Taxonomic and size structures of phytophilous macroinvertebrate communities in *Vallisneria* and *Trapa* beds of the Hudson River, New York

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Abstract

Phytophilous macroinvertebrates (PMI) were sampled from the surfaces and surrounding water of two aquatic plant species, *Vallisneria americana* and *Trapa natans,* which have substantially different morphologies. It was expected that the plants would harbor invertebrate communities of different structure. Total density of PMI was consistently greater in *Vallisneria* than in *Trapa*, e.g. $6\times$ greater per m^3 water and $21\times$ greater per m^2 leaf surface in August. Each macrophyte harbored taxa that were either significantly more abundant or present only with that macrophyte; the herbivore *Galerucella nymphaceae* (Coleptera: Chrysomelidae) was abundant on *Trapa. Vallisneria* harbored 34 taxa vs. 40 taxa in *Trapa*, but similarity was low (Morisita's C=0.55–0.66). Predaceous invertebrates were more prevalent in *Trapa* than in *Vallisneria,* as were larger individuals. Both PMI communities exhibited shifts in size distribution between July and August. Standing crop of *Trapa* was $3\times$ greater than for *Vallisneria*. These two macrophyte beds clearly support PMI communities of different taxonomic and size structure, which is believed to be related to the differences in macrophyte morphology.

Introduction

Aquatic vegetation influences macroinvertebrate community structure by affecting both the physical characteristics of a habitat and the biotic interactions that occur there (Crowder & Cooper, 1982; Heck & Crowder, 1991). Compared to unvegetated habitats, invertebrate abundance and richness is typically greater among aquatic plants, for both sediment- and plant-associated fauna (Gilinsky, 1984; Orth, Heck & Van Montfrans, 1984; Richardson et al., 1998). Furthermore, different aquatic plant species support different communities of plant-associated invertebrates (Gerking, 1957; Keast, 1984; Engel, 1985). These phytophilous macroinvertebrates (hereafter PMI) live in, on, or in close proximity to the shoots and leaves of aquatic plants. The biotic and abiotic conditions associated with the microhabitat of different plant species is believed to differ, with likely consequences for PMI community structure (Stoner, 1982; Heck & Crowder, 1991). Among the factors creating different conditions are leaf morphology and plant density, which are regarded as important for determining PMI distribution (Krecker, 1939; Crowder & Cooper, 1982; Cyr & Downing, 1988). These two factors formed the basis of comparisons of PMI density, taxonomic distribution and size distribution in this study.

Fish predation is a major factor in determining the size structure of invertebrate communities, with some freshwater fish, notably sunfish, recognized as size-selective feeders (Werner & Mittelbach, 1981; Mittelbach, 1988; Laughlin & Werner, 1989). Therefore, characterization of PMI size distributions provides a potentially valuable description of the influence of fish upon the PMI community and of the fish prey resource. Size-selective predation upon PMI may also be influenced by aquatic plants, since foraging efficiency is influenced by the density or morphology of aquatic plants (Crowder & Cooper, 1982; Diehl, 1988). Given the importance of size-selective predation by species such as sunfish, and that different aquatic plants create different conditions for predator–prey relations,

I hypothesized that PMI community size structure would differ among aquatic plant species. Although differences in total abundance and taxonomic distribution of PMI have been demonstrated among aquatic plant species (Gerking, 1957; Engel, 1985), no such comparisons exist for PMI size distributions.

This paper focuses on the community structure (taxonomic and size distributions) of PMI associated with plant parts above the sediment surface. I hypothesized that PMI community structure would differ between monospecific beds of two aquatic plants, *Vallisneria americana* Michx. (wild celery) and *Trapa natans* L. (water chestnut). These aquatic plants have distinctly different morphologies and growth habits, which were expected to influence invertebrate densities, species occurrence and sizes of individuals. Differences in leaf morphology, density of vegetation, and resultant light penetration are the most apparent botanical factors that may influence PMI community structure in these two beds. *Trapa* creates a dense floating canopy that greatly diminishes light penetration into the water column. This creates different conditions for PMI and fish compared to the more open growth morphology of *Vallisneria*; under less light it is expected that larger invertebrates would persist, less readily detected by fish. I hypothesized that lower light penetration under *Trapa* would skew the size distribution to larger individuals than among *Vallisneria*. It was expected that *Trapa* would harbor more large predaceous invertebrates that would be less likely to survive the fish foraging among the better lit water column of *Vallisneria*.

Materials and methods

Study area

Two aquatic plant beds were studied in the Thompson Island Pool of the upper, non-tidal section of the Hudson River. This is an 8 km stretch extending from the location of the former dam at Ft. Edward, NY to another small dam. One bed was dominated by *Vallisneria*, in a channel between the east shore and three islands, opposite Snook Kill, 3 km south of Champlain Canal Lock 7, at 43° 14′ N, 73° 36′ W. The other was dominated by *Trapa*, in a channel between the west shore and Griffen Island, 6 km south of Lock 7, at 43° 12′ N, 73° 36′ W. This unavoidable separation of the two plant beds leads to potential confounding of effects between plant species and location. However, as described below, there is evidence that plant morphology can have marked effects on invertebrate community structure.

Both plants reach peak biomass in July or August, and senesce in autumn. *Vallisneria* is a submerged aquatic plant with basal rosettes of flexible ribbon-like leaves that can occupy the full height of the water column, forming an underwater meadow. *Trapa* develops into a floating plant, with compact rosettes of succulent rhombic leaves, forming a dense canopy with leaves in, on and above the water; submerged finely dissected modified leaves grow sparsely from the stem. At Griffen Island, this dense canopy prevented submerged macrophyte species from growing under it. The majority of *Trapa*'s biomass is near or above the water surface, whereas for *Vallisneria* it is distributed through the water column, although late in the growing season some concentration at the surface occurs as longer leaves lie immediately under the water surface. These differences in plant morphology and growth habit were expected to contribute to differences in the associated PMI communities.

