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EPIPHYTIC MACROINVERTEBRATES ALONG A GRADIENT OF EURASIAN WATER MILFOIL (*MYRIOPHYLLUM SPICATUM* L.): THE ROLE OF PLANT SPECIES AND ARCHITECTURE

By

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ABSTRACT

EPIPHYTIC MACROINVERTEBRATES ALONG A GRADIENT OF EURASIAN WATER MILFOIL (*MYRIOPHYLLUM SPICATUM* L.): THE ROLE OF PLANT SPECIES AND ARCHITECTURE

BY

KENDRA SPENCE CHERUVELIL

An important feature of lake foodwebs are the interactions between submerged macrophytes, macroinvertebrates, and the spread of the exotic macrophyte Eurasian water milfoil (hereafter milfoil, *Myriophyllum spicatum* L.). To examine these interactions, I had the following five objectives: 1) Design a sampler to sample macroinvertebrates associated with submerged plants; 2) Assess the sample size and statistical power to detect differences in macroinvertebrate density and biomass among plant species and architecture types; 3) Examine macroinvertebrate density and biomass on different species and architecture types of submerged plants; 4) Use meta-analysis to quantitatively synthesize the published literature on the relationship between macroinvertebrates and plant architecture; and 5) Examine patterns between macroinvertebrate density and biomass and percent cover of milfoil. I designed and used a mesh bag sampler to sample epiphytic macroinvertebrates from one lake in 1998 and six lakes in 1999, all located in southern MI. To plan my 1999 sampling, I used results from 1998 that indicated high power to detect differences between two plant architecture types associated with a moderate number of samples. Based on the 1999 field study and meta-analysis, I found higher macroinvertebrate densities and biomass on dissected plants than undissected plants. I also found that as percent milfoil increased, macroinvertebrate density and biomass decreased along the six-lake gradient.

DEDICATION

There are many, many special people who have helped me make this degree possible. Rather than name them all (and accidentally leave someone out!), I wish to dedicate this thesis to two pivotal people. First, my mother. Noel Lynne Hogarth Spence sacrificed her own Master's degree to marry my father and bring me into the world, and later gave up her demanding job to stay at home with me. I have learned so much from her, and continue to do so. Her dream that I get my M.S. has finally come true, and I owe her a lot. The second person I dedicate this piece of work to is my husband, Jubin Joseph Cheruvelil. He gave up everything he had and everyone he knew to marry me, and had enough faith for both of us that we would be happy and successful in Michigan. Through the last three years he has done much more than understand late nights and grumpy moods - he has encouraged and supported me every step of the way. Mom, Jubin – this one's for you.

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PREFACE

Chapters 1 and 2 are written as manuscripts that either has been (Chapter 1) or will soon be (Chapter 2) submitted. I would like to acknowledge my co-authors for their contributions.

Chapter 1:

Cheruvelil, K.S., P.A. Soranno, and R.D. Serbin. Macroinvertebrates associated with submerged macrophytes: Sample size and power to detect effects. Submitted to Hydrobiologia February 2000.

Chapter 2:

Cheruvelil, K.S., P.A. Soranno, J.D. Madsen, and M.J. Sanborn. The effects of Eurasian water milfoil invasion on interactions between plant architecture and epiphytic macroinvertebrates. To be submitted to Canadian Journal of Fisheries and Aquatic Sciences August 2000.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure

Figure

Figur

Figur

Figu

Figu

Cor

Fig

INTRODUCTION

To fully understand lake ecosystems, ecologists must concentrate not on individual ecosystem components, but examine the many complex inter-relationships between components. Complex interactions result from multiple pathways linking organisms and abiotic resources, and involve both direct and indirect effects and time lags (Carpenter 1988). An example of a complex lake interaction occurs among macrophytes, macroinvertebrates, fish, and humans. 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 Kornijow1998; Persson and Crowder 1998). However, macrophytes are diverse in shape and form, and their role in the food web is dependent on their abundance and community composition, both of which are affected by human management practices (Olson et al.1998).

Interactions among macrophytes, macroinvertebrates, and fish

Specifically, the interaction between juvenile bluegill sunfish (*Lepomis macrochirus*) and its major predator, the largemouth bass (*Micropterus salmoides)* depends on macrophyte populations. Adult bluegills make use of macrophytes for cover and make daily migrations from the pelagic zone where they feed on zooplankton, to the edges of the littoral zone where they are more protected from predators (Werner and Hall 1988). Juvenile bluegills also use macrophytes for cover and food. They feed on epiphytic macroinvertebrates within the vegetated littoral zone where they compete with young-of-year largemouth bass for epiphytic macroinvertebrates until bass reach a sufficiently large size to make the switch to the more energetically profitable fish diet (Olson et al. 1995).

Questions still surround this macrophyte-mediated interaction between macroinvertebrates and fish. Mittelbach (1988) experimentally studied the effects of fish on macroinvertebrates in a natural lake, where predator and prey have co-occurred for many generations. He found that the fish in this lake had strong effects on macroinvertebrate size structure, little or no effect on species richness, and variable effects on total macroinvertebrate densities (Mittelbach 1988). Macroinvertebrates, in turn, can affect fish abundance and growth. Crowder and Cooper (1982) found that bluegill in experimental ponds with intermediate macrophyte density exhibited higher growth than bluegill in low or high plant density ponds because at low macrophyte densities there was insufficient food and at high densities fish search and capture times were long. However, laboratory and mesocosm studies show that plant density does not influence bluegill growth beyond relatively low densities owing to the interaction between capture probabilities and macroinvertebrate densities (Savino et al. 1992). Therefore, high plant densities may have either no effect or a negative effect on bluegill growth, which is driven by both macrophyte and macroinvertebrate densities.

Most studies examining interactions among fish and macroinvertebrate prey have either considered the effects of introduced fish in a previously fishless system (Crowder and Cooper 1982), or were conducted in artificial ponds (Savino et al. 1992). In addition, most studies concentrate on the effects of macrophyte density or biomass only, even though it has been suggested that macrophyte species composition, architecture, and growth form all have effects on fish foraging (Dionne and Folt 1991; Dibble and Harrel 1997). We know surprisingly little about the potential effects of submerged macrophyte

species composition, architecture, and growth form on macroinvertebrate colonization, and how these effects are translated up the food chain to fish.

Macrophytes and epiphytic macroinvertebrates

Macrophytes, the largest sessile organism in fresh water ecosystems, have large effects on physical, biogeochemical, and biotic habitats (Carpenter and Lodge 1986; Engel 1990; Barko and James 1998). The most important physical effects of macrophyte structure are those on 1) light: extinction coefficients vary among plant species and significantly alter the depth profile of photosynthesis, 2) temperature: vertical gradients within macrophyte stands are much steeper than neighboring unvegetated areas, 3) water flow: flow is reduced among macrophyte beds, and 4) substrate: macrophyte beds enhance deposition of fine sediments that would otherwise be eroded (Carpenter and Lodge 1986; Engel 1990; Barko and James 1998). Biogeochemically, macrophyte growth alters 1) diel and annual oxygen dynamics, 2) dissolved inorganic carbon speciation and pH, 3) dissolved organic carbon levels, and 4) dissolved nutrient levels such as the limiting nutrient, phosphorus (Carpenter and Lodge 1986; Engel 1990; Barko and James 1998). In addition, macrophyte decomposition changes the biogeochemical habitat through 1) the release of dissolved substances such as organic carbon, phosphorus, and nitrogen, 2) deoxygenation, and 3) sediment accretion (Carpenter and Lodge 1986; Engel 1990; Barko and James 1998).

The effects of macrophytes on biotic interactions are dependent upon macrophyte physical structure, biomass and productivity, which all vary substantially within and among lakes (Crowder and Cooper 1982; Carpenter and Lodge 1986; Engel 1990). The level of productivity drives how much organic carbon macrophytes release, which in turn

provides a substrate for periphyton and macroinvertebrates. In turn, periphyton exchange dissolved nutrients with the water, assimilate phosphorus released from decomposing macrophytes, and provide food for many macrophyte-associated grazers. Commonly these macroinvertebrate grazers use macrophytes for food, refuge from predation, oviposition sites, and access to the air-water interface (Carpenter and Lodge 1986; Engel 1990; Newman 1991; Merritt and Cummins 1996).

The relationship between macroinvertebrates and submerged macrophytes can be partly explained by macrophyte physical structure, also known as architecture. Submerged macrophytes can be grouped according to architecture based on plant morphology (the number, morphometry, and arrangement of stems, branches, and leaves; Lillie and Budd 1992). Macrophytes are diverse in shape and form, and the architecture of plants has been suggested to influence the importance and colonization of epiphytic macroinvertebrates (Jackson 1997). Specifically, plants with finely dissected leaves have been found to support more macroinvertebrates than plants with broader, undissected leaves (Krecker 1939; Andrews and Hasler 1943; Gerking 1957; Mrachek 1966; Gerrish and Bristow 1979; Cattaneo and Kalff 1980; Dvorak and Best 1982). This pattern may occur because dissected-leaf plants have a higher surface area to volume ratio and therefore provide more habitat for macroinvertebrate colonization, more food for grazing macroinvertebrates in the form of periphyton, or additional complexity which offers better refuge from predators (Krull 1970; Pardue 1973; Dvorak and Best 1982; Gilinsky 1984; Jackson 1997). In fact, with surface area held constant, Jeffries (1993) found that habitat complexity (measured by fractal dimensions) is an important factor in determining invertebrate densities on macrophytes of differing morphologies.

Whereas many studies have found that dissected-leaf plants support more macroinvertebrates than undissected-leaf plants (Krecker 1939; Andrews and Hasler 1943; Gerking 1957; Mrachek 1966; Gerrish and Bristow 1979), a more recent study found that macroinvertebrate density did not vary predictably with leaf dissection across multiple lakes (Cyr and Downing 1988a and b). Instead, macroinvertebrate density was plant species-specific and related to plant biomass rather than dissection (Cyr and Downing 1988a and b). In their study of high surface area, finely divided, and thinly leafed plants, Parsons and Matthews (1995) suggest that the nature of the colonizable surface (soft or hard stems, brittle or pliable leaves, whorled or non-whorled leaves) is at least as important as the surface area. In addition, a study relating biomass and surface area of six submerged plants did not find that all dissected-leaf plants had higher surface areas than plants with undissected leaves (Sher-Kaul et al. 1995). This lack of consensus has contributed to the many questions that remain regarding the macroinvertebrate-macrophyte relationship.

Because macroinvertebrate densities are much higher in vegetated areas than open–water areas, these organisms are an extremely important component of lake food webs (Gerking 1957; McLachlan 1969; Krull 1970; Biggs and Malthus 1982; Watkins et al. 1983; Pardue and Webb 1985; Engel 1988; Jackson 1997). Although we recognize the importance of epiphytic macroinvertebrates and the macrophytes they colonize, the relationship between macrophytes and epiphytic macroinvertebrates, and the roles these organisms play in lake food webs has been difficult to quantify (Downing and Cyr 1985), leading to uncertainty and misinterpretation of the importance of epiphytic macroinvertebrates in lake ecosystems. This uncertainty is partly because sampling

macroinvertebrates on submerged plants is difficult. Many sampling methods are expensive, cumbersome, time consuming, and often require trained SCUBA personnel, which can limit the number of replicates taken (Mittelbach 1981a; Downing 1986; Creed and Sheldon 1992; Galanti 1995). Other methods are semi-quantitative because the sampling method disturbs the plants causing a loss of organisms that does not occur consistently and thus cannot be quantified (e.g. Krecker 1939; Rosine 1955; Schramm and Jirka 1989; Beckett et al. 1992). Also, many samplers combine benthic and epiphytic macroinvertebrates, not allowing for the separation of organisms between these two very different habitats (e.g. Hanson 1990; Hargeby 1990; James et al. 1998). In addition to these sampling issues, most studies have sampled only one lake, a small number of plant species, or have not used comparable methods to sample, process, analyze, and report data (e.g. macroinvertebrates expressed as density per plant, density per plant biomass, density per plant surface area, density per unit bottom surface, or density per unit water volume; Downing 1984; Kornikova 1971; Downing and Cyr 1985; Jackson 1997). Therefore, it is difficult to determine what factor(s) contribute to the different study conclusions.

To further complicate the study of epiphytic macroinvertebrates, these organisms exhibit large plant-to-plant variability. This variability has been attributed to predation, periodic macroinvertebrate emergence, irregular plant density, