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# Plant architecture and epiphytic macroinvertebrate communities: the role of an exotic dissected macrophyte

KENDRA SPENCE CHERUVELIL[1] AND PATRICIA A. SORANNO

*Department of Fisheries and Wildlife, 13 Natural Resources Building, Michigan State University,*
*East Lansing, Michigan 48824 USA*

JOHN D. MADSEN[2]

*US Army Engineer Research and Development Center, 3909 Halls Ferry Road,*
*Vicksburg, Mississippi 39180 USA*

MARLA J. ROBERSON

*Department of Fisheries and Wildlife, 13 Natural Resources Building, Michigan State University,*
*East Lansing, Michigan 48824 USA*

*Abstract.* The abundance of epiphytic macroinvertebrates on aquatic macrophytes can be influenced by different plant architecture types. For example, dissected plants can provide epiphytic macroinvertebrates more substrate for foraging and more cover from predators than undissected plants. Large changes in macrophyte community composition have the potential to strongly influence whole-lake macroinvertebrate abundance if overall plant architecture changes. For example, when the exotic macrophyte Eurasian watermilfoil (*Myriophyllum spicatum* L., EWM), a dissected plant, invades a lake and becomes dominant, fundamental changes in lake-wide plant architecture occur. We conducted a 6-lake field study and a meta-analysis to examine whether macroinvertebrate density and biomass varies predictably with plant architecture and, if so, whether these relationships are evident at the whole-lake scale when EWM dominates the plant community. We found that higher macroinvertebrate densities and biomass per g of plant were associated with dissected plants than undissected plants in both our field study and our meta-analysis of published studies. However, in our field study, macroinvertebrate densities and biomass per g of plant decreased as the % of EWM cover increased across lakes, although not always significantly. This result suggests that EWM provides different habitat for macroinvertebrates than native dissected plants. Therefore, the macrophyte community may support lower densities and biomass of macroinvertebrates when EWM is dominant at the whole-lake scale. Reduced abundance of macroinvertebrates could have strong impacts on other components of lake food webs.

*Key words:* Eurasian watermilfoil, *Myriophyllum spicatum*, epiphytic macroinvertebrates, plant architecture, macrophyte, meta-analysis.

Epiphytic macroinvertebrates are an important forage base for many species of juvenile fish that use macrophyte beds for cover and as a source for food (Keast 1984, Diehl and Kornijow 1998, Persson and Crowder 1998). However, epiphytic macroinvertebrate abundance and diversity are variable and sensitive to macrophyte abundance and community composition, making predictions of macroinvertebrate distribution, diversity, and abundance difficult (Gaufin et al. 1956, Downing and Cyr 1985). Macrophytes are diverse in form, and can be grouped according to architecture based on the number, morphometry, and arrangement of stems, branches, and leaves (Lillie and Budd 1992). Plant architecture may influence the colonization of epiphytic macroinvertebrates (Jackson 1997) and, therefore, may partly explain the relationship between macroinvertebrate abundance and submersed macrophytes. Macroinvertebrate densities are often greater on plants with dissected leaves than plants with undissected leaves (Krecker 1939, Andrews and Hasler 1943, Cattaneo and Kalff 1980, Dvorak and Best 1982). Dissected plants have a higher surface area to plant mass ratio and, therefore, may provide more habitat for macroinvertebrates,

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[1] E-mail address: spencek1@msu.edu

[2] Present address: S-242 Trafton Science Center, Minnesota State University, Mankato, Minnesota 56001 USA.

more food in the form of periphyton for grazing macroinvertebrates, or additional complexity, which offers better refuge from predators (Krull 1970, Gilinsky 1984, Pardue and Webb 1985). However, 2 recent studies found that macroinvertebrate density did not vary predictably with leaf dissection, but rather was plant-species specific (Cyr and Downing 1988a, b). Contrary to previous studies that examined macroinvertebrates in a single lake, these studies combined macroinvertebrates sampled from multiple lakes, which may have introduced interlake variability that could have masked patterns observed in previous single-lake studies. Because no studies have explicitly compared within- and across-lake variation in epiphytic macroinvertebrate abundance relative to plant architecture, we still do not know the role that plant architecture plays in determining macroinvertebrate abundance across lakes.

Further, previous within-lake studies have not been designed to address questions at the whole-lake scale. For example, many of these studies included relatively few plant species and made little attempt to characterize whole-lake plant community composition or cover, which makes it difficult to extrapolate macroinvertebrate abundance to the whole-lake scale. However, if variability across lakes is high and we wish to understand and manage lakes at the whole-lake scale, then situations may arise for which whole-lake plant composition may become especially important, such as when a single plant species or architecture dominates the macrophyte community. For example, Eurasian watermilfoil (*Myriophyllum spicatum* L., EWM), an exotic, submersed, dissected macrophyte species can become dominant in lakes. EWM was introduced to North America prior to 1950 from Europe and now occurs in many temperate North American lakes (Couch and Nelson 1985, Smith and Barko 1990, Creed 1998). EWM typically forms dense surface mats or canopies that suppress native plant growth and result in homogeneous macrophyte beds (Aiken et al. 1979, Madsen et al. 1991).

Several characteristics of EWM suggest that it should have high macroinvertebrate abundance. Along with having dissected leaves, EWM has a greater surface area for the same unit of biomass than 4 other plant species (Sher-Kaul et al. 1995). However, studies have shown that EWM supports fewer macroinvertebrates per g plant than native plant species, despite its greater surface area (Soszka 1975, Dvorak and Best 1982, Keast 1984, Cattaneo et al. 1998). Low macroinvertebrate densities on EWM are expected based upon research showing that homogeneous beds of other macrophyte species supported fewer macroinvertebrates than heterogeneous macrophyte beds (Brown et al. 1988). Unfortunately, we do not know whether differences in EWM cover in lakes affect total macroinvertebrate abundance at the whole-lake scale.

We address 2 questions in this study: 1) Do macroinvertebrate density and biomass vary predictably with plant architecture? and 2) Do lakes with a higher % of EWM cover have lower macroinvertebrate density and biomass at the whole-lake scale? We answered these questions with a field study of 6 lakes that varied in the % of EWM cover and with a meta-analysis of past studies examining the relationship between plant architecture and epiphytic macroinvertebrate abundance. We hypothesized 1) that macroinvertebrate density and biomass are related to plant architecture, with dissected plants having higher macroinvertebrate densities and biomass than undissected plants, and 2) that macroinvertebrate density and biomass per g of plant biomass would decrease as % EWM cover increases across lakes.