Sampling

PMI were sampled at 10 randomly selected points along a transect placed on the water surface at each site on 29 July and 20 August 1988. Transects were laid in the middle of each bed where water depth was 1.5 m. The plants were fully developed by 29 July and were expected to be well-colonized by PMI at that time. The later sampling was conducted to account for the phenologies of different invertebrates, and to increase the generality of the findings to these sites. Aquatic plants were collected by use of a diver-operated collapsible polyethylene tube (designed by Sallie Sheldon, Middlebury College) that isolated plants and associated invertebrates (Fig. 1), with minimal disturbance of the water column. This permitted more complete sampling of organisms that are sensitive to turbulence, e.g. amphipods, than traditional methods. The sampler was 25 cm in diameter, reinforced with tubular rings to maintain a cylinder in the water, with the bottom edge fused to a ring of metal duct. In operation, the collapsed tube was positioned by an assistant on board a canoe over the vegetation to be sampled, and a diver gently moved the ring downward over the plant. For *Trapa* it was necessary to isolate an individual plant for sampling. At 5 cm from the bottom, the plant was clipped and a sieve (0.5 mm mesh openings) was placed snugly against the duct ring. The volume of water column sampled was approximately

Figure 1. Phytophilous macroinvertebrate tube sampler brought to surface above *Vallisneria*. Plants and invertebrates are retained by sieve at bottom of tube, held by diver.

0.045 m^3. The isolated, enclosed sample of plants and animals was brought to the surface, consolidated in the sieve, transferred to a plastic bag and stored on ice until lab processing and preservation.

In the lab, plants were rinsed under a slow flow of tap water, with sieves (minimum mesh openings of 0.5 mm) underneath to capture invertebrates dislodged by sliding fingers over the plant surfaces. The resulting invertebrate samples were preserved in 70% ethanol, with rose bengal added to aid in separating specimens from plant material (Williams & Williams, 1974). Sorting, identification and counting of all specimens was conducted at 8–40× magnification. Most taxa were identified to family, many to genera (Pennak,

1978; McCafferty, 1981), and a few to class; taxonomic statistics were conducted on data at the family level (and class level when that was the greatest resolution). All individuals were sized at $10\times$ along the longest dimension, using an ocular micrometer. This length measurement included cerci and anal gills, but not antennae. Amphipods were not extended beyond their natural curvature.

Densities are expressed as numbers of individuals/water volume, and also as individuals/leaf area, individuals/leaf dry mass and individuals/water surface area. The volume measurement is preferred because the invertebrates and their fish predators exist in a three-dimensional habitat, and because the sampling device sampled a water volume containing plants and invertebrates. The other measures are included to facilitate comparison with other studies.

When estimating density per leaf area, the area of both sides of the leaves was used since invertebrates were collected from both sides. *Vallisneria* leaf area was determined by measuring the length and mid-leaf width of 30 leaves, and approximating the shape as a parallel-edged ribbon. This subsample was dried at 85 °C for 24 h to determine a dry weight:area ratio, which was applied to the dry weights of all *Vallisneria* samples. An equivalent relationship was supplied by Stuart Findlay (unpublished data) for *Trapa*. These measurements allowed for calculation of invertebrate densities per gram dry weight (gdw) and per leaf area (m^2). They also provided an estimate of plant dry mass per river surface area (in addition to standing crop, below).

The sampling technique used in the present study probably introduced bias in density measures per water volume and per water surface. In July, when *Trapa* rosettes were closely packed against each other, PMI densities may have been underestimated, since only one rosette usually fit into the sampler (two samples, however, included two small rosettes). The 0.05 m^2 area of the sampler was large enough to contain one rosette plus part of another one, but parts of rosettes could not be sampled. The patchier distribution of *Vallisneria* may have resulted in overestimation of PMI, since sampling occurred only where plants existed, not accounting for open areas between plants. The open areas likely had much lower densities of invertebrates.

Standing crop of aquatic plants was measured at each site on 29 July by harvesting the above-sediment biomass within a 1 m^2 quadrat in the center of each bed at 1.5 m depth. Three samples were taken at each site at randomly chosen locations 1 m parallel to the

PMI sampling transect, after PMI sampling. Biomass was measured after drying at 85 °C for 24 h. Mean dry weights of these plant samples were calculated as standing crop.

Statistical analysis

Differences in densities were evaluated with *t*-tests, using separate rather than pooled variances in SYSTAT (Wilkinson, 1989), since sample sizes were unequal and variances often differed substantially between habitats (Zar, 1984). Taxonomic similarity was calculated with the Morisita index (*C*):

$$C = \frac{2\Sigma X_{iv} X_{it}}{\frac{\Sigma[X_{iv}(X_{iv}-1)]}{N_v(N_v-1)} + \frac{\Sigma[X_{it}(X_{it}-1)]}{N_t(N_t-1)} N_v N_t},$$

where X_{iv} and X_{it} = abundance of taxon i in *Vallisneria* (v) and *Trapa* (t), and N_v and N_t = total abundance in *Vallisneria* and *Trapa* samples. It considers relative abundance of taxa, and is the least sensitive to abundance and number of taxa (Wolda, 1981; Krebs, 1989). The expected maximum value for *C* is 'about one' (Wolda, 1981).

The difference in size structure of communities associated with *Vallisneria* and *Trapa* was assessed with the Kolmogorov-Smirnov test, which is more powerful than the chi-squared test (Siegel & Castellan, 1988). The algorithm described by Sokal & Rohlf (1981) for samples of $n>40$ was used. All tests were conducted on sums of abundances, since variance and replication are not accounted for in this nonparametric test. Although measuring and contrasting mean lengths among treatments has been done in the past (Mittelbach, 1981), describing and contrasting entire size distributions was considered to be more informative in this study.

