feeding determinant for this insect. In contrast, a specialist weevil preferred its host plant in choice assays, regardless of whether fresh tissue or reconstituted macrophytes were used, suggesting this insect cued on a unique, non-structural property of its host plant.

5. These results suggest that herbivory on freshwater macrophytes is of a similar magnitude to that on terrestrial plants. The findings of this study are consistent with the hypothesis that herbivorous insects of primarily terrestrial groups have a narrower diet breadth than insects of primarily aquatic groups.

Introduction

Herbivores can reduce the biomass and change the species composition of marine (Lubchenco & Gaines, 1981; Lewis, 1986; Morrison, 1988; Hay & Steinberg, 1992) and stream (Feminella & Hawkins, 1996) algal and terrestrial vascular plant communities (Crawley,

1983; McNaughton, 1985; Rosenthal & Berenbaum, 1992). Although past texts and reviews suggested this was rarely the case for freshwater macrophytes (Shelford, 1918; Hutchinson, 1975; Wetzel, 1983; Lamberti & Moore, 1984) much recent work on fresh-

water macrophyte–herbivore interactions (Wallace & O'Hop, 1985; Jacobsen & Sand-Jensen, 1992, 1994; Lodge *et al.*, 1994; reviewed by Lodge, 1991; Newman, 1991; Lodge *et al.*, 1997) suggests that freshwater herbivores, like their marine and terrestrial counterparts, often have an appreciable impact on macrophytes.

For freshwater macrophytes, there are assessments of the diversity of herbivorous invertebrates associated with different species (e.g. Soska, 1975), and estimates of *in situ* consumption rates on selected macrophytes (Otto & Wallace, 1989; Jacobsen & Sand-Jensen, 1994; Kornijow, 1996). However, little experimental work has tested whether herbivore–plant associations result from food preferences by the consumers or from other mechanisms; for example, several species of generalist freshwater herbivores prefer senescent rather than fresh watercress (*Nasturtium officinale*, R. Brown) because the chemical defence of watercress is inactive following plant death (Newman, Kerfoot & Hanscom, 1996). However, whether most herbivores exhibit preferences among different macrophyte species, and if any such preferences are mediated by chemical defence or other plant characteristics, is unknown.

Better knowledge of the selective impact that herbivores have on macrophytes is important for understanding whether herbivores modify the functional role of macrophytes in aquatic ecosystems and whether herbivores might regulate desirable and nuisance macrophytes (Carpenter & Lodge, 1986). Basic information about the impact and selectivity of herbivores on freshwater macrophytes is also necessary to make comparisons among terrestrial, marine, and freshwater habitats, providing insights into the ecology and evolution of plant–herbivore interactions in general (Hay & Steinberg, 1992; Cyr & Pace, 1993; Lodge *et al.*, 1997).

Freshwater macrophytes with floating or emergent leaves must contend with both aquatic and terrestrial herbivores because even their leaves destined to be exposed to air are initiated under water. Given that floating or emergent leaves are exposed to both aquatic and terrestrial herbivores, one might predict that floating or emergent leaves should experience higher levels of grazing damage than submersed leaves. In the present study the amount of grazing damage to submersed and floating leaves of water lilies was measured and the feeding preferences of five common insect herbivores were tested among submersed, floating, emergent and entirely terrestrial plants. Rates of graz-

ing damage to submersed and floating leaves of a heterophyllous (*Nuphar variegata* Engelm) and non-heterophyllous (*Nymphaea odorata* Ait.) water lily were measured and the feeding selectivity of their herbivores was assessed. The experiments used five herbivorous insects with a range of affinities for water, including a primary aquatic insect [caddisfly larva, *Limnephilus infernalis* (Banks), Trichoptera: Limnephilidae], three secondary aquatic insects (i.e. at least one life stage is submersed), which are placed phylogenetically in families or orders of primarily terrestrial groups that have secondarily invaded the aquatic habitat [midge larva, *Hyporhygma quadripunctatum* (Malloch), Diptera: Chironomidae; weevil adult, *Bagous americanus* Le Conte, Coleoptera: Curculionidae; and beetle adult, *Donacia cincticornis* Newman, Coleoptera: Chrysomelidae], and a semi-terrestrial insect [no life stage is submersed; beetle adult, *Galerucella nymphaeae* (L.) = *Pyrrhalta nymphaeae*, Coleoptera: Chrysomelidae]. The feeding preferences of these insects were compared with the prediction that the primary aquatic insect would have a more generalized diet than the insects of primarily terrestrial groups that have recently (evolutionarily) invaded aquatic habitats (Hynes, 1984; Newman, 1991). For *Limnephilus* and *Bagous*, by comparing preferences for whole-plant tissue with preferences for reconstituted samples of the same plant species (freeze-dried ground plant tissue reconstituted in an alginate gel), the present study tested whether feeding preferences were partly a function of the gross architecture (shape, surface toughness) of the whole tissue.

Materials and methods

Study sites and plant species

During the summers of 1993, 1994 and 1995, field surveys of herbivore damage were conducted and laboratory feeding selectivity assays carried out focusing on the macrophytes and herbivores in four small oligotrophic–mesotrophic softwater lakes at the University of Notre Dame Environmental Research Centre (UNDERC) in the Upper Peninsula of Michigan (46°N, 89°W). Central Long (2.1 ha., max. depth = 5 m) and West Long (3.4 ha, max. depth = 17 m) Lakes were characterized by sandy-peaty sediments and sparse littoral vegetation (20–30% areal coverage), mostly of *Isoetes* and *Nuphar variegata* (D.M. Lodge,

unpublished data). Kickapoo Lake (6.1 ha, max. depth = 3 m) had soft, organic-rich sediments throughout and almost 100% macrophyte coverage of mostly *Nuphar variegata*, *Nuphar pumila* (Pers.) Fernald., *Nymphaea odorata*, *Potamogeton robinsii* Oakes, *P. amplifolius* Tuckerm., and *Ceratophyllum demersum* L. (D.M. Lodge, unpublished data). Roach Lake (35 ha, max. depth = 11 m) had a sandy littoral zone with extensive coverage of softwater macrophytes, including *Nuphar variegata*, *Sparganium fluctuans* (Morong) Robinson, *Juncus pelocarpus* Mey, *Eleocharis acicularis* (L.) R. & S., *Myriophyllum tenellum* Bigel., *Isoetes braunii* Dur., *Elatine minima* (Nutt.) Fisch. & Meyer, and *Lobelia dortmanna* L. (Carpenter & McCreary, 1985). Plant nomenclature followed Voss (1972, 1985).

Rates of herbivore damage

During the summer of 1994, the rates of herbivore damage to floating and submersed leaves of *Nuphar variegata* and *Nymphaea odorata* (Nymphaeacea) were measured by tagging young, undamaged leaves with flagging tape on 22 May ($n = 5\text{--}14$ leaves per lake) and 27 May ($n = 4\text{--}8$), and then quantifying with a digitizer the area of leaves damaged 2.3–3.0 weeks later. *Nuphar variegata* leaves were tagged in Kickapoo Lake and West Long Lake and leaves of *Nymphaea odorata* (which did not occur in West Long Lake) were tagged in Kickapoo Lake only. Submersed leaves of *Nuphar* are morphologically distinct from floating leaves and never grow to the water surface (*Nuphar* is heterophyllous). In contrast, submersed leaves of *Nymphaea* ultimately grow to the water surface and become floating leaves (mature *Nymphaea* is non-heterophyllous).