## Methods

### *Study area*

Epiphytic macroinvertebrates were sampled in July and August 1999 from 6 mesotrophic lakes in southern Michigan, USA, that exhibited a range of % EWM cover. The 6 lakes had similar summer mean values for Secchi depth, chlorophyll concentration, total N concentration, and total P concentration (Table 1), and were part of a study examining the direct and indirect effects of whole-lake fluridone (Sonar®, SePRO Corporation, Indianapolis, Indiana) treatments on plants, fish, and invertebrates. The 3 lakes with low % EWM cover (Camp, Big Crooked, and Lobdell) were treated in May 1997 with 5 ppb fluridone to reduce EWM abundance.

Fluridone treatments were unlikely to influence our results for several reasons. First, fluridone was applied at very low concentrations,

TABLE 1. Characteristics of the 6 Michigan study lakes. All water-quality data are averages from integrated epilimnetic samples taken monthly (June, July, and August 1999). Lakes are in order of increasing % Eurasian watermilfoil cover (see Table 4). Chl *a* = chlorophyll *a*, TP = total P, and TN = total N.

| Lake | Latitude, longitude (°) | Lake area (ha) | Mean depth (max., m) | % Littoral area | Secchi depth (m) | Pelagic Chl *a* (μg/L) | TN (μg/L) | TP (μg/L) |
|---|---|---|---|---|---|---|---|---|
| Camp | 43.11 N, 85.40 W | 53 | 7.3 (15) | 39 | 3.0 | 11.1 | 479 | 32.3 |
| Big Crooked | 43.03 N, 85.23 W | 64 | 4.5 (18.3) | 55 | 3.4 | 9.2 | 497 | 25.6 |
| Lobdell | 42.47 N, 83.50 W | 197 | 2.7 (21.3) | 83 | 3.5 | 3.6 | 431 | 16.7 |
| Heron | 42.81 N, 83.52 W | 53 | 3.4 (12.2) | 80 | 4.1 | 5.3 | 381 | 16.8 |
| Clear | 42.30 N, 85.16 W | 72 | 2.2 (4.6) | 89 | 3.6 | 11.6 | 544 | 23.0 |
| Big Seven | 42.49 N, 83.40 W | 64 | 3.2 (15) | 82 | 4.3 | 3.9 | 422 | 18.2 |

which are highly selective for EWM (Netherland and Getsinger 1995). Native plant cover was not reduced in the treatment lakes; in fact, it increased post-treatment. EWM biomass remained low for 2 y after the fluridone treatment (Getsinger et al. 2001). Second, fluridone is not toxic to macroinvertebrates (Muir et al. 1982, 1983, Hamelink et al. 1986, Haag and Buckingham 1991), and no difference in macroinvertebrate abundance was found between reference and treatment lakes (M. T. Bremigan, Michigan State University, East Lansing, Michigan, unpublished data). Last, we sampled 2 y after the fluridone treatment so that the littoral communities of the lakes should have recovered. Therefore, any differences in macroinvertebrate abundance found in this study should not be related to the herbicide treatments.

### *Sampling*

*Macrophytes.*—Plants were sampled in August 1999 in the 6 Michigan lakes using the point intercept method (Madsen 1999), which estimates plant cover, but does not quantify plant density or biomass. Each lake was mapped using a geographic information system and then overlaid with a grid of points to be surveyed (150–250 points per lake covering the entire lake). Points were located in the field with a global positioning system. Water depth was measured at each survey point, a 2-sided macrophyte rake was thrown, and plant species presence was recorded.

We determined 2 gradients using macrophyte data collected in 1999: 1) % dissected plant cover, and 2) % EWM cover. To develop the gradients, we included all submersed and floating-leaved macrophytes, thus excluding emergent and free-floating plants. Within the littoral zone (defined as the zone from shore to the deepest point at which plants consistently occurred), we then calculated the % of sites that were vegetated. Thus, we calculated the % of the vegetated littoral zone that had either dissected plants or EWM present to determine the gradients for each lake.

*Macroinvertebrates.*—We sampled epiphytic macroinvertebrates from the 5 dominant submersed plant species in each lake to characterize whole-lake macroinvertebrate density and biomass. We identified dominant plant species using vegetation survey results from the 6 lakes conducted in August 1998 (Getsinger et al. 2001). We adapted the final species list onsite for seasonal and interannual changes that may have occurred from 1998 to 1999. We sampled less common species in a few cases to collect at least 2 species within the 2 plant architecture types (dissected and undissected) and to include EWM in each lake. Therefore, the number of dissected and undissected plants sampled was similar across all lakes. We included *Potamogeton pectinatus* as dissected because it has thin branching leaves like the other dissected plants.

We sampled each lake for macroinvertebrates twice during the summer of 1999 (June 28–July 7 and August 16–24). To sample epiphytic macroinvertebrates, a snorkeller enclosed ~30 to 60 cm of an individual plant stem with a 500-μm-mesh bag sampler that measured 65 cm long by 24 cm in diameter (Cheruvelil et al. 2000). We sampled 13 individuals of each plant species for a total of 65 samples per lake per date (except Camp Lake in July when only 4 plant species were sampled), totaling ~800 samples. We chose our sample size based on power and sample size analyses from data collected in Heron Lake in August 1998 (Cheruvelil et al. 2000). We sampled epiphytic macroinvertebrates in each lake at 3 to 5 sites separated by >100 m. Each site was ~2 m deep, consisted of heterogeneous macrophyte beds, and formed approximately a 10 m radius around an anchored boat. We haphazardly sampled 2 to 4 stems from each of the 5 macrophyte species at each site. Samples were stored in a sealed plastic bag and kept cool and dark until further processing.

In the lab, we rinsed individual macrophyte stems with water to detach macroinvertebrates, and plants were dried at 105°C for 48 h and weighed to estimate plant biomass. Macroinvertebrates were preserved in 95% ethanol. We were interested in macroinvertebrate variability across plant species and across lakes, so it was not necessary to count the 13 individual samples. Therefore, the 13 replicate samples from each plant species for each lake were pooled, and subsamples from the pooled sample were used to estimate macroinvertebrate abundance and biomass per plant species. We subsampled by using a rotating apparatus developed by Waters (1969). Subsamples were counted until at least 140 individuals had been counted overall, which resulted in density and biomass estimates within 20% of the mean. Macroinvertebrates were identified to the lowest taxonomic level possible (genus, tribe, or family). Each individual was measured to the nearest μm using a drawing tube and digitizing tablet. Individual macroinvertebrate biomass was estimated using length–dry mass regressions from the literature (Rogers et al. 1977, Smock 1980, Meyer 1989, Burgherr and Meyer 1997) and unpublished data from G. G. Mittelbach (Michigan State University, East Lansing, Michigan).