Results

Density

The density of all invertebrates, expressed per m^3 water, was significantly greater in the *Vallisneria* bed than in *Trapa* in both July and August; in July, the difference was two-fold, and in August it was nearly six-fold (Fig. 2a). Expressed per water surface area the proportions and significance were the same as per water volume (Fig. 2b). When expressed per m^2 leaf surface, the difference was more than four-fold in July, and more than 21 times as great in *Vallisneria*
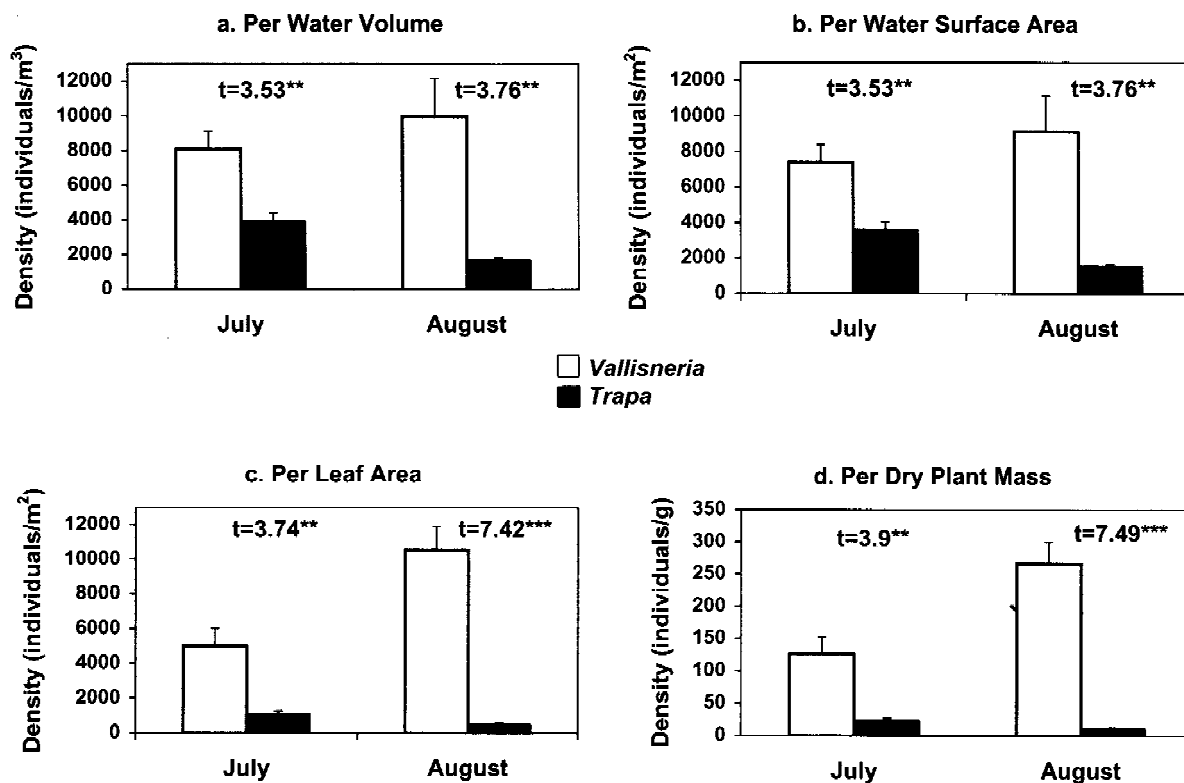
Figure 2. Total density of phytophilous macroinvertebrates from two macrophyte beds. Data are means+1se; *n*=10. Comparisons of means between sites each month by *t*-tests where **$p<0.01$ and ***$p<0.001$.

in August (Fig. 2c). Expressed per gram dry weight of plant tissue, *Vallisneria* had significantly greater densities during both months, five-fold in July and 26-fold in August (Fig. 2d). Density, by any measure, tended to increase for *Vallisneria* and decrease for *Trapa* communities from July to August. These changes were significant at *p*=0.005 for *Vallisneria* PMI measured per leaf surface area and dry plant mass, and at *p*=0.001 for *Trapa* PMI measured by each of the units. *Trapa* PMI decreased 57% per water volume, 56% per leaf area, 58% per dry plant mass and 57% per water surface area (Fig. 2). *Vallisneria* PMI increased 24% per water volume, 112% per leaf area, 111% per dry plant mass and 24% per water surface area (Fig. 2).

In *Vallisneria*, 7 of the 10 most abundant taxa were either significantly more abundant there than in the *Trapa* bed or did not occur in *Trapa*. In July, these seven taxa all occurred at significantly greater densities in *Vallisneria*: Planorbidae, Hydrobiidae and Ancylidae Cladocera, Coenagrionidae, Leptoceridae and Chironomidae (Tables 1, 2). In August, four taxa –

Table 1. Summary of taxa that were significantly more abundant or occurred exclusively at one site. Selected from the 10 most abundant taxa at each site, each month

	July	August
Number of taxa significantly more abundant among Vallisneria	7	4
Number of taxa occurring exclusively with Vallisneria	0	3
Number of taxa significantly more abundant among Trapa	4	3
Number of taxa occurring exclusively with Trapa	1	2

Cladocera, Copepoda, Ostracoda and Chironomidae – were significantly more abundant with *Vallisneria*, and three taxa – Planorbidae, Ancylidae and Hydroptilidae – also occurred exclusively there (Tables 1, 3).