In addition to measuring the rate of herbivore damage to tagged leaves, snapshot measurements of grazing damage were obtained on 28 June 1993 and 28 June 1994 by measuring the damaged area of *Nuphar variegata* from Central Long, West Long, Kickapoo, and Roach Lakes. The shoreline of each lake was divided into ten equal sectors and one or two leaves of each leaf type (i.e. floating and submersed) were randomly collected from each sector. The leaf area grazed by herbivores was estimated by overlaying each leaf with a clear grid and counting the number of grid cells (1.5 mm × 1.5 mm) covering the damage.

Grazing rate data and snapshot data were initially analysed with ANOVA with macrophyte species, leaf

type (i.e. floating or submersed), lake and sampling period as main factors. Separate, species-specific ANOVAs with leaf type, lake and sampling period as factors were also performed.

Feeding selectivity assays

The goal of the feeding assays was to determine the feeding preferences of various herbivores when offered macrophytes of various architectures and plant families. Feeding selectivity assays were performed with all the insect herbivores that were apparently consuming *Nuphar variegata* or *Nymphaea odorata*, including the caddisfly *Limnephilus infernalis* (Wiggins, 1977; Ruiter, 1995), the midge *Hyporhygma quadripunctatum* (Wiederholm, 1983), the weevil *Bagous americanus* (McGaha, 1952), and two chrysomelid beetles *Donacia cincticornis* (Dillon & Dillon, 1972) and *Galerucella nymphaeae* (Dillon & Dillon, 1972) (Table 1). Hereafter, the organisms will be referred to by their generic names only. Herbivores and macrophytes were generally collected at UNDERC sites on the same day that assays were performed (Table 1). When this was not possible, herbivores were maintained at room temperature in containers with available host plant and macrophytes were kept in plastic bags at 4°C for up to 3 days. Each herbivore was offered a choice of two–nine macrophytes presented simultaneously to determine feeding preferences (Table 1).

On 28 June 1994, *Limnephilus* was offered a choice of nine macrophyte types (Table 1). A portion of each macrophyte was selected to provide a similar encounter rate (i.e. volume of water occupied) as estimated by eye. Therefore, masses differed among macrophytes (see below). Depending on the structure of the macrophyte, the portions were either blotted with a paper towel or spun in a salad spinner to remove excess water, weighed to the nearest mg, and anchored to the bottom of a shallow aquarium with a rubber suction cup. Three late instar larvae (length 16.9 ± 1.6 mm; mean ± 1 SD) were placed in each of fourteen aquaria (25 × 31 cm plastic dish pans) for 25 h with a leaf portion of *Potamogeton amplifolius* (0.052–0.060 g, blotted), a shoot of *Myriophyllum alterniflorum* (0.357–0.367 g, spun), a portion of submersed (0.105–0.113 g, blotted) and floating (0.174–0.181 g, blotted) leaves of *Nuphar variegata*, a portion of an emergent leaf of *Pontederia cordata* (0.200–0.207 g, blotted), a plant (with roots removed) of *Lobelia dortmanna*

Table 1 Identity and source of plants and insects used in experiments. An 'X' indicates that the plant was offered to the herbivore during laboratory feeding assays. Macrophyte names in **bold** indicate water lilies and an 'X' in **bold** indicates plants were natural host plants (where the animal was usually observed in the field). Sources of organisms are indicated with a numerical superscript: ¹West Long Lake; ²Kickapoo Lake; ³Roach Lake; ⁴Morris Lake; ⁵Tenderfoot Creek; ⁶Allequash Lake; ⁷Paul Lake; ⁸temporary pond. Growth forms of leaves used in assays are indicated in parentheses following plant name: fl = floating; sub = submersed; em = emergent; ter = terrestrial. Fresh = assays with fresh plants and Reconst. = assays with reconstituted plants

Plant species	¹ <i>Limnephilus</i>			² <i>Hyporhygma</i>		² <i>Bagous</i>		² <i>Donacia</i>	¹ <i>Galerucella</i>
	Fresh 6/94	Fresh 6/95	Reconst. 6/95	Fresh 6/95	Fresh 6/95	Fresh 6/95	Reconst. 6/95	Fresh 6/94	Fresh 6/93
<i>Nuphar variegata</i> Engelm (sub)	¹X		⁴X	⁴X		⁴X	⁴X	²X	¹X
<i>Nuphar variegata</i> (fl)	¹X	⁴X	⁴X	⁴X		⁴X	⁴X	²X	^{1,2}X
<i>Nuphar pumila</i> (Pers.) Fernald (sub)								²X	
<i>Nuphar pumila</i> (fl)			²X	²X	²X	²X	²X	²X	²X
<i>Nymphaea odorata</i> Ait. (fl)			⁵X	⁵X	²X	⁵X	⁵X	²X	²X
<i>Brasenia schreberi</i> Gmel. (fl)								⁶X	
<i>Pontederia cordata taenia</i> Fassett (sub)			²X	²X		²X	²X	²X	
<i>Pontederia cordata</i> typical L. (em)	²X		²X	²X		²X	²X	²X	²X
<i>Potamogeton amplifolius</i> Tuckerm. (sub)	²X	⁴X	⁴X	⁴X		⁴X	⁴X		
<i>Typha latifolia</i> L. (em)	⁸X		⁸X	⁸X		⁸X	⁸X	⁸X	⁸X
<i>Calla palustris</i> L. (em)		⁷X	⁷X	⁷X		⁷X	⁷X		
<i>Potamogeton natans</i> L. (sub)								⁶X	
<i>Isoetes braunii</i> Dur. (sub)	^{2,4}X								
<i>Lobelia dortmanna</i> L. (sub)	³X								
<i>Myriophyllum alterniflorum</i> DC. (sub)	²X								
<i>Zygnema</i> sp. (sub)	³X								
<i>Polygonum</i> sp. (fl)		²X							
<i>Acer saccharum</i> Marsh. (ter)									X
<i>Populus tremuloides</i> Michx. (ter)									X

(0.338–0.348 g, spun), a plant (with roots removed) of *Isoetes braunii* (0.311–0.321 g, spun), and a leaf portion of *Typha latifolia* (0.171–0.180 g, blotted). The larvae were also offered the alga *Zygnema* sp., but this food was not included in analyses because we were unable to recover the fine filaments and quantify the amount consumed. Another fourteen aquaria were set up with water and macrophytes, but without *Limnephilus*, to control for changes in mass not caused by herbivory; each control aquarium was paired with an experimental aquarium. For each pair of aquaria (i.e. replicate), the amount of each plant portion that was consumed was calculated with the equation $[(H_0 \times C_f / C_0) - H_f]$, where H_0 and H_f were pre-assay and post-assay wet masses of tissue exposed to herbivores and C_0 and C_f were pre-assay and post-assay wet masses of controls for changes in mass not due to herbivory. For all macrophytes in this and all other experiments, a large portion of tissue remained at the conclusion of the assay (i.e. all plants remained available).