## *Data analysis*

*Macroinvertebrates.*—Cumulative macroinvertebrate taxa richness was calculated for each lake using only those plant species that were sampled in both July and August (3–5 plant species per lake). Macroinvertebrates for all other analyses were standardized by plant dry mass (g), which allowed for the comparison of macroinvertebrates among different plant species and architecture types that exhibited large differences in biomass per stem of plant. We report abundance results for July and August separately rather than as an average because macroinvertebrate life cycles are short and periodic (Gaufin et al. 1956, Soszka 1975, Merritt and Cummins 1996). Thus, density, biomass, and species composition varied throughout the summer. Macroinvertebrate density (number of individuals per g dry plant biomass), biomass (dry mg per g dry plant biomass), average individual biomass (mg), and cumulative taxa richness were ln- transformed.

We tested whether macroinvertebrate density and biomass varied predictably by plant architecture using ANOVA and adjusted Bonferroni post-hoc comparisons. We used regression analyses across the 6 lakes to determine if macroinvertebrate density, biomass, individual biomass, and cumulative taxa richness were related to the % of EWM cover in the vegetated littoral zone.

## *Meta-analysis*

We performed a meta-analysis to quantitatively synthesize data from published studies on the relationship between epiphytic macroinvertebrate density and plant architecture. We included all field studies in which only lentic, epiphytic macroinvertebrates were sampled from submersed plants with dissected and undissected leaves. Sampling methods differed among studies, but we compared results from the studies by calculating a dimensionless overall effect size for each individual study (the ratio of the means of the 2 architecture types). Because we calculated a separate dimensionless metric for each study, the different sampling methods and different approaches should not confound comparisons across studies (Fernandez-Duque and Valeggia 1993, Gurevitch and Hedges 1999).

*Data selection.*—We found the published articles included in the meta-analysis using computer databases (Aquatic Sciences and Fisheries Abstracts [Cambridge Scientific Abstracts], Biological Abstracts, and Institute for Scientific Information Science Citation Index Expanded [ISI Citation Databases]). We identified and collected older articles not included in these databases from the reference sections of the more recent articles. These searches resulted in ~75 articles. We excluded articles that did not include all of the following data: 1) number of times macroinvertebrates were sampled, 2) sample date, 3) study location, 4) number of macrophyte species sampled, 5) number of individual plants sampled within each species, 6) sampler used, 7) organisms sampled, and 8) results for single plant species or plant architecture. This selection process resulted in data from 13 articles for our final analysis (Table 2). For articles that reported data in figure form only (Pip and Stewart 1976, Gerrish and Bristow 1979, Kornijow 1989, Chilton 1990), we scanned the graphs and interpolated the values using Scion Image software (1998. Scion Corporation, Frederick, Maryland).

Three of the articles included results from >1 lake or pond (Krull 1970, Cyr and Downing 1988a, Kornijow 1989), resulting in 18 lakes as independent observations. Cyr and Downing (1988a) and Krull (1970) averaged macroinvertebrate density across multiple lakes. Because these means included among-lake variability, meta-analyses were done with and without these 2 studies. Three articles (Andrews and Hasler 1943, Cyr and Downing 1988a, Cheruvelil et al. 2000) reported macroinvertebrate density from 1 sample date only. Four articles (Pip and Stewart 1976, Gerrish and Bristow 1979, Keast 1984, Chilton 1990) reported multiple estimates within a season (May–October), so we averaged densities across the season. For the 2 articles that reported multiple years of data (Soszka 1975, Kornijow 1989), we only used the final year of data to be consistent with all other studies that only had 1 year of data. The remaining articles presented single mean density estimates for the summer season. We obtained raw data from Cyr and Downing (1988a), but we removed littoral microcrustaceans from their dataset because no other studies included them. We also eliminated single samples that included >1 architecture type from Cyr and Downing (1988a).

*Data processing.*—We performed both weighted and unweighted meta-analyses because many of the articles did not provide variance estimates. Weighted meta-analysis incorporates sample variance into the overall effect size (using the variance as the weighting variable), whereas unweighted meta-analysis does not. Our weighted meta-analysis used the 6 lakes that had variance estimates and the 6 lakes in our field study after averaging across months to be consistent with all other studies. Two articles included in the weighted analysis reported variance estimates directly (Cyr and Downing 1988a, our study). We calculated variance for the other studies (Andrews and Hasler 1943, Mrachek 1966, Krull 1970, Kornijow 1989) by averaging macroinvertebrate density across >2 plant species within each architecture group (viewing plant species as replicates within architecture groups as in our study).

For both the weighted and unweighted meta-analyses:

$$\text{Effect size} = \ln\left[\begin{array}{l}(\text{Average macroinvertebrate density per plant biomass on dissected plants})\\ \div\ (\text{Average macroinvertebrate density per plant biomass on undissected plants})\end{array}\right]$$

(Cooper and Hedges 1994, Hedges et al. 1999). This natural-log response ratio is centered on 0 (Cooper and Hedges 1994, Hedges et al. 1999), so values >0 indicate that dissected plants have higher densities of macroinvertebrates than undissected plants on a plant biomass basis.

The weighted meta-analysis was performed with MetaWin (M. S. Rosenberg, D. C. Adams, and J. Gurevitch. 1997. MetaWin: statistical software for meta-analysis with resampling tests. Sinauer Associates, Sunderling, Massachusetts). MetaWin calculates weights for each effect size as (1/variance) and uses the weighted effect sizes for hypothesis testing. Because the weighted meta-analysis of 12 lakes included estimates of variance calculated in different ways, and the 6 lakes from our study, we grouped studies according to author and type of variance estimate and tested for differences between groups using $\chi^2$ tests. We calculated mean effect size and 95% confidence intervals (CI) for the 18 studies included in the unweighted analysis, and performed ANOVAs to examine whether mean effect size differed among study groups according to the number of lakes sampled (1 or multiple), study area (North America or elsewhere), number of plant species sampled, number of dates sampled (1, multiple, or unknown), organisms sampled (all macroinvertebrates, snails only, chironomids only), whether or not EWM was sampled, or decade sampled.

## Results

### *Macrophyte and macroinvertebrate communities*

Each of the 6 lakes in our field study had different plant assemblages, with a range of 13 to

TABLE 2. Published studies used in the meta-analyses. The number of times sampled is the number of times organisms were sampled within 1 season. The studies sampled all epiphytic macroinvertebrates unless otherwise denoted.

| Citation | Lake | Location | Plants sampled | Sampler[a] | No. of times sampled |
|---|---|---|---|---|---|
| Andrews and Hasler 1943 | Mendota | Wisconsin, USA | *Ceratophyllum demersum, Potamogeton pectinatus, Myriophyllum spicatum, Vallisneria americana, P. amplifolius, P. richardsonii, P. americanus* | Zippered net | Once |
| Cheruvelil et al. 2000 | Heron | Michigan, USA | *Myriophyllum spicatum, Potamogeton pectinatus, P. richardsonii, P. illinoensis, P. zosteriformis, Ranunculus* sp. | Mesh bag | Once |
| Chilton 1990 | Onalaska | Wisconsin, USA | *Myriophyllum spicatum, Vallisneria americana, Ceratophyllum demersum* | Mesh bag | Multiple[b] |
| Cyr and Downing 1988a | Champlain | Quebec, Canada | *Ceratophyllum demersum, Myriophyllum spicatum, Vallisneria americana, Najas flexilis, Elodea canadensis* | Box sampler | Once |
|  | Memphremagog | Quebec, Canada | *Myriophyllum spicatum, Vallisneria americana* | Box sampler | Once |
|  | 8 lakes: Brome, Des Isles, Echo, Fournelle, Ludger, Magog, Massawippi, Quenouilles | Quebec, Canada | *Elodea canadensis, Myriophyllum spicatum, Vallisneria americana, Potamogeton robbinsii, P. amplifolius, Utricularia* spp. | Box sampler | Once |
| Dejoux 1983[c] | Chad | Central Africa | *Potamogeton schweinfurthi, Najas* spp., *Ceratophyllum demersum* | Phytoisolator | Unknown |
| Gerrish and Bristow 1979 | Opinicon | Ontario, Canada | *Myriophyllum spicatum, Vallisneria americana, Potamogeton richardsonii* | Plastic bags | Multiple |
| Keast 1984 | Opinicon | Ontario, Canada | *Myriophyllum spicatum, Vallisneria americana, Potamogeton robbinsii* | Plastic bags | Multiple |
| Kornijow 1989 | Piaseczno | Poland | *Potamogeton praelongus, Myriophyllum alterniflorum, Ceratophyllum demersum, Elodea canadensis* | Self-made apparatus | Multiple |
|  | Glebokie | Poland | *Potamogeton lucens, Myriophyllum spicatum, Ceratophyllum demersum* | Self-made apparatus | Multiple |
| Krull 1970 | Montezuma Main Pool | New York, USA | *Ceratophyllum demersum, Potamogeton foliosus, P. pectinatus* | Ekman dredge and plastic bag | Multiple |
|  | Black Duck Pond | New York, USA | *Utricularia vulgaris, Elodea canadensis* | Ekman dredge and plastic bag | Multiple |

TABLE 2. Continued.

| Citation | Lake | Location | Plants sampled | Sampler[a] | No. of times sampled |
|---|---|---|---|---|---|
| | 3 ponds[d]: Montezuma Spring Hole, Reagan Pond, Labrador Pond | New York, USA | *Najas marina, N. flexilis, Myriophyllum spicatum* | Ekman dredge and plastic bag | Multiple |
| Mrachek 1966 | Clear Lake | Iowa, USA | *Ceratophyllum demersum, Potamogeton pectinatus, Najas flexilis, Myriophyllum spicatum, P. richardsonii, P. nodosus* | Net | Multiple |
| Parson and Matthews 1995 | Cannery Pond | Washington, USA | *Ceratophyllum demersum, Potamogeton pusillus, P. natans* | Net | Multiple |
| Pip and Stewart 1976[e] | Manitoba | Manitoba, Canada | *Potamogeton pectinatus, P. richardsonii* | Box-like sampler | Multiple |
| Soszka 1975 | Mikolajskie | Poland | *Elodea canadensis, Myriophyllum spicatum, Potamogeton perfoliatus, P. lucens* | Plastic bags | Multiple |

[a] Author's terminology
[b] Sampled 4 to 22 times
[c] Only chironomids sampled
[d] The 3 ponds in this study included plant species of only 1 architecture type, so we combined the 3 ponds for the meta-analyses
[e] Only snails sampled