Table 2. Density of phytophilous macroinvertebrate taxa in July. Densities are individuals per cubic meter water; *n*=10. Identified genera are listed in parentheses, and represent the most common, if not exclusive forms found. The ten most abundant taxa are ranked

Significance level[a]		Taxon	*Vallisneria*				*Trapa*			
			Density		% of	Density	Density		% of	Density
			mean	se	total	rank	mean	se	total	rank
*	Gastropoda	Planorbidae (*Gyraulus*)	151±	30.9	1.9	8	53±	16.3	1.3	
		Physidae (*Physella*)	25±	10.8	0.3		31±	12.5	0.8	
*		Hydrobiidae (*Amnicola*)	580±	190.4	7.2	4	2±	2.2	<0.1	
**		Ancylidae (*Ferrisia*)	1111±	263.3	13.9	3	40±	17.5	1.0	
		Lymnaeidae (*Psuedosuccinea*)	0±	0.0	0.0		18±	13.2	0.5	
	[b]Pelecypoda		10±	5.4	0.1		9±	4.9	0.2	
	[b]Turbellaria		0±	0.0	0.0		7±	4.7	0.2	
	Annelida									
*		Glossiphonidae	15±	5.2	0.2		173±	64.9	4.3	7/8
	[b]Naididae (*Stylaria*)		0±	0.0	0.0		31±	21.8	0.8	
	Nematoda		0±	0.0	0.0		4±	3.0	0.1	
	Cladocera									
**		Chydoridae	217±	49.0	2.7	7	4±	4.4	0.1	
ns	Copepoda		321±	59.0	4.0	6	267±	101.7	6.7	6
	Ostracoda		44±	21.6	0.5		22±	7.4	0.6	
	Amphipoda									
ns		Talitridae (*Hyallela azteca*)	1523±	413.0	19.0	2	1393±	171.9	34.8	1
	Isopoda									
**		Asellidae (*Caecidotea*)	2±	2.5	<0.1		309±	79.1	7.7	4
	Arachnoidea									
ns		Hydracarina	79±	19.3	1.0	10	122±	23.5	3.1	10
		Araneae	0±	0.0	0.0		18±	7.3	0.5	
	Odonata									
*		Coenagrionidae	506±	123.8	6.3	5	173±	27.3	4.3	7/8
	[b]Corduliidae		0±	0.0	0.0		9±	3.6	0.2	
	[b]Libellulidae		2±	2.5	<0.1		2±	2.2	<0.1	
	[b]Gomphidae		2±	2.5	<0.1		0±	0.0	0.0	
	Ephemeroptera									
***		Caenidae (*Caenis*)	27±	13.2	0.3		440 ±	64.2	11.0	2
	Coleoptera									
		Hydrophilidae (*Berosus*)	2±	2.5	<0.1		0±	0.0	0.0	
	[b]Staphylinidae (*Stenus*)		0±	0.0	0.0		2±	2.2	<0.1	
***		Chrysomelidae (*Galerucella nymphaeae*)	0 ±	0.0	0.0		293±	55.8	7.3	5
	Lepidoptera									
		Pyralidae (*Paraponyx*)	10±	5.4	0.1		0±	0.0	0.0	
	Hemiptera									
		Pleidae (*Neoplea*)	0±	0.0	0.0		4±	4.4	0.1	
	[b]Corixidae		44±	19.6	0.5		0±	0.0	0.0	
	[b]Gerridae		15±	7.4	0.2		0±	0.0	0.0	
		Mesovelidae (*Mesovelia*)	2±	2.5	<0.1		51±	11.0	1.3	
	[b]Velidae		2±	2.5	<0.1		0±	0.0	0.0	
	[b]Nepidae (*Ranatra*)		0±	0.0	0.0		13±	6.8	0.3	
	[b]Belostomatidae		0±	0.0	0.0		2±	2.2	<0.1	
		Notonectidae (*Notonecta*)	0±	0.0	0.0		7±	3.4	0.2	
		Aphididae	0±	0.0	0.0		2±	2.2	<0.1	
	Trichoptera									
		Hydroptilidae (*Orthotrichia, Ochrotichia, Hydroptila*)	54±	1.2	0.7		0±	0.0	0.0	
**		Polycentropodidae (*V: Neureclipsis; T: Polycentropus*)	7±	3.7	0.1		151±	43.5	3.8	9
**		Leptoceridae (*Oecetis, Triaenodes*)	91 ±	23.6	1.1	9	0±	0.0	0.0	
	Diptera									
*		Chironomidae	3104±	1067.4	38.7	1	322±	56.3	8.1	3
	[b]Chaoboridae		0±	0.0	0.0		2±	2.2	<0.1	
		Ceratopogonidae	2±	2.5	<0.1		13±	7.6	0.3	
		Ephydridae	35±	13.9	0.4		0±	0.0	0.0	
		Empididae	5±	3.3	0.1		0±	0.0	0.0	
		Psychodidae	0±	0.0	0.0		2±	2.2	<0.1	
	[b]Culicidae		0±	0.0	0.0		2±	2.2	<0.1	
		Diptera1	20±	17.2	0.2		0±	0.0	0.0	
		Diptera2	0±	0.0	0.0		2±	2.2	<0.1	
Totals:		47 taxa	8012±	1073.0	100.0		4000±	461.0	100.0	

[a] Significance of difference of mean density between sites; *t*-tests of 10 most abundant taxa in each site, * $p<0.05$, ** $p<0.01$, ns non-significant.
[b] Absent from both sites in August.

Table 3. Density of phytophilous macroinvertebrate taxa in August. Densities are means (per cubic meter water) +/- 1 SE; n=10. Identified genera are listed in parentheses, and represent the most common, if not exclusive forms found. The ten most abundant taxa are ranked