On 24 June 1995, late instar *Limnephilus* were offered a simultaneous choice of nine macrophytes (Table 1)

that had been freeze-dried, ground to a powder, and reconstituted at natural dry mass concentrations using an alginate gel (methods modified from Hay *et al.*, 1994). Macrophytes included six of the nine species that had been used the previous summer, plus *Nuphar pumila*, *Calla palustris* and *Nymphaea odorata*. A 0.3-mm thick layer of reconstituted macrophyte was embedded on a fibreglass window screen and offered to twenty-seven individual *Limnephilus* for 32 h in shallow aquaria (13 × 16 cm plastic trays). The amount of each macrophyte that was consumed was measured by counting the number of window screen squares that had been cleared of the reconstituted macrophyte. Twenty replicates in which no food was consumed were excluded from statistical analysis, resulting in a sample size of seven. Food was not lost from the fibreglass screen in the absence of herbivores; thus controls for autogenic changes in size were not necessary.

Because *Limnephilus* preferred one of the reconstituted plants that had not been offered as fresh tissue in the previous assay (*Calla palustris*; see Results), an additional experiment was conducted on 28 June 1995

in which larvae were allowed to choose from fresh leaf portions of *Potamogeton amplifolius* (0.069–0.226 g, blotted), floating *Nuphar variegata* (0.373–0.671 g, blotted), *Polygonum* sp. (0.140–0.469 g, blotted), and *Calla palustris* (0.194–0.450 g, blotted) using the methods described above for the June 1994 experiment, with the exception that one larva per replicate ($n = 20$) fed for 108 h.

The feeding preferences of *Hyporhygma*, *Bagous*, *Donacia* and *Galerucella* were determined by offering each insect squares cut from the leaves of nine macrophytes (see Table 1 for a list of macrophytes offered to each herbivore). For any feeding assay, only one square was taken from any leaf. The squares were placed on top of a moist paper towel in a 3×3 array randomly assigned for each arena. *Hyporhygma* (1.2×1.2 cm squares, one larva/replicate, $n = 15$), *Bagous* (1.2×1.2 cm squares, one adult/replicate, $n = 11$), *Donacia* (2.1×2.1 cm squares, two adults/replicate, $n = 13$), and *Galerucella* (2.5×2.5 cm squares, one adult/replicate, $n = 20$) were allowed to feed until leaf area damaged was great enough to show clear preferences, resulting in durations of 56, 65, 34 and 23 h, respectively. The area of leaf damaged by herbivory was determined with a 9×9 transparent grid for *Donacia* and by visually estimating the percentage of damage caused by *Hyporhygma*, *Bagous* and *Galerucella*. Visual estimates by a 'calibrated' eye allowed rapid accurate measurement of leaf damage ($r^2 = 0.917$ for visual estimate vs. digitized measure). Because the squares did not change in area and remained undamaged in the absence of herbivores, controls for autogenic changes were unnecessary.

In addition to the assay using squares from fresh leaves, *Bagous* was offered a choice of nine species of reconstituted macrophytes using the methods described for *Limnephilus* (Table 1), except that the reconstituted macrophytes were placed on moist paper towels. Because *Bagous* did not eat a noticeable amount of the reconstituted macrophytes, preferences were determined by noting the location of each animal on five occasions during the 35 h assay.

Data from the multiple-choice feeding assays cannot be analysed with parametric statistics because the assumption of independence among treatments (macrophyte species) is violated (Peterson & Renaud, 1989). Therefore, P -values and multiple comparisons groupings were calculated with a non-parametric Friedman test ($\alpha = 0.05$; Conover, 1980).

Results

Qualitative patterns of water lily phenology, grazer abundance and damage

In the authors' experience, the timing of the following events varies considerably on an annual basis, depending on factors including timing of spring warming and ice-melt. In 1994, *Nuphar* produced submersed leaves in early to mid-May only, but many of these leaves persisted throughout the summer. Production of floating *Nuphar* leaves began in late May and continued until autumn. *Nymphaea* produced leaves from early May until autumn.

Five insect herbivores were found to be common on *Nuphar* and *Nymphaea* at UNDERC. Herbivores ranged from being a primary aquatic insect (*Limnephilus* larvae) to being semi-terrestrial (*Galerucella*). *Hyporhygma* larvae and *Bagous* and *Donacia* adults are secondary aquatic insects. The larvae of these insects are aquatic and the adults are semi-aquatic. For the present study, a herbivore's host plant was considered to be the macrophyte with which it was associated in the field.

Limnephilus larvae were common (about 30 m^{-2} , Y. Vadeboncoeur & D.M. Lodge, unpublished data) in the littoral zones of Central and West Long Lake in May, but densities declined greatly when adults emerged in late June. The caddisfly larvae were observed consuming submersed and developing (i.e. still submersed) floating leaves of *Nuphar*, periphyton growing on sediments and on other submersed substrata, and detritus. Their feeding left irregular holes or leaf margin damage cut entirely through the leaves of *Nuphar*.

Hyporhygma larvae were observed only on the floating leaves of *Nymphaea* at UNDERC. However, populations of this midge in southern Michigan were also found on floating leaves of *Brasenia* (Nymphaeaceae) and *Potamogeton* (G. Cronin, unpublished observations). In Kickapoo Lake, the midge attained high densities in late May: leaf dissections of *Nymphaea* floating leaves yielded five to ten midge larvae per leaf. The midge cut a trench entirely through the leaves as it fed and lived in a silken tube constructed at one end of the trench.

Adult *Bagous*, like *Hyporhygma*, were observed only on *Nymphaea odorata*. The weevils were rarely seen on the upper surface of floating leaves, but many were obtained from haphazard collections of *Nymphaea* (petioles and leaves) in mid-June 1995, suggesting that they spend most of the day on submersed portions of

Nymphaea. In the laboratory, *Bagous* left irregular, shallow grazing scars on the surface of *Nymphaea*, but did not chew entirely through the leaf.

Adult *Donacia* occurred from mid-June to mid-July in 1994 and were also observed in mid-June 1995. Adults were very mobile and readily flew from one plant to another, but were observed feeding only on *Nymphaea*, *Nuphar variegata* and *Brasenia* (all in the family Nymphaeaceae) in the field. *Donacia* was usually found on the dry surface of floating leaves and in emergent flowers. It would sometimes enter the water and cling to the underside of floating leaves when alarmed, although mostly would fly. *Donacia* feeding scars were holes (2–5 mm diameter) chewed entirely through the leaf, through which female *Donacia* would oviposit on the underside of floating leaves.