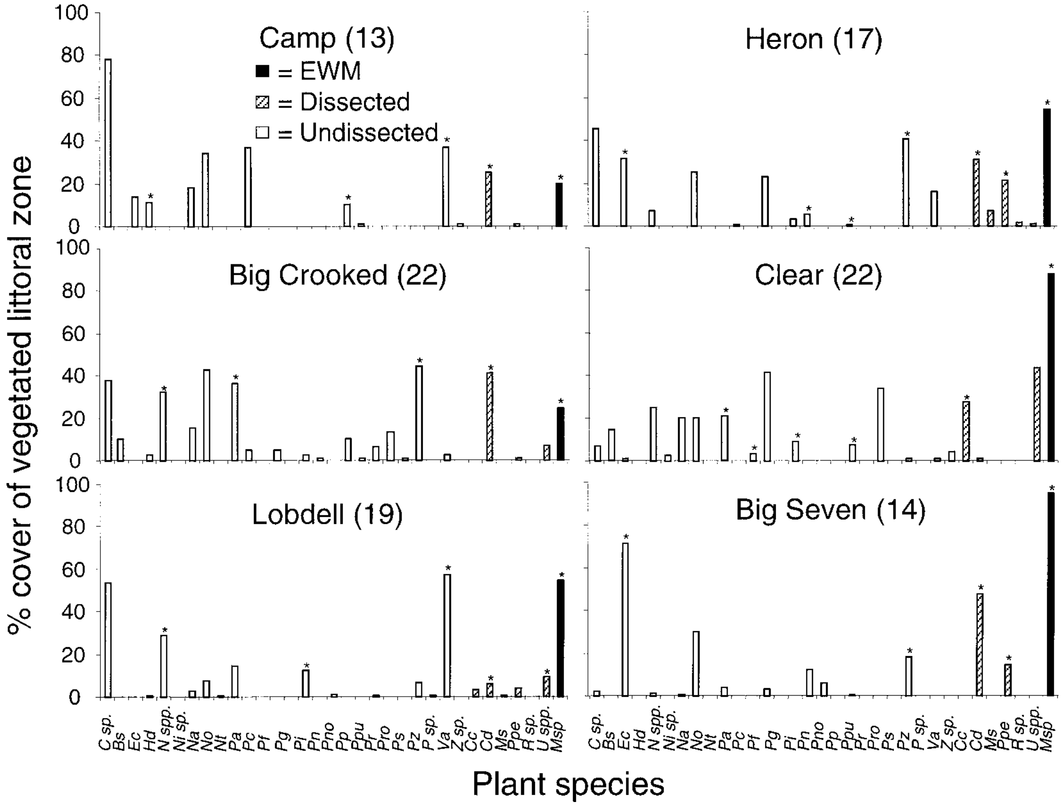

FIG. 1. Percent cover of plant species in the vegetated littoral zone of each study lake in August 1999. Lakes are in order from low % Eurasian watermilfoil (EWM) cover to high % EWM cover (Table 4). Species richness appears in parentheses beside each lake name. * = plant species that were sampled for epiphytic macroinvertebrates. Total % plant cover does not sum to 100% in each lake because >1 plant species could be found at any 1 point. Species: *C sp.* = *Chara* sp., *Bs* = *Brasenia schreberi* Gmel., *Ec* = *Elodea canadensis* Michx., *Hd* = *Heteranthera dubia* Jacq., *N spp.* = *Najas* spp. (including *Najas* sp., *N. flexilis* Willd., *N. guadalupensis* Spreng., and *N. marina* L.), *Ni sp.* = *Nitella* sp., *Na* = *Nuphar advena* Ait., *No* = *Nymphaea odorata* Ait., *Nt* = *Nymphaea tuberosa* Paine., *Pa* = *Potamogeton amplifolius* Tuckerm., *Pc* = *Potamogeton crispus* L., *Pf* = *Potamogeton foliosus* G., *Pg* = *Potamogeton gramineus* L., *Pi* = *Potamogeton illinoensis* Morong., *Pn* = *Potamogeton natans* L., *Pno* = *Potamogeton nodosus* Poir., *Pp* = *Potamogeton praelongus* Wulf., *Ppu* = *Potamogeton pusillus* L., *Pr* = *Potamogeton richardsonii* Benn., *Pro* = *Potamogeton robbinsii* Oakes., *Ps* = *Potamogeton strictifolius* Benn., *Pz* = *Potamogeton zosteriformis* Fernald., *P sp.* = *Potamogeton* sp., *Va* = *Valisneria americana* Michx., *Z sp.* = *Zannichellia* sp., *Cc* = *Cabomba caroliana* Gray, *Cd* = *Ceratophyllum demersum* L., *Ms* = *Myriophyllum sibiricum* Kom., *Ppe* = Potamogeton *pectinatus* L., *R sp.* = *Ranunculus* sp., *U spp.* = *Utricularia* spp. (including *U. intermedia* Hayne., *U. minor* L., and *U. vulgaris* L.), and *Msp* = *Myriophyllum spicatum* L.

22 submersed plant species in the vegetated littoral zones and a total of 33 species across lakes (Fig. 1). Each lake had different plant assemblages and plant species richness, but species richness was not related to % EWM cover ($r^2$ = 0.07, $p$ = 0.62). Macroinvertebrate density and biomass were variable across lakes and months, and there was no clear trend in dominant taxa with % EWM cover. A total of 32 macroinvertebrate taxa were identified across the 6 lakes, although most taxa were uncommon (averaging <1% of total macroinvertebrate density or biomass; Cheruvelil 2000). The 6 lakes had similar dominant (>70% biomass) epiphytic macroinvertebrate taxa (Table 3). Only 1 to 6 taxa made up >70% of total macroinvertebrate biomass across lakes and months, including amphipods, chironomids, gastropods, and oligochaetes. Some species of weevil (Curculionidae) feed on EWM and have contributed to its decline in

TABLE 3. Dominant macroinvertebrate taxa in the 6 Michigan study lakes in (A) July and (B) August 1999. These taxa made up >70% of the total macroinvertebrate biomass per g of plant in each lake. Taxa are numbered in descending order of dominance. Percent EWM cover for each lake is shown in parentheses.

| Camp (20) | Big Crooked (25) | Lobdell (55) | Heron (54) | Clear (88) | Big Seven (95) |
|---|---|---|---|---|---|
| **A: July** | | | | | |
| 1) Amphipoda<br>*Hyalella* | 1) Amphipoda<br>*Hyalella* | 1) Oligochaeta<br>Naididae | 1) Diptera<br>Orthocladiinae | 1) Oligochaeta<br>Naididae | 1) Oligochaeta<br>Naididae |
| 2) Diptera<br>Orthocladiinae | 2) Gastropoda<br>Hydrobiidae | 2) Gastropoda<br>Hydrobiidae | 2) Gastropoda<br>Physidae | 2) Gastropoda<br>Planorbiidae | 2) Diptera<br>Orthocladiinae |
| 3) Gastropoda<br>Physidae | 3) Gastropoda<br>Physidae | 3) Diptera<br>Orthocladiinae | 3) Gastropoda<br>Hydrobiidae | 3) Ostracoda | 3) Gastropoda<br>Planorbiidae |
| 4) Diptera<br>Chironomini | 4) Ostracoda | 4) Oligochaeta<br>Tubificidae | | 4) Gastropoda<br>Hydrobiidae | 4) Oligochaeta<br>Tubificidae |
| | 5) Oligochaeta<br>Naididae | | | 5) Amphipoda<br>*Hyalella* | 5) Amphipoda<br>*Hyalella* |
| **B: August** | | | | | |
| 1) Gastropoda<br>Hydrobiidae | 1) Amphipoda<br>*Hyalella* | 1) Oligochaeta<br>Naididae | 1) Gastropoda<br>Hydrobiidae | 1) Gastropoda<br>Hydrobiidae | 1) Amphipoda<br>*Hyalella* |
| 2) Amphipoda<br>*Hyalella* | 2) Gastropoda<br>Hydrobiidae | 2) Gastropoda<br>Hydrobiidae | | 2) Gastropoda<br>Planorbiidae | 2) Diptera<br>Chironomini |
| | 3) Trichoptera<br>*Nectopsyche* | 3) Diptera<br>Chironomini | | 3) Oligochaeta<br>Naididae | 3) Oligochaeta<br>Tubificidae |
| | 4) Diptera<br>Orthocladiinae | | | 4) Odonata<br>Coenagrionidae | 4) Diptera<br>Orthocladiinae |
| | 5) Odonata<br>Coenagrionidae | | | | 5) Gastropoda<br>Hydrobiidae |
| | 6) Gastropoda<br>Planorbiidae | | | | |