Significance level[a]		Taxon	Vallisneria				Trapa			
			Density		% of	Density	Density		% of	Density
			mean	se	total	rank	mean	se	total	rank
	Gastropoda									
***		Planorbidae (*Gyraulus*)	322±	53.5	3.2	9	0±	0.0	0.0	
		Physidae (*Physella*)	13±	4.9	0.1		0±	0.0	0.0	
		Hydrobiidae (*Amnicola*)	82±	29.8	0.8		2±	2.5	0.2	
***		Ancylidae (*Ferrisia*)	309±	102.0	3.1	7	0±	0.0	0.0	
		Lymnaeidae (*Psuedosuccinea*)	0±	0.0	0.0		5±	3.3	0.3	
	Annelida									
		Glossiphonidae	13±	6.8	0.1		15±	6.4	0.9	
	Nematoda		0±	0.0	0.0		2±	2.5	0.2	
*	Cladocera		722±	269.0	7.2	3	2±	2.5	0.2	
*	Copepoda		349±	99.4	3.5	5	30±	12.3	1.8	
*	Ostracoda		798±	334.0	8.0	2	17±	14.7	1.0	
	Amphipoda									
ns		Talitridae (*Hyalella azteca*)	207±	60.1	2.1	9	222±	59.5	13.3	2
	Isopoda									
*		Asellidae (*Caecidotea*)	11±	6.0	0.1		67±	17.0	4.0	9/10
	Arachnoidea									
ns		Hydracarina (*Arrenurus; V: Piona, Oxus*;	209±	91.0	2.1	8	82±	23.7	4.9	8
		T: Hydrovolzi, Athienemannia, Arrenurus, Lebertia)								
		Araneae	2±	2.2	<0.1		32±	12.3	1.9	
	Odonata									
ns		Coenagrionidae	44±	14.8	0.4		84±	12.7	5.0	7
	Ephemeroptera									
*		Caenidae (*Caenis*)	47±	25.1	0.5		116±	19.9	6.9	4
	Coleoptera									
		Hydrophilidae (*V:Berosus; T: Hydrophilus, Paracymus*)	4±	3.0	<0.1		27±	8.1	1.6	
***		Chrysomelidae (*Galerucella nymphaeae*)	0±	0.0	0.0		106±	25.6	6.3	6
		Pyralidae	4±	3.0	<0.1		2±	2.5	0.2	
	Neuroptera									
		Sisyridae (*Climacia*)	2±	2.2	<0.1		0±	0.0	0.0	
	Megaloptera									
		Sialidae (*Sialis*)	13±	7.5	0.1		0±	0.0	0.0	
	Hemiptera									
		Saldidae	0±	0.0	0.0		2±	2.5	0.2	
		Pleidae (*Neoplea*)	0±	0.0	0.0		59±	13.4	3.5	
		Mesovelidae (*Mesovelia*)	0±	0.0	0.0		20±	12.0	1.2	
		Notonectidae (*Notonecta*)	0±	0.0	0.0		12±	3.9	0.7	
***		Aphididae	0±	0.0	0.0		114±	60.2	6.8	5
	Trichoptera									
***		Hydroptilidae (*Orthotrichia, ochrotichia, Hydroptila*)	487±	129.0	4.9	4	0±	0.0	0.0	
ns		Polycentropodidae (*V: Neureclipsis; T: Polycentropus*)	173±	108.0	1.7	10	67±	19.9	4.0	9/10
		Leptoceridae (*Oecetis, Triaenodes*)	116±	34.7	1.2		0±	0.0	0.0	
		Brachycentridae	0±	0.0	0.0		2±	2.5	0.2	
		Phyrganeidae	4±	3.0	0.0		0±	0.0	0.0	
	Diptera									
**		Chironomidae	5967±	1308.0	59.7	1	432±	65.0	25.8	1
*		Ceratopogonidae	29±	11.0	0.3		148±	52.8	8.8	3
		Ephydridae	2±	2.2	<0.1		0±	0.0	0.0	
		Empididae	2±	2.2	<0.1		0±	0.0	0.0	
		Psychodidae	0±	0.0	0.0		5±	4.9	0.3	
		Diptera1	56±	17.3	0.6		2±	2.5	0.2	
Totals:	37 taxa		9990±	2194.0	100.0		1676	±114.0	100.0	

[a] Significance of difference of mean density between sites; *t*-tests of 10 most abundant taxa in each site, * $p<0.05$, ** $p<0.01$, ns non-significant.
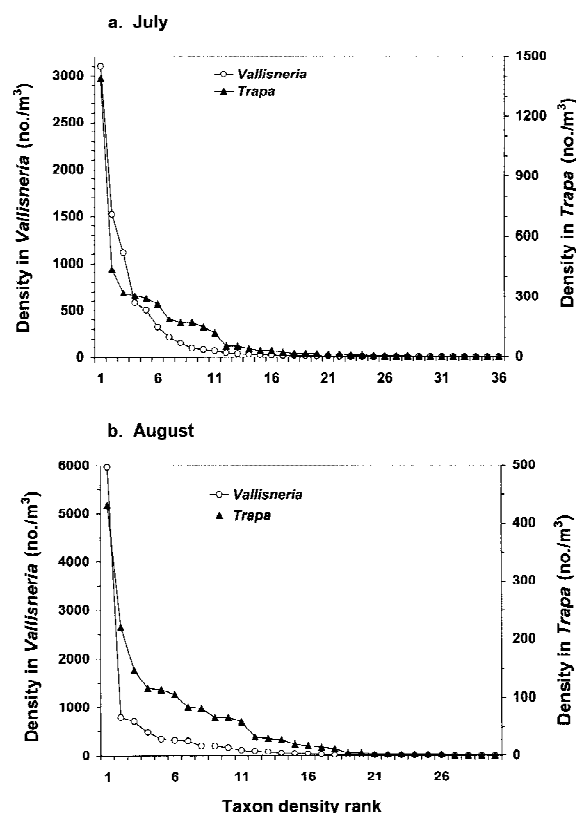
a. July

b. August

Figure 3. Distribution of phytophilous macroinvertebrate density among invertebrate taxa in two macrophyte beds. Taxa are ranked by density.

In *Trapa*, 5 of the 10 most abundant taxa were either significantly more abundant there than in the *Vallisneria* bed, or did not occur in *Vallisneria*. In July, 4 of the 10 most abundant taxa associated with *Trapa* were significantly more abundant than in *Vallisneria* (Tables 1, 2): Hirudinea, Asellidae, Caenidae and Polycentropodidae. Chrysomelidae, as the herbivore *Galerucella nymphaeae* (L.), were also exclusively on *Trapa*. In August, three taxa – Asellidae, Caenidae and Ceratopogonidae – were significantly more abundant with *Trapa*, and two taxa – *G. nymphaeae* and Aphididae – occurred exclusively with *Trapa* (Tables 1, 3).