Galerucella was found only on the floating leaves of *Nuphar variegata* in the field, and first appeared on these plants in mid-July in 1994 and mid-June in 1995. *Galerucella* larvae and adults fed on the upper surface of floating and emergent *Nuphar*, leaving shallow (i.e. not entirely through the leaf), irregular trenches in the leaves. No life stage of *Galerucella* occurs in the water. Rather, it is a terrestrial beetle that lives on islands of dry macrophyte leaves (i.e. semi-terrestrial), except for overwintering adults which occur on land or trees.

Other herbivore species that were observed in the lakes, but at densities too low to work with, included a pyralid caterpillar, a noctuid caterpillar (*Bellura* sp.), and another midge larvae. The pyralid caterpillars were aquatic, had gills, and were observed in laboratory experiments to cause localized damage by cutting away a section of the leaf and cementing it to another area of the leaf surface for use as a domicile. The noctuid caterpillars were semi-terrestrial, remained dry by boring into the petioles of *Nuphar*, and consumed large portions of the floating or emergent *Nuphar* leaves. The aquatic midge larvae were found only in the young, unopened, submersed leaves of *Potamogeton amplifolius*. The hole grazed through the rolled leaf by the midge resulted in a straight row of holes after the leaf unfurled.

Rates of herbivore damage

On all plants, secondary infections at grazing scars (presumably of fungi, bacteria and other pathogens) often damaged a greater area of leaf than the herbivores, especially when the leaves were in contact with

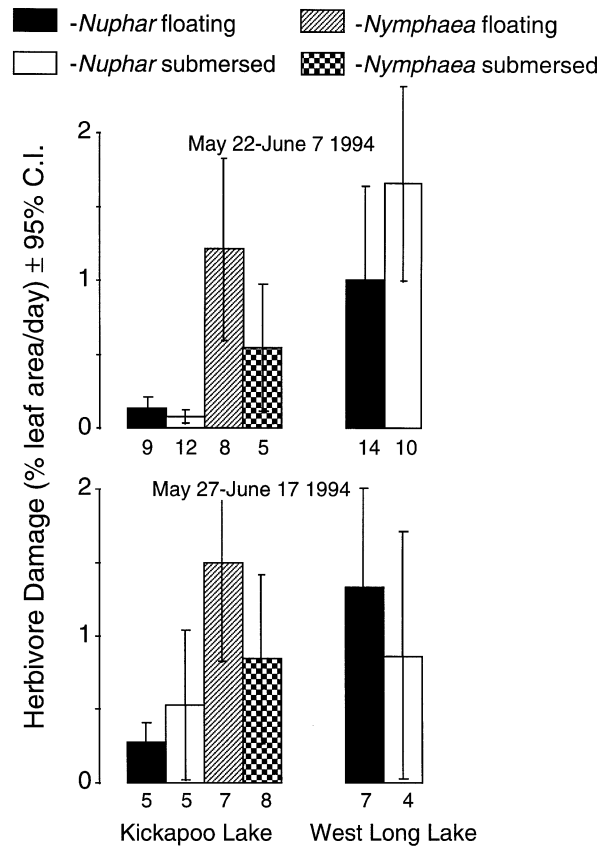


Fig. 1 Rates of herbivore damage experienced by marked floating and submersed leaves of the water lilies *Nuphar variegata* and *Nymphaea odorata* in two lakes during 1994. Sample sizes (leaf numbers) are given below each bar. Bars represent mean \pm 95% CI.

water (i.e. floating and submersed leaves apparently rotted more than emergent leaves). It was possible to distinguish grazing damage from necrosis caused by secondary infection, but it may be that necrosis masked prior grazing damage. Thus, the measurements of grazing damage in the present study are conservative.

Approximately 0.2–1.7% of water lily leaf area was grazed daily from 22 May to 17 June 1994 (Fig. 1), resulting in some leaves with more than 60% of their surface damaged by herbivores. The most abundant herbivore during this period was *Limnephilus*, although numbers of *Donacia* adults were beginning to increase in mid-June towards the end of the measurement period. *Galerucella* was absent during this period. Overall, a mean of 16% of leaf surface was damaged by herbivores during the two sampling periods. These rates differed significantly among plant species, leaf type and lake, but not between the overlapping sampling periods ($P = 0.37$). *Nymphaea* was grazed more

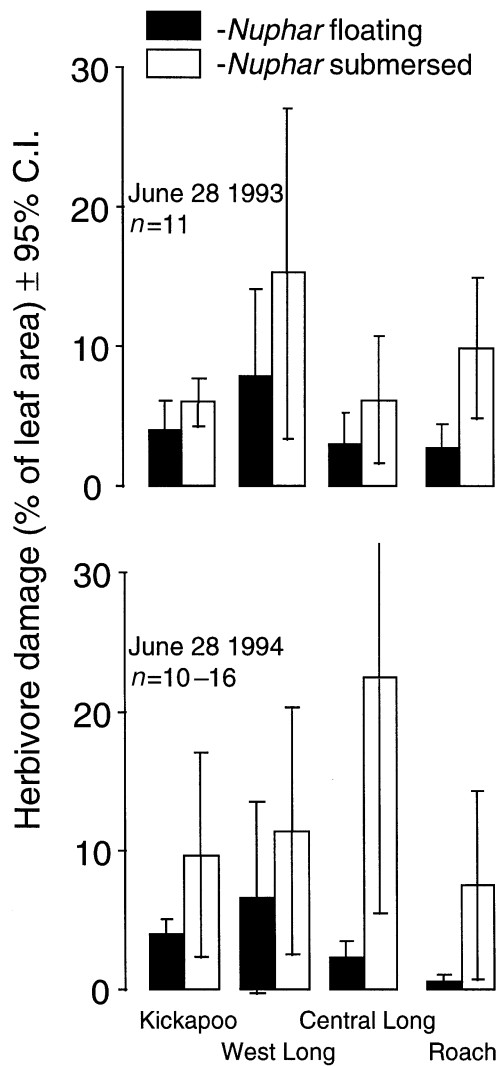


Fig. 2 Snapshot estimates of herbivore damage experienced by floating and submersed leaves of *Nuphar variegata* in different lakes on 28 June 1993 and 28 June 1994 (based on 10–16 leaves of each type and lake). Bars represent mean \pm 95% C.I.

heavily than *Nuphar* ($P = 0.0002$). *Nuphar* experienced higher rates of grazing in West Long Lake, where it was the only available water lily, than in Kickapoo Lake ($P < 0.0001$), but there was no significant difference in herbivore damage to floating vs. submersed *Nuphar* leaves ($P = 0.39$). In contrast, the floating leaves of *Nymphaea* experienced about twice the herbivory of submersed *Nymphaea* leaves ($P = 0.036$).

The snapshot levels of herbivore damage measured from randomly collected *Nuphar* leaves differed significantly between leaf types ($P = 0.00002$) (Fig. 2). Submersed leaves were more heavily grazed than floating leaves at every lake and date. Damage did not differ

between years ($P = 0.444$), or lakes ($P = 0.102$) (Fig. 2). Overall, the 176 *Nuphar* leaves had 7.2% of their area damaged by herbivores.