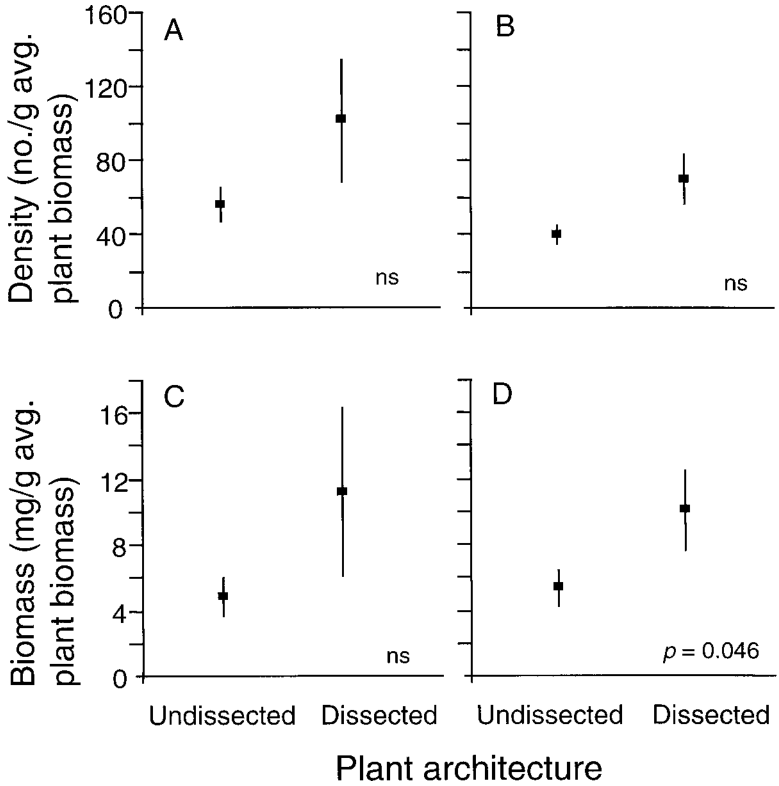

FIG. 2. Mean (±SE) macroinvertebrate density (A: July and B: August) and biomass (C: July and D: August) for the 2 plant architecture groups. n = 6 for each architecture type. ns = non significant (ANOVA). Statistics were performed on ln-transformed data.

some lakes (Trebitz et al. 1993, Creed and Sheldon 1995, Sheldon and Creed 1995). However, in our lakes, this family was only found in 1 lake in July and it accounted for only 0.5% of the total biomass.

### *Macroinvertebrates and plant architecture*

We found patterns of higher macroinvertebrate densities and biomass on dissected compared to undissected plants in both July and August in our 6 study lakes, although many of these comparisons were not statistically significant (Fig. 2). The results of our meta-analysis more strongly supported the hypothesis that dissected plants harbor more macroinvertebrates than undissected plants (Fig. 3A, B). In fact, the weighted meta-analysis showed that dissected plants had almost twice as many macroinvertebrates per unit of macrophyte biomass as undissected plants (Fig. 3B). We also found that studies grouped according to the number of plant species sampled, the number of samples within a season (once, multiple, unknown), the decade, the organisms sampled (all macroinvertebrates, chironomids only, snails only), and whether or not EWM was sampled were not significantly different from one another ($p > 0.11$). In addition, for the weighted meta-analysis, there were no differences between the 2 methods of estimating variance (with raw data or averaging across plant species within architecture groups, $p > 0.343$) or between studies conducted by ourselves versus other authors ($p > 0.825$). However, the 4 studies conducted outside of North America (Soszka 1975, Dejoux 1983, Kornijow 1989 [2 lakes: Table 2]) had significantly lower mean effect sizes than the 14 North American studies ($p = 0.017$). The 2 multiple-lake studies (Krull 1970, Cyr and Downing 1988a) had lower mean effect sizes than the other 16 studies and the difference was marginally sig-

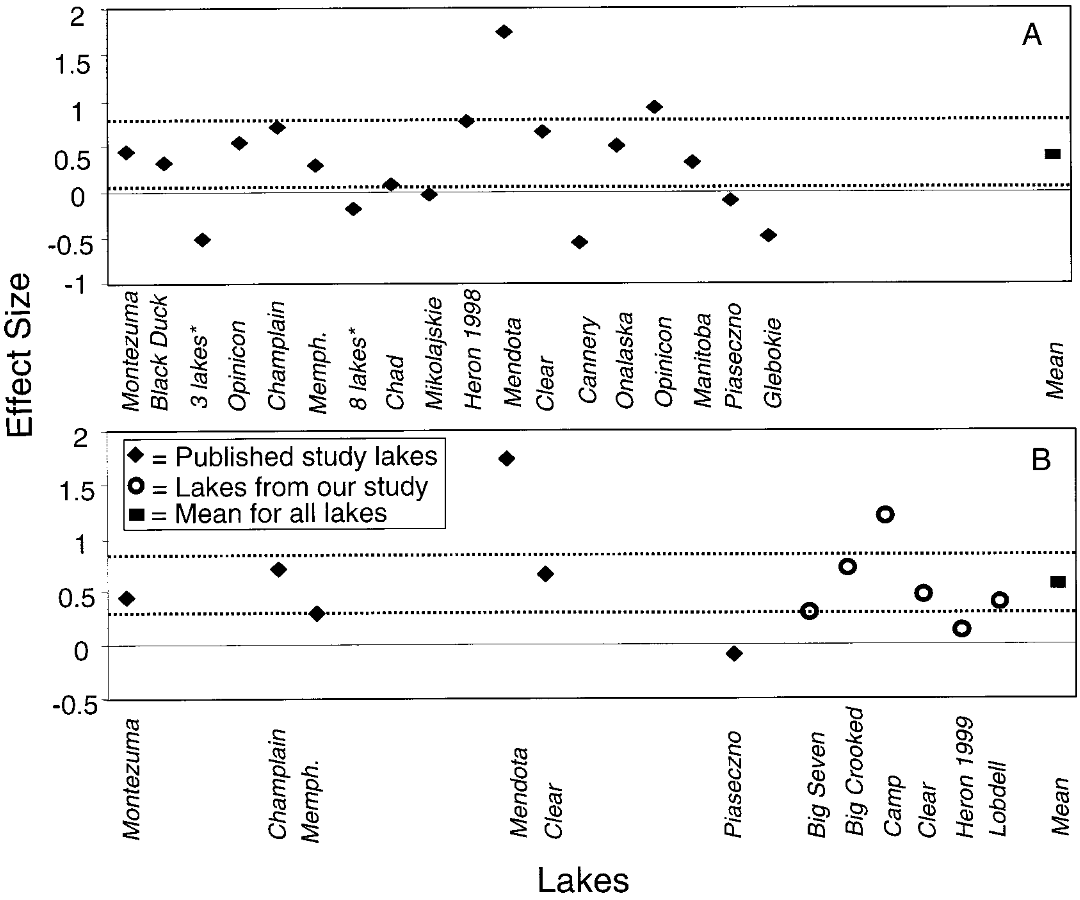

FIG. 3. Effect size (ln response ratio) for each study included in the unweighted meta-analysis (A) and the weighted meta-analysis (B). An effect size >0 means that dissected plants exhibited higher macroinvertebrate densities than undissected plants. Dashed lines are the 95% confidence intervals. * = those studies that averaged macroinvertebrate densities across multiple (4–22) lakes. Memph. = Memphremagog.

nificant ($p$ = 0.091). Upon removing these 6 studies, the mean effect size increased from 0.30 (95% CI: 0.01–0.59) to 0.55 (95% CI: 0.22–0.89).

### *Macroinvertebrates and EWM*

Our study lakes fell along a gradient of dissected plant cover ranging from 40 to 98% and a gradient of EWM cover ranging from 20 to 95% of the vegetated littoral zone (Table 4). Percent dissected plant cover along the 6-lake % EWM cover gradient significantly increased (Fig. 4). To examine how macroinvertebrates and EWM were related at the whole-lake scale, we regressed macroinvertebrate cumulative taxa richness, densities, biomass, and individual biomass for the 5 dominant plant species in each lake against the % EWM gradient. Cumulative species richness significantly decreased with increasing % EWM (Fig. 5) and macroinvertebrate density and biomass significantly decreased with increasing % EWM in July but not in August (Fig. 6A, B). Average individual biomass was negatively correlated with % EWM cover in both July and August (Fig. 6C).

## Discussion

### *Macroinvertebrates and plant architecture*

This study has 2 important conclusions. First, higher macroinvertebrate densities and biomass are associated with dissected plants than undissected plants. Use of both a field study and a

TABLE 4. Macrophyte patterns in the 6 Michigan study lakes. The % dissected plant cover and % Eurasian watermilfoil (EWM) cover refer to the % of the vegetated littoral-zone sites that had dissected plants and EWM present, respectively.

| Lake | % EWM cover | No. of dissected plants sampled[a] in July, August | % Dissected plant cover | % Vegetated littoral zone covered by sampled plants[a] |
|---|---|---|---|---|
| Camp | 20 | 2, 2 | 40 | 66 |
| Big Crooked | 25 | 2, 2 | 58 | 75 |
| Lobdell | 55 | 2, 3 | 62 | 84 |
| Heron | 54 | 2, 2 | 70 | 75 |
| Clear | 88 | 2, 2 | 93 | 56 |
| Big Seven | 95 | 3, 3 | 98 | 95 |

[a] Only the 5 plant species that were sampled for epiphytic macroinvertebrates

meta-analysis enabled us to examine patterns from multiple lakes and studies, which helped improve our understanding of the relationship between plant architecture and epiphytic macroinvertebrates. The results of our meta-analysis clearly supported the hypothesis that macroinvertebrate abundance is higher on dissected plants than undissected plants. However, the results of our field study demonstrated that, although dissected plants exhibited higher densities and biomass of macroinvertebrates than undissected plants, the differences were not always statistically significant. This result suggests that examining patterns across only 6 lakes may not be enough to detect differences because of high interlake variability; however, significant patterns emerge across multiple studies and more lakes. Thus, organizing plants into plant architecture categories should help reduce some of the inherent variability associated with estimating epiphytic macroinvertebrate abundance.

Our study was not designed to determine why most dissected plants harbor more macroinvertebrates than undissected plants, but others have postulated that it is because dissected-leaf plants have a higher surface area to plant mass ratio (e.g., Krull 1970, Pardue and Webb 1985, Gilinsky 1984, but see Sher-Kaul et al. 1995, Parsons and Matthews 1995). Whatever the underlying cause, leaf dissection is a much easier and a potentially more reliable metric than surface area to plant mass ratio, which is difficult to measure. Thus, grouping plants by architecture for the purposes of describing patterns of epiphytic macroinvertebrate abundance on macrophytes should be transferable to other whole-lake studies.

### *Macroinvertebrates and EWM*

Our 2nd important conclusion is that EWM dominance may alter the above relationship at the whole-lake scale. Lakes with high % EWM cover may have low macroinvertebrate abundance, despite high % cover of dissected plants. We found patterns of decreasing macroinvertebrate density, biomass, average individual bio-

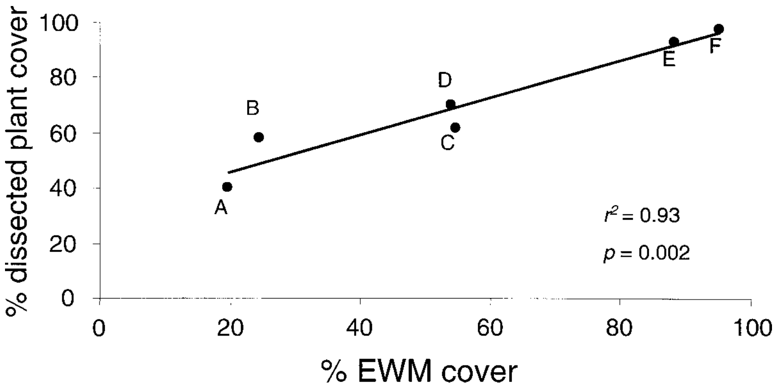

FIG. 4. Percent dissected plant cover along the Eurasian watermilfoil (EWM) cover gradient in August 1999. Lakes: A = Camp, B = Big Crooked, C = Lobdell, D = Heron, E = Clear, and F = Big Seven. Statistics were performed on ln-transformed data.

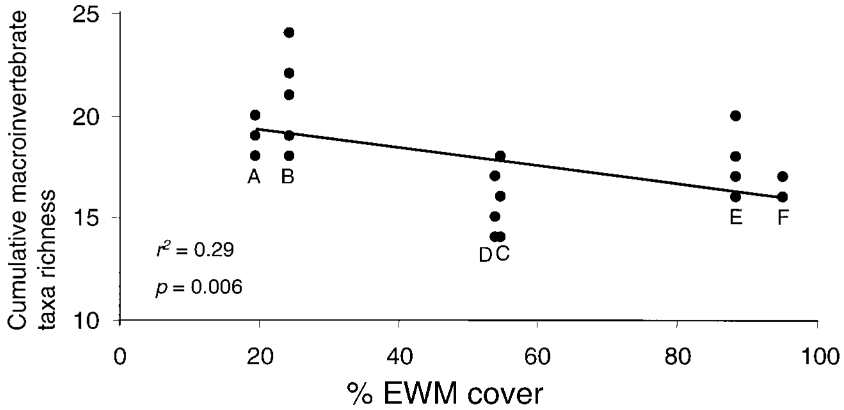

FIG. 5. Cumulative macroinvertebrate taxa richness along the Eurasian watermilfoil (EWM) cover gradient. Each data point represents cumulative (July and August 1999) macroinvertebrate taxa richness for each plant species within each lake. Lakes A to F as in Fig. 4 caption. For lakes A, C, and F there are multiple data points with the same taxa richness value. Statistics were performed on ln-transformed data.

mass, and cumulative taxa richness with increasing % EWM cover, although not all regressions were significant (Fig. 6). However, the fact that macroinvertebrate abundance never increased with increasing % EWM cover, and actually decreased significantly with increasing % EWM cover on some dates, suggests that EWM may alter the relationship between macroinvertebrate abundance and plant architecture. The mechanisms for these patterns are not clear, but there are several possible explanations. First, the results may be a consequence of EWM's dense homogeneous canopies, which can alter the underlying chemical and physical environment, making it inhospitable for some macroinvertebrate taxa (Unmuth et al. 2000). Second, it is possible that EWM exudes inhibitory chemicals. It has been suggested that other plant species induce a chemically mediated avoidance reaction in zooplankton (Lauridsen and Lodge 1996, Burks et al. 2001), although this idea has not been well tested for either epiphytic macroinvertebrates or for EWM. Our results demonstrate the need for further research to determine how EWM alters the relationship between plant architecture and macroinvertebrate abundance in North American lakes.

An alternative explanation for the observed decrease in macroinvertebrate abundance along the % EWM gradient is fish predation. Juvenile bluegill (*Lepomis macrochirus* Rafinesque) are often the dominant littoral-zone macroinvertebrate predators in these types of lakes (Mittelbach 1988). If bluegill densities were influencing the observed relationship between macroinvertebrate abundance and % EWM cover, we would expect to see an increase in juvenile bluegill density with increasing % EWM cover. However, juvenile bluegill density (measured as catch per unit effort) and % EWM cover were not related ($r^2$ = 0.333, $p$ = 0.301; R. D. Valley, Michigan State University, East Lansing, Michigan, unpublished data). Thus, bluegill predation does not appear to affect the observed macroinvertebrate abundance patterns.

Although we found decreases in macroinvertebrate abundance with increasing % EWM cover, not all regressions were significant. There are several possible explanations for these weak relationships. First, the lake lowest on the EWM gradient (Camp Lake) experienced a decrease in macroinvertebrate densities and biomass from July to August ($p$ = 0.001; Fig. 6A, B), which was caused by the emergence of odonates and chironomids in July (Cheruvelil 2000). Therefore, seasonal macroinvertebrate fluctuations may have contributed to our inability to detect a pattern with macroinvertebrates and % EWM cover across the 6 lakes in August. Second, macrophyte senescence, which starts in late summer for some plants, may have affected macroinvertebrate density and biomass, and our ability to detect patterns in August. Third, we sampled epiphytic macroinvertebrates from plants in relatively heterogeneous macrophyte beds, even in lakes dominated by EWM. However, macroin-

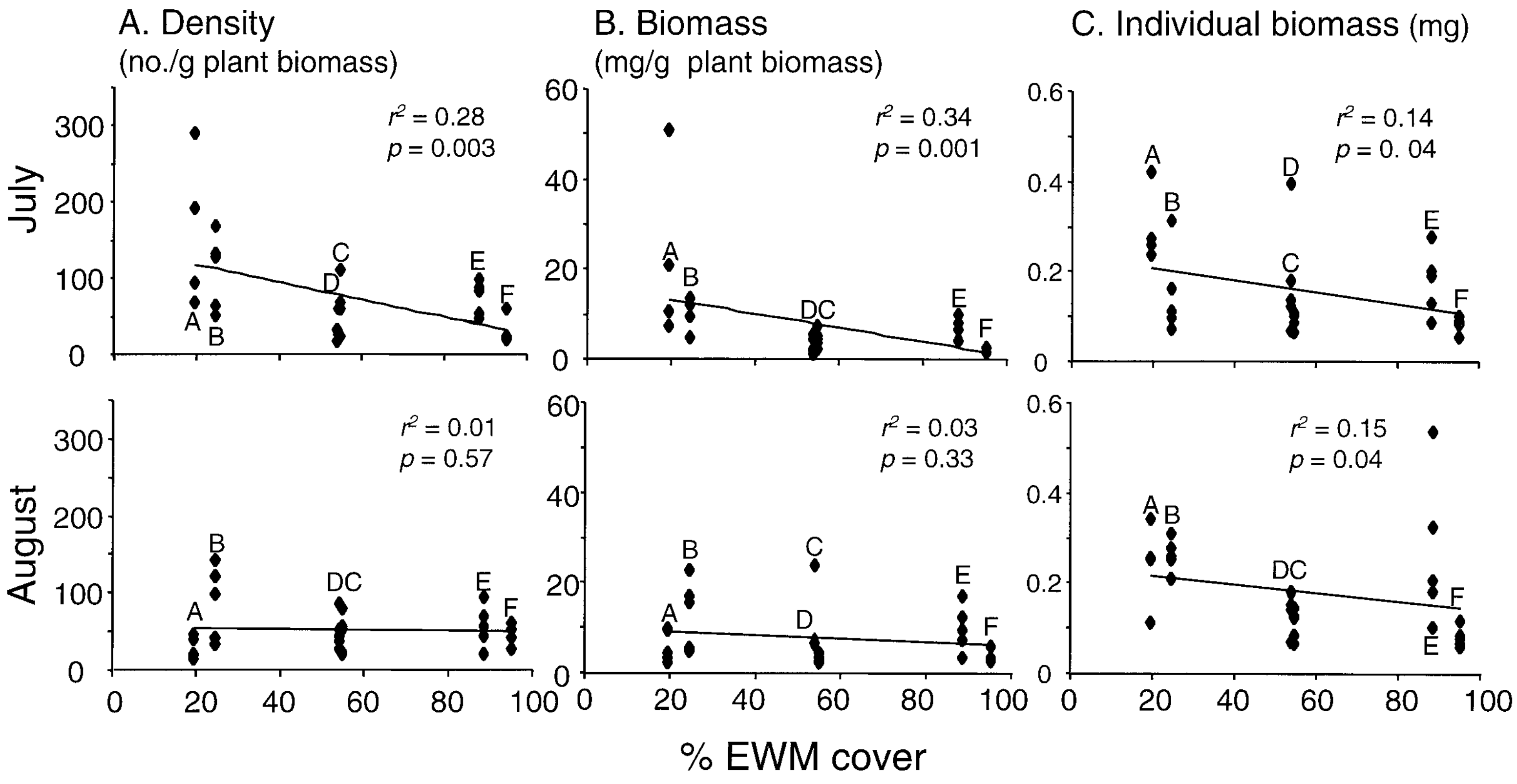

FIG. 6. Macroinvertebrate density (A), macroinvertebrate biomass (B), and average individual macroinvertebrate biomass (C) along the Eurasian watermilfoil (EWM) gradient in July and August 1999. Each data point represents the average density, biomass, or average individual biomass for each plant species within each lake. Lakes A to F as in Fig. 4 caption. Statistics were performed on ln-transformed data.

vertebrate abundance and taxa richness are low within the interior of dense homogeneous beds (Sloey et al. 1997). Therefore, we may have underestimated the effect of EWM on macroinvertebrate abundance by only sampling plants from heterogeneous beds. Had we sampled the characteristic dense mats of EWM, we might have seen stronger negative relationships between macroinvertebrates and % EWM cover.

In conclusion, additional research is needed to examine the complex relationship between macroinvertebrates and % EWM cover at the whole-lake scale. The results of our study have implications for lake food webs and management because macroinvertebrates are an integral component linking macrophytes, fish that consume macroinvertebrates, and piscivorous fish. Research on foodweb effects of EWM on multiple trophic levels should help improve lake management.

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