The distribution of invertebrate density across taxa differs between *Vallisneria* and *Trapa* PMI. In *Vallisneria*, fewer taxa contribute high numbers of individuals to total density than in *Trapa*. The 10 most abundant taxa comprised 96% of the total of *Vallisneria* PMI density in July and 96% in August; for *Trapa* PMI the corresponding values were 91% and 86%. Plots of abundance vs. taxon abundance rank

Table 4. Richness of phytophilous macroinvertebrates (mean number of taxa +/− 1 SE) and similarity (Morisita's index (C)) between aquatic plant habitats. C range=0–1

	July	August
Richness		
Vallisneria	17.7±0.6	16.6±0.8
Trapa	18.7±0.8	14.4±0.8
	$t=1.02$ $p=0.320$	$t=1.56$ $p=0.137$
Similarity (C)	0.55	0.66

(Fig. 3) illustrate the contribution of individual taxa to total density. The X axis was approached sooner for *Vallisneria* PMI than for *Trapa* PMI; particularly in August, it is apparent that total densities were distributed more evenly over the taxa in *Trapa* than in *Vallisneria*. The August plot for *Trapa* is for a community with fewer invertebrates and for a greatly decreased population of *Hyalella azteca* (Saussure), the most abundant taxon in July. This plot consequently illustrates greater evenness than the July *Trapa* plot or either of the *Vallisneria* plots.

Richness and similarity

A total of 50 taxa occurred across both sites over the two sampling dates, 34 in *Vallisneria* and 40 in *Trapa*. Richness, as the mean number of taxa, was similar between sites, for both months (Table 4). However, there was only limited overlap of taxa between these PMI communities. The relatively low similarity, C, in both months (Table 4) was probably influenced by abundant taxa that exhibited significant differences in densities (above). Also, some abundant taxa occurred in only one habitat or the other, e.g. Chrysomelidae, Leptoceridae, Hydroptilidae, Aphididae and Corixidae, which also contributed to lowering similarity. Lastly, Morisita's index omits single occurrences of taxa, further reducing similarity values.

Taxa that were predominantly or exclusively predaceous comprised a higher proportion of total density in *Trapa* than in *Vallisneria*: 15.1% vs. 8.3% in July, and 27.1% vs. 3.1% in August (Tables 2, 3).

Size

Both communities in both months were dominated by size class II (1.1–3.0 mm), with that size being at least twice as abundant as the next most abundant size class (Fig. 4). The increased density of *Vallisneria* PMI in
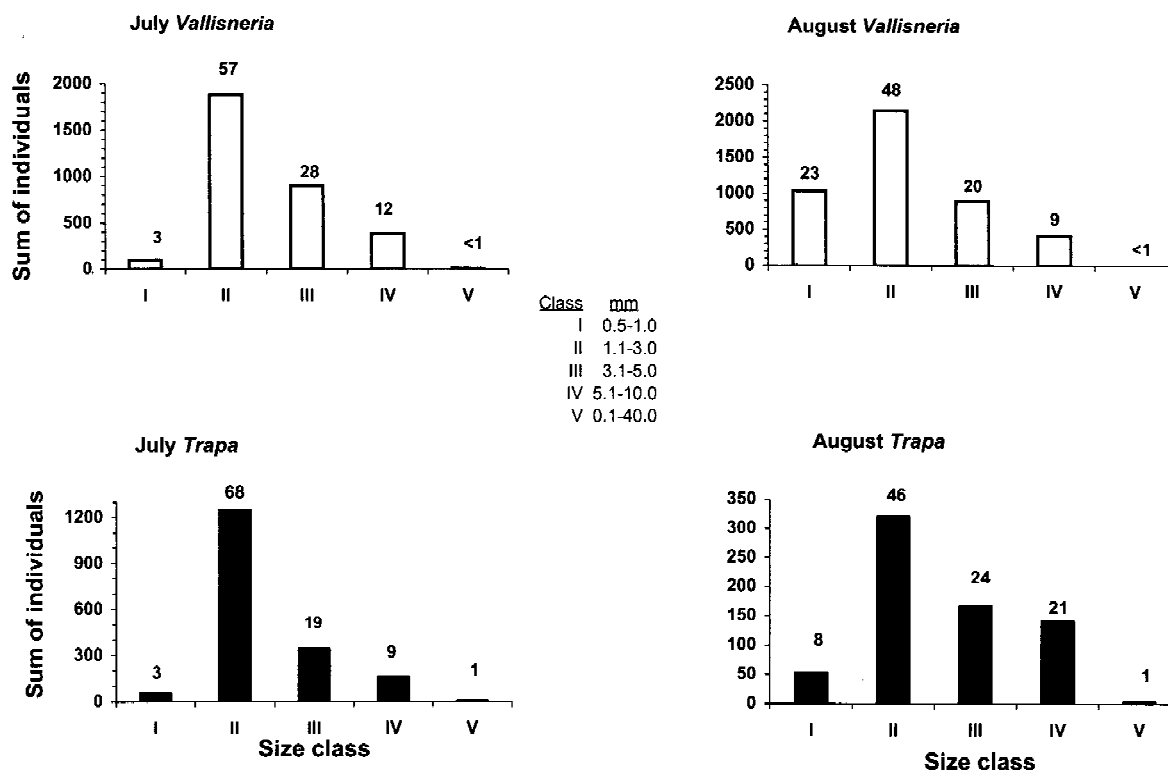
Figure 4. Size distributions of total abundance of phytophilous macroinvertebrates from two macrophyte beds. Comparisons of difference of distributions between sites and between months were all significant, at $p<0.01$ by the Kolmogorov–Smirnov comparison. Values above each bar are% of total abundance.

August was due largely to a great increase in class I, the greatest representation of this size for either community, either month. In contrast, *Trapa* PMI in August exhibited a greater proportion of the two largest size classes (22%), compared to July (10%) and to *Vallisneria* (9–13%). Kolmogorov–Smirnov tests (*D* statistic) of size class distributions were significant at $p<0.01$ for all four comparisons (*Trapa* vs. *Vallisneria* in July *D*=0.11, in August *D*=0.166, and between months for *Trapa* *D*=0.20 and *Vallisneria* *D*=0.22). The sensitivity of this test to differences in distributions is high when distributions have >1000 individuals, as in these samples. In July, the relative differences between size classes II and III likely accounted for much of the difference between the size distributions of *Vallisneria* and *Trapa*. In August, classes I and IV accounted for much of the difference between sites.

Plant mass

Mean standing crop ($\pm$ se) of *Vallisneria* was 31.6 ± 5.2 g dw/m^2 and of *Trapa* was 103.6 ± 11.4 g

dw/m^2. Mean *Vallisneria* mass from PMI samples was 67.0 ± 9.9 g dw/m^2 in July and 39.6 ± 8.3 in August; for *Trapa* it was 159.9 ± 16.5 in July and 150.3 ± 17.9 in August. These latter measures unlike standing crop, do not incorporate the spaces between rosettes in the beds, having been taken with a 25 cm diameter sampler.

Discussion

Density

The decreased density per water volume of *Trapa* PMI in August corresponds with a thinning of the *Trapa* bed after late July (pers. obs.). This was partially due to herbivory by the beetle *Galerucella nymphaeae* (Chrysomelidae), which has also been found on *Trapa* in Europe (Pemberton, 1999). A congener, *G. birmanica* Jacoby, is recognized as a major consumer of *Trapa* in Asia, particularly as adults (Lu et al., 1984; Pemberton, 1999). The reduction of PMI density per leaf area was equivalent to that per water volume. The

decreased density was manifested in population declines of previously abundant species, e.g. *Hyalella azteca* (Talitridae), *Caenis* sp. (Caenidae), *Caecidotea* sp. (Asellidae) and *G. nymphaeae*; Chironomidae, however, did not reflect this decline. *Hyalella* and *Caecidotea* are very mobile and may have become more visible to predatory fish as the floating canopy thinned, thereby permitting more light penetration. *Caenis* and *G. nymphaeae* metamorphosed into adults; *Caenis* became aerial, and *G. nymphaeae* continued to utilize *Trapa*. Larval mortality may have contributed to *G. nymphaeae's* decline, since it is conspicuous potential prey for surface feeding fish (Juliano, 1988), semiaquatic spiders, and possibly birds; all of these potential predators were observed at the surface of the *Trapa* bed. The larval stage is also particularly susceptible to drowning, and increased mortality is correlated with rainfall (Lu et al., 1984).

In contrast to *Trapa* PMI, *Vallisneria* PMI density increased from July to August, during which time this specie's density decreased (dry weights of *Vallisneria* from PMI samples decreased by 40%); concurrently, there were denser periphyton communities in August (pers. obs.). Greater algal food levels for grazers is thus a possible cause for the greater *Vallisneria* PMI total density in August and between *Vallisneria* PMI and *Trapa* PMI. Increased periphyton densities may have also reduced foraging efficiency of fish (Power et al., 1992). The increased PMI density in August compared to July was much greater on a leaf surface area basis (112%) compared to a water volume basis (24%). This may be due simply to the reduction in leaf surface area, without a large increase in PMI abundance. Alternatively, the higher PMI density per water volume may have been due to other factors, e.g. increased food base, reduced predation and increased egg hatchings. In contrast, Keast (1985) found a more direct correspondence between PMI abundance and the development and senescence of an aquatic plant bed in Ontario, with peak PMI abundance and aquatic plant biomass in mid-July; by late August, plants and invertebrates had greatly declined.

Taxa that were primarily responsible for the greater total density in *Vallisneria* include Gastropoda, Cladocera, Coenagrionidae, Hydroptilidae (August) and especially Chironomidae (Tables 2, 3). The Gastropoda included genera that were also found by Vincent et al. (1991) on *Vallisneria* in the St. Lawrence River. However, their comparison with *Myriophyllum spicatum* indicated no effect of plant species upon gastropod distribution.

The most relevant comparison of total density of *Vallisneria* PMI comes from Chilton & Margraf (1990), who found 100–220 ind/g dw in a monospecific *Vallisneria* bed, which is similar to densities found in this study (126–266 ind/g dw). Their methods were comparable (but see below), as was their study site, a backwater of the upper Mississippi River. Other studies revealed much lower densities, such as 3 ind/g dw by Andrews & Hasler (1943), but their sampling methods probably did not capture as high a percentage of PMI as techniques developed by subsequent investigators. Gerrish & Bristow (1979) found 2045 ind/m² leaf area on *Vallisneria* (but it is not known if this represents one or two sides of leaf area), lower than found in this study (4981–10 538 ind/m²). In both of these studies, *Vallisneria* may have been sampled from mixed species beds rather than monospecific beds. Neighbor plants of different species would likely influence PMI densities differently than neighbors of the same species.

In a tidal freshwater bay of the Hudson River, *Trapa* PMI total density was 1500–3000 ind/m² leaf area (two sides), or 9000–20 000 ind/m² water surface area during July and August (Schoeberl & Findlay, 1988; Findlay et al., 1989). This is substantially greater than seen in the present study, which may be related to differences in ecosystem characteristics between tidal and non-tidal sections of the Hudson River. In contrast, densities of *Trapa* PMI in Lago di Candia were about one-tenth of those in the present study (Cattaneo et al., 1998). However, as with the present study, PMI densities were significantly higher among submerged macrophytes (*Myriophyllum, Ceratophyllum* and *Najas*) than in *Trapa*; the sampling method was also similar to the present study.

Richness and similarity

The differences in percentages of taxa between habitats, plus the absence of certain taxa from one or the other habitat, influenced similarity, as measured by Morisita's index (C). The floating rosettes of *Trapa* created a semiaquatic habitat, which probably provided more suitable habitat for Arachnida, Coleoptera and Hemiptera, which include taxa that are semi-aquatic. All of these orders were observed in the field to be on *Trapa* leaves, at or above the water surface. The higher proportion and diversity of Arachnida, Odonata and Hemiptera in *Trapa* contributed to the greater and more diverse representation of invertebrate predators than in *Vallisneria*, as pre-

dicted. The thickly vegetated *Trapa* bed may have lead to less effective fish predation upon these fairly large invertebrates (Crowder & Cooper, 1982; Diehl, 1988).

Taxonomic richness was similar between the two sites and was also similar to those found in another study that compared *Trapa* PMI with submerged macrophyte PMI (Cattaneo et al., 1998).

Temporal variation in richness was apparent in both communities. From July to August, total richness declined by 10 taxa (21%) over both sites, which was reflected in decreased mean richness of both sites (Table 4). Most of the species that did not occur in August were rare in July, and all such species occurred at less than 50/m^3 in July (Table 2). Likely factors influencing their absence in August samples and changes in taxonomic richness are fish predation, metamorphosis to aerial stages and sampling error. For example, Odonata and Mollusca were more prevalent in these sites in July, and are recognized prey of pumpkinseed (*Lepomis gibbosus* (L.)) and brown bullhead (*Ictalurus nebulosus* (Leseur)) (Keast & Webb, 1966; Keast & Welsh, 1968; Laughlin & Werner, 1980). Pumpkinseed and bullhead were the only fish species at the *Trapa* site, and pumpkinseed was the most common at the *Vallisneria* site. Limited gut content analysis indicated that Mollusca were by far the most common diet items of adult pumpkinseed; Odonata were the most common diet items in bullhead (Feldman, 1993). It is possible that these fish species suppressed the populations of their preferred prey by August. Sampling error, which is dependent upon patchiness of invertebrate distributions, would be biased toward not sampling rare taxa.

Compared to prior studies that measured PMI and benthos richness, *Vallisneria* PMI richness in this study was relatively high. Using a similar level of taxonomic definition as the present study, mean taxonomic richness of *Vallisneria* PMI in the upper Mississippi in late July was 8.2±0.5, and in early September was 10.9±0.6 (Chilton, unpublished data), with a total of 27 taxa across the two sampling periods. The much lower richness in these samples compared to the present study was probably due to shorter length of plants sampled, and preservation only by refrigeration. *Vallisneria* PMI mean richness in this study was significantly higher than found at the same site the following year (Feldman, 1993), indicating expected annual variation in community structure. Studies that have compared PMI and benthos consistently show higher taxonomic richness among PMI (Gerking, 1957; Engel, 1985; Feldman, 1993), indicating the importance of aquatic plants for maintaining invertebrate diversity in littoral habitats.

Size

The examination of size structure in this study complements earlier and present findings that have shown differences in taxonomic distributions and abundance within and among different aquatic plant species. From July to August the size structure of *Vallisneria* PMI shifted toward smaller individuals, with a 10-fold increase in class I (0.5–1.0 mm, mostly Chironomidae; Fig. 4). All *Trapa* PMI classes declined in abundance, but its distribution shifted toward larger individuals, with classes III (3.1–5.0 mm) and IV (5.1–10.0 mm) comprising a larger proportion of the total. These results support the hypothesis that size distribution in *Trapa* would be skewed toward larger individuals than in *Vallisneria*. The differences may have resulted from the different taxa present between the two sites, exhibiting differing life cycles, and related differences in size and metamorphic stages. Some cohorts in *Trapa* that were too small to be captured in the sieves in July may have become large enough for capture in August. Conversely, in *Vallisneria*, some cohorts may have developed into adults and emerged from the river, leaving behind a higher proportion of smaller, immature insects. The same developmental changes may have led to changes in susceptibility to predation. Furthermore, the efficacy of different predators may have changed between months, which may have influenced the change in PMI size distributions.

Prey size is an important parameter in predicting fish diet (Werner & Mittelbach, 1981) and in determining fish feeding efficiency and growth (Bannon & Ringler, 1986). Sustained fish growth is often dependent upon the presence of large prey (Werner & Hall, 1976); indeed, prey size is recognized as constraining predator-prey relationships in open water (Strayer, 1991) and the littoral zone (Werner & Hall, 1976). Pumpkinseed sunfish (*Lepomis gibbosus*), in particular, rely heavily upon the littoral zone throughout their lives, as observed during this study, first for refuge from predators and later as adults, when snails on the plants become an important food (Mittelbach, 1984).

An outcome of size-selective feeding is that the size structure of the prey community can be determined by its predators. Introduction of predatory fish generally causes a reduction in mean body size of benthos, but some relatively small taxa may still experience more predation than larger ones (Strayer, 1991).

In benthic habitats, it appears that prey activity, exposure, density and defenses can override selection based upon size by foraging fish. Thus, it appears that there may not be as strong a relation between fish predation and invertebrate size structure for benthos as there is for zooplankton (Strayer, 1991). However, PMI may be more influenced by size-selective predation than benthos; data from Mittelbach (1981) show a much lower mean size of PMI compared with a nearby benthic community. In vegetated habitats visual feeders, e.g. sunfish, are known to "suppress large, active prey and enhance simpler, more cryptic forms" (Heck & Crowder, 1991). In the present study, juvenile and adult pumpkinseed sunfish were common, particularly at the *Vallisneria* site (Feldman, 1993), and given the evidence for their size-selective feeding, they may have influenced PMI size structure, especially at the *Vallisneria* site.

Conclusion

The structure of phytophilous macroinvertebrate communities clearly differs between the beds of *Vallisneria* and *Trapa* sampled. This is evident from comparisons of the presence and relative abundance of taxa (as Morisita's similarity index), from comparisons of total density, as well as densities of individual taxa, and from comparisons of size distributions. Some of the difference in structure may also be due to location effects, since the plant beds were not at the same site. However, prior studies also support the importance of plant morphology in influencing PMI community structure (Gerking, 1957; Keast, 1984; Engel, 1985). Temporal variations in PMI community structure were also apparent within each habitat. The differences in PMI community structure between aquatic plant habitats and over time may enhance the overall macroinvertebrate diversity of the upper Hudson River. Such differences may also affect ecosystem processes, e.g. the movement of substances through food chains, as with polychlorinated biphenyls (PCBs) in the Hudson River (Feldman & Titus, 2001).

Acknowledgements

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