Feeding selectivity assays

Among fresh plants, *Limnephilus* consumed appreciable amounts of *Myriophyllum*, *Potamogeton*, *Polygonum* and submersed *Nuphar* (Fig. 3 a & b). In other, non-experimental arenas in the laboratory, *Limnephilus* readily ate the green alga *Zygnema* and submersed leaves of *Nuphar* when offered no choice. Apparently negative consumption occurred for some plants (e.g. *Typha*) with substantial aerenchyma because biting and sampling of these species by *Limnephilus* provided additional pathways for absorption of water into the air spaces, resulting in these plants gaining more wet mass (i.e. apparent negative consumption) than plants in the control arenas. Results for these species are artefacts, but observations of the present study support the conclusion that little, if any, tissue from these species was actually consumed. Thus, the rank order for consumption reflected in Fig. 3 is accurate.

Among reconstituted macrophytes, *Limnephilus* overwhelmingly preferred *Calla*, largely ignoring the remaining eight choices (Fig. 3c), including *Potamogeton*, a species preferred as a fresh macrophyte. However, *Calla* was not consumed when offered to the caddisflies as fresh tissue (Fig. 3b).

Hyporhygma preferred the floating leaves of *Nuphar pumila* over other macrophytes (Fig. 4a). Submersed leaves of *Nuphar variegata* and its host plant *Nymphaea odorata* were moderately preferred. Very little of the remaining six macrophytes was consumed (Fig. 4).

In contrast to the midge, the weevil preferred its host plant during the laboratory feeding assay (Fig. 5). *Bagous* consumed *Nymphaea* and some *Nuphar* when the macrophytes were offered as fresh tissue. They did not consume enough of the reconstituted macrophytes to quantify the amount eaten, but the weevils were located on reconstituted *Nymphaea* most often, were observed on *Nuphar variegata*, *Nuphar pumila* and *Typha latifolia* a few times, and were never observed on the remaining reconstituted macrophytes (Fig. 5).

Adult *Donacia* consumed appreciable amounts of only their host plants *Brasenia* and *Nymphaea* when offered fresh leaves of nine macrophytes (Fig. 6). They sampled *Potamogeton*, *Pontederia* and submersed leaves

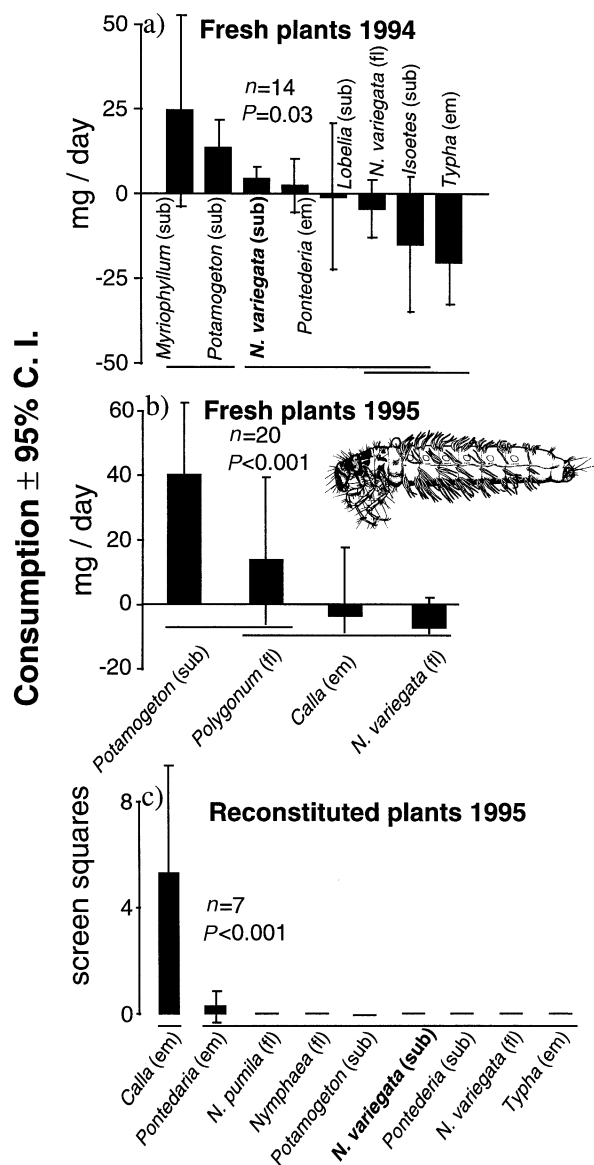


Fig. 3 (a) 1994 and (b) 1995 feeding preferences of the caddisfly *Limnephilus* when offered pieces of fresh macrophytes; and (c) when offered reconstituted macrophytes (em = emergent; fl = floating; sub = submersed leaves). The plant on which *Limnephilus* was seen in the field and from which it was collected is indicated in bold. Bars represent mean \pm 95% CI. Lines below the bars connect means that do not differ significantly from each other (Friedman test).

of *Nuphar variegata*, but did not eat any *Typha*, *Nuphar pumila* or floating *Nuphar variegata* (Fig. 6).

Adult *Galerucella* consumed only their host genus *Nuphar* during the feeding assay, without even sampling the five non-*Nuphar* plants offered (Fig. 7). Floating leaves of *Nuphar variegata* were consumed to about a four times greater extent than the submersed leaves.

Discussion

Live macrophytes in foodwebs

The present study found that consumption of live water lilies was common, and often very marked. Because herbivore damage can increase the turnover rate of water lily leaves (Wallace & O'Hop, 1985; Juliano, 1988; Otto & Wallace, 1989), snapshot measurements of herbivore damage can underestimate the degree of herbivory because heavily damaged leaves have a shorter lifespan than undamaged leaves (Jacobsen & Sand-Jensen, 1992, 1994). By following individual leaves through time, in addition to making snapshot measurements, it was found that herbivores damaged up to 1.7% of leaf area daily (Fig. 1), resulting in damage to leaves that averaged from 1 to 22% of leaf area, depending on species, leaf type, time and location. These results, and those of others that have measured levels of herbivore damage to freshwater macrophytes (Wallace & O'Hop, 1985; Sheldon, 1987; Otto & Wallace, 1989; Sand-Jensen & Madsen, 1989; Jeffries, 1990; Kouki, 1991a, b, c; Setälä & Mäkelä, 1991; Jacobsen & Sand-Jensen, 1992, 1994; Lodge *et al.*, 1994), indicate that freshwater macrophytes experience herbivory to an extent similar to that reported for terrestrial plants (Coley & Aide, 1991; Cyr & Pace, 1993; Lodge *et al.*, 1997), but less than herbivory to freshwater or marine algae (Hay, 1992a; Steinman, 1996; Lodge *et al.*, 1997). Thus, there is no *a priori* reason to suggest that freshwater herbivores should affect the ecology and evolution of plants any less than their terrestrial counterparts. Living macrophytes not only serve as substratum, habitat and environmental modifiers in the littoral zone, but also enter the foodweb via direct herbivory (Carpenter & Lodge, 1986).

Comparison of damage to submersed vs. floating leaves

Predicting the relative grazing damage to floating and submersed leaves is difficult. One could predict that floating leaves would be more damaged than submersed leaves because the former are exposed to a greater variety of herbivores. Floating leaves are initiated underwater and then grow to the water surface, where they are exposed to aquatic herbivores from underneath and terrestrial herbivores from above. On the other hand, submersed leaves have less structural material and thinner cuticles than floating or emergent leaves, which could make the delicate submersed

Fig. 4 (a) Feeding preference of the midge *Hyporhygma* when offered nine different macrophyte types (em = emergent; fl = floating; sub = submersed leaves). (b) The inset shows results of an assay that was performed with plants collected from the same site as the midges to control for any unknown between-lake differences in macrophytes (see Table 1). The host plant is in bold. Bars represent mean \pm 95% CI. Lines below the bars connect means that do not differ significantly from each other (Friedman test).

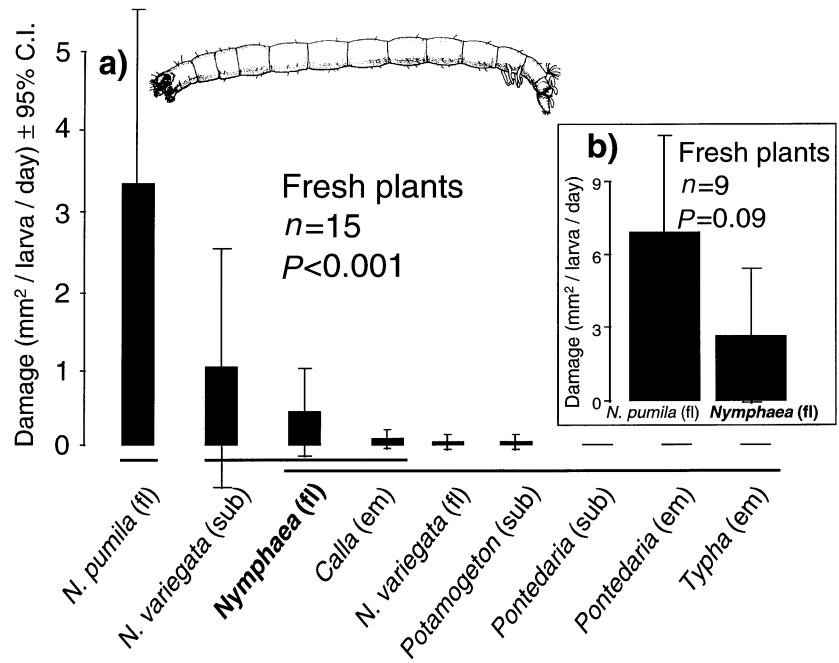
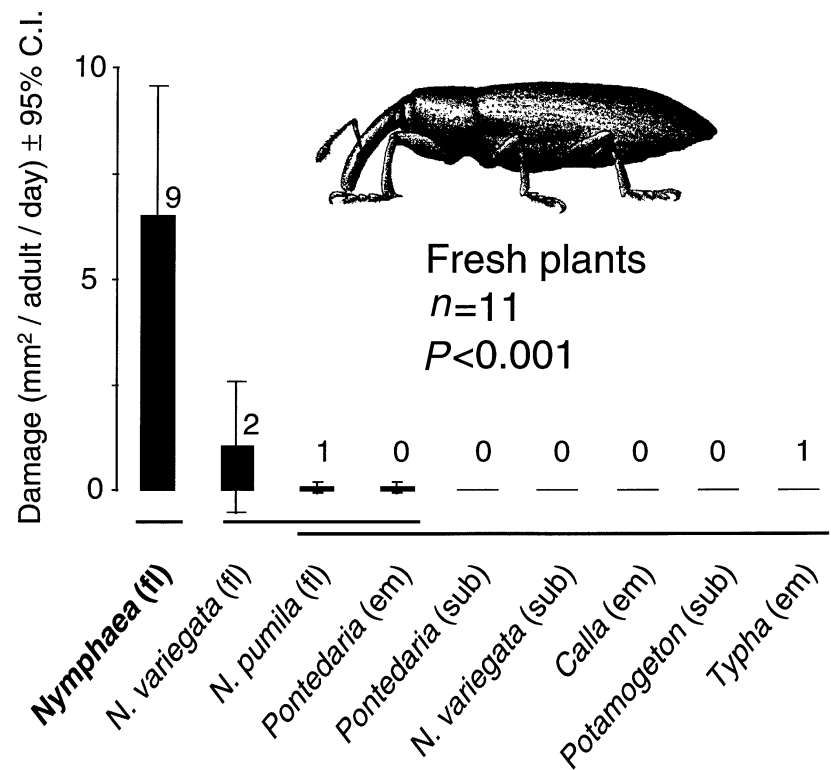


Fig. 5 Feeding preference of the weevil *Bagous* when offered fresh tissue of nine different macrophytes (em = emergent; fl = floating; sub = submersed leaves). The number above each bar represents the number of weevils out of fourteen that were located on the reconstituted macrophyte. The host plant is in bold. Bars represent mean \pm 95% CI. Lines below the bars connect means (for fresh tissue) that do not differ significantly from each other (Friedman test).



leaves more susceptible to herbivory than floating or emergent leaves (Chambers, Hanson & Prepas, 1991; Cronin, 1997).

When rates of grazing damage to submersed and

floating leaves were measured, no clear pattern emerged (Fig. 1). However, snapshot measurement of grazing damage consistently showed that submersed leaves were more heavily damaged than floating leaves

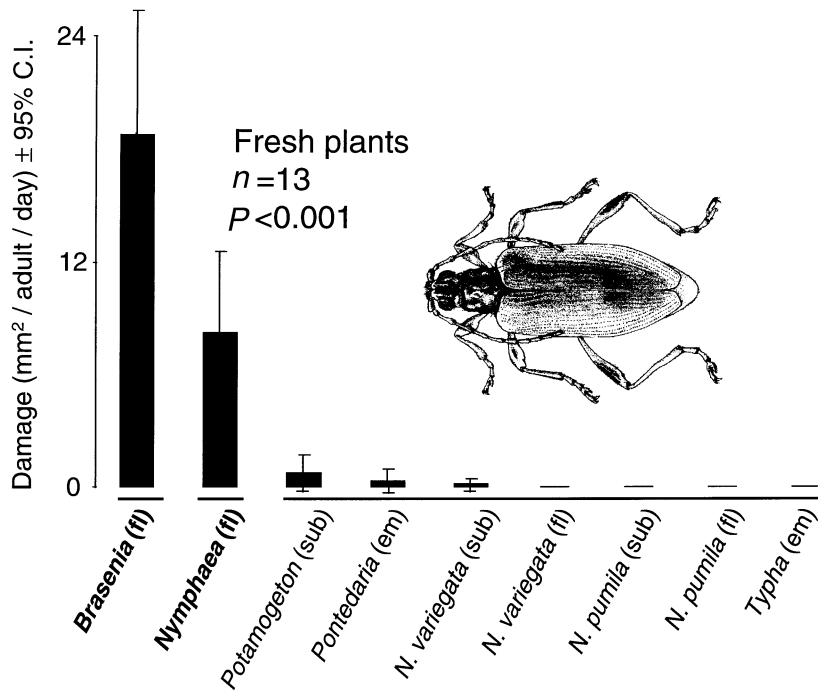


Fig. 6 Feeding preference of the chrysomelid beetle *Donacia* when offered fresh leaf squares of nine different macrophytes (em = emergent; fl = floating; sub = submersed leaves). Host plant is in bold and bars represent mean ± 95% CI. Lines below the bars connect means that do not differ significantly from each other (Friedman test).

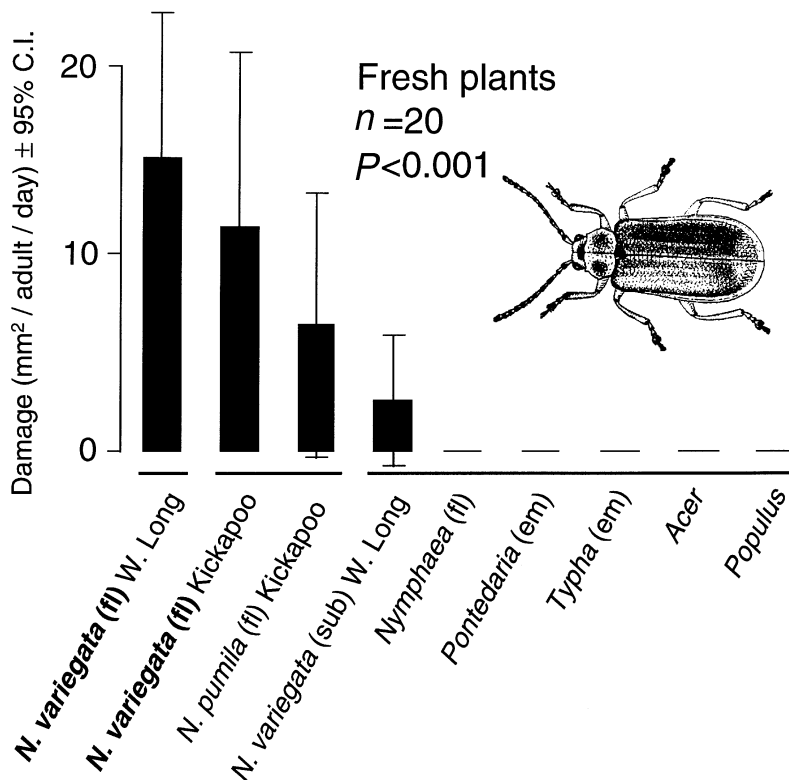


Fig. 7 Feeding preference of the chrysomelid beetle *Galerucella* when offered fresh leaf squares of nine different macrophytes (em = emergent; fl = floating; sub = submersed leaves). The host plant is in bold and bars represent mean ± 95% CI. Lines below the bars connect means that do not differ significantly from each other (Friedman test).

(Fig. 2). The apparent inconsistency for *Nuphar variegata* between data in Figs 1 and 2 could be explained if the longevity of submersed leaves was greater than the longevity of floating leaves. This study has no

data to address this possibility. The observations in these lakes suggest that changing abundance of different herbivores in different lakes (driven by species-specific phenology) contributes to these apparent

discrepancies; for example, in West Long Lake, shape and size of holes in *Nuphar* leaves indicated that *Limnephilus* was solely responsible for the damage to submersed leaves, while *Galerucella* was almost solely responsible for damage to floating leaves. While snorkeling in West Long Lake, the authors often observed *Limnephilus* feeding on submersed *Nuphar* and never saw other herbivores doing so. However, the abundance of pupating *Limnephilus* and empty cases increased during late May through to early June, while the abundance of actively feeding larvae declined, consistent with the decline in damage rate to submersed *Nuphar* in West Long Lake (Fig. 1). As the number of submersed-leaf-feeding *Limnephilus* larvae declined in this lake, the number of floating-leaf-feeding *Galerucella* increased. Thus, the relative amount of grazing to submersed and floating leaves changes temporally. The grazing damage to floating *Nuphar* that was measured in May–June 1994 was less than damage reported in other studies (Wallace & O'Hop, 1985; Otto & Wallace, 1989; Kouki, 1991b; Setälä & Mäkelä, 1991), probably because *Galerucella* was not yet active and *Donacia* populations were low during this period. Measurements of damage rates over the entire growing season would be necessary to evaluate more confidently the relative herbivory on submersed and floating leaves.

Diet breadth of primary vs. secondary aquatic insects

Findings of this study support the suggestion that primarily aquatic insects have a broader diet breadth than aquatic insects from primarily terrestrial groups (Hynes, 1984; Newman, 1991). Of the five herbivores studied here, the four from primarily terrestrial groups (two chrysomelids, one curculionid and one dipteran) specialized on water lilies (Figs 4–7), while the primarily aquatic trichopteran consumed *Myriophyllum*, *Potamogeton*, *Zygnema*, submersed *Nuphar* and reconstituted *Calla* (Fig. 3 and authors' personal observations). Additionally, the caddisfly is known to consume periphyton and detritus (Y. Vadeboncoeur, University of Notre Dame, personal communication).

The disparity in the occurrence of feeding specialization between marine (where specialization is rare) vs. terrestrial (where > 90% of species are specialists; Bernays, 1989) herbivores provides insight into herbivore traits that promote host specificity (Hay, 1992b; Hay & Steinberg, 1992). Marine generalist herbivores

(e.g. fish, urchins and molluscs) are often large relative to their hosts, have generation times similar to their hosts, have planktonic propagules that disperse over great distances, and avoid chemically rich plants (Hay, 1992b; Hay & Steinberg, 1992). In contrast, terrestrial specialists (e.g. insects) are often small relative to their hosts, have generation times shorter than their hosts, deposit their eggs directly on the host, and associate with hosts that are chemically defended against other herbivores (Bernays, 1989). The few marine specialist consumers are usually small animals that brood or oviposit on their chemically defended host (Hay *et al.*, 1990; Hay, 1992b; Cronin *et al.*, 1995).

Some life history traits of the generalist vs. specialist herbivores in the present study fit the above patterns well. What is known about their life histories, much of it from the authors' personal observations, is summarized here. Adult *Limnephilus* lay their eggs on the water surface where eggs or larvae can be dispersed by air and/or water currents before the larvae hatch and begin feeding in the benthos (Wiggins, 1996). *Limnephilus* larvae then feed on algae, macrophytes, and detritus for 1–2 years before metamorphosing into adults (i.e. have longer generation times than most specialist insects) (Wiggins, 1996).

In contrast, for the specialist *Hyporhygma*, adult females oviposit on the upper surface of floating *Nymphaea* leaves. The larvae have been observed feeding only on the floating leaves of *Nymphaea*, where they pupate and then emerge as adults. This midge completes at least one life cycle per growing season (i.e. < 5 months), but how it overwinters is unknown. Adult *Donacia* feed and mate on leaves or in flowers of water lilies and oviposit on the underside of their floating leaves, usually through a feeding hole. Larvae then drop or crawl to the sediments, where they attach to the host's rhizome with two respiratory hooks through which oxygen is acquired while surrounded by anoxic sediments. The grubs of most *Donacia* spp. presumably feed on roots, rhizomes and petioles for 2 years, pupate underwater, and then crawl to the surface after emerging as adults (White & Brigham, 1996). Thus, *Donacia* is a long-lived specialist with ontogenetic shifts in feeding behaviour. *Galerucella* is a semi-terrestrial beetle in which all life stages must remain above water to avoid drowning. Adults feed, mate and oviposit on the dry surface of floating or emergent *Nuphar* leaves. The larvae begin feeding on the leaf immediately after hatching, go through three

instar stages, pupate and emerge as adults, all in about a month (Wallace & O'Hop, 1985; Juliano, 1988; Otto & Wallace, 1989; G. Cronin *et al.*, unpublished observations). *Galerucella* overwinter as adults in leaf litter or under tree bark (Almkvist, 1984; Kouki, 1991b, c). Adult *Bagous* spend long periods of time on the underside of floating leaves of *Nymphaea*, where eggs are oviposited into plant tissues. The larvae mine the leaves of the host and pupate in the petioles and junctions of the leaves, thereby avoiding direct contact with the water (McGaha, 1952). Thus, the one generalist herbivore (*Limnephilus*) in the present study belongs to a primarily freshwater order and disperses its eggs or larvae, while the four specialists on water lilies are insects of primarily terrestrial groups and mate on and/or oviposit on their host plant.

Proximal cues for feeding choices

While host chemistry is a primary proximal cue for the feeding choices of many specialists (Futuyma, 1983; Futuyma & Moreno, 1988; Courtney & Kibota, 1990), generalists are likely to base feeding decisions on a combination of plant nutritive, textural, morphological and chemical cues (Newman, 1991; Cronin, 1997; Lodge *et al.*, 1997). The texture or morphology of *Potamogeton* and *Calla* was an important proximal feeding cue for *Limnephilus* because the relative palatability of these plants changed when their structure was altered. Delicate *Potamogeton* leaves were a preferred food as fresh tissue but were untouched after freeze-drying, grinding and reconstituting in an alginate gel (Fig. 3). In contrast, tough, emergent *Calla* leaves were not consumed as whole tissue but were highly preferred as reconstituted tissue (Fig. 3). Just as plant structure was an important feeding determinant of *Limnephilus*, the feeding preferences of generalist crayfishes appear to be partly determined by macrophyte structure (Chambers *et al.*, 1991; Cronin, 1997). Plant chemical defences and nutritive value become important feeding determinants for generalists only after any structural constraints are overcome (Cronin, 1997; Lodge *et al.*, 1997).

Unlike the generalist *Limnephilus*, the feeding preference of the specialist *Bagous* did not change when plants were freeze-dried and reconstituted; the weevil preferred its host plant *Nymphaea* in both cases (Fig. 5), suggesting the specialist was cueing on plant compounds unique to *Nymphaea* and not on structural features when making its feeding choices. Thus, this

behavioural information on a few aquatic herbivores (for oviposition behaviour see Solarz, 1995; Solarz & Newman, 1996) is consistent with what is known about proximal feeding cues of terrestrial and marine herbivores: specialists cue on specific host chemistry and generalists cue on multiple plant traits, including plant structure or texture.

Plant attributes favouring feeding specialization

There appeared to be more specialists associated with water lilies than the other freshwater macrophytes observed in the lakes. This pattern could be an artefact of floating and emergent leaves being more apparent to humans than submersed plants. However, considerable time was spent snorkeling in these lakes, qualitatively surveying for herbivores, and only one insect herbivore predictably associated with a submerged plant species was seen (the midge on *Potamogeton*). What properties of water lilies might make them more apt to be hosts of specialist grazers? Considerable disagreement remains about factors that promote the origin of feeding specialization (see Bernays & Graham, 1988 and subsequent responses in *Ecology* (1988) 69, pp. 886–915). However, it is generally believed that behavioural responses to host chemistry are important in maintaining specialized associations (Futuyma, 1983; Futuyma & Moreno, 1988; Courtney & Kibota, 1990). Nymphaeaceae is a chemically rich family of macrophytes (Hutchinson, 1981; Ostrofsky & Zettler, 1986), which might provide insects with unique chemical cues to maintain specialized associations.

Also, by occurring at the water–air interface, water lilies are more available than many other aquatic macrophytes to terrestrial insect groups, which have a high propensity for feeding specialization (Bernays, 1989). Because insect larvae usually have limited mobility, host-plant specificity is maintained more by the oviposition behaviour of adult insects than the feeding selectivity of the larvae (Futuyma & Moreno, 1988), suggesting that water lilies may have more specialist herbivores because oviposition sites for adult terrestrial insects are numerous. This is especially true for *Galerucella*, which would be unable to use *Nuphar* if the leaves did not reach the surface of the water, because eggs, larvae, pupae and adults cannot survive long periods of submersion (Juliano, 1988; Kouki, 1991a, 1993).

Terrestrial ecologists have also suggested that insects may specialize on a few host plants because the plants

are used as mating rendezvous (i.e. they concentrate potential mates) (Colwell, 1986). Floating leaves of water lilies would be ideal mating sites because they are long-lived perennials that predictably occur along the edge of lakes. Additionally, the two-dimensional space that floating leaves represent would concentrate potential mates more than the three-dimensional space that most terrestrial or submersed plants occupy, all else being equal.

As others have recently found (Wallace & O'Hop, 1985; Juliano, 1988; Sand-Jensen & Madsen, 1989; Kouki, 1991a, b, c, 1993; Lodge, 1991; Newman, 1991; Setälä & Mäkelä, 1991; Jacobsen & Sand-Jensen, 1992, 1994; Lodge *et al.*, 1994, 1997; Cyr & Pace, 1993; Kornijow, 1996), the data presented here dispute the long-held assumption that living macrophytes are rarely eaten by herbivores. While we know that freshwater macrophytes are eaten by herbivores, no apparent pattern emerged from our data regarding relative grazing rates on submersed and floating leaves of macrophytes. Grazing damage to submersed and floating leaves was the result of complex factors, including leaf longevity, leaf palatability and relative population size and activity of herbivore taxa. The diet breadth of herbivores in the present study was consistent with the pattern observed by Newman (1991) concerning the propensity of feeding specialization of primarily aquatic and primarily terrestrial insects. The primarily aquatic *Limnephilus* fed on many plant species and appeared to use multiple feeding cues while foraging. Primarily terrestrial insects consumed only water lilies and unique plant chemistry seemed to be the important feeding cue for the one specialist for which it was possible to eliminate plant structure/texture as a factor. Overall, these freshwater plant–insect interactions have much in common with plant–insect interactions studied by terrestrial ecologists. Further study of freshwater plant–herbivore interactions will not only increase our understanding of freshwater habitats, but will undoubtedly complement our knowledge of terrestrial and marine plant–herbivore interactions, providing insight into the factors governing the evolution and ecology of herbivory in general.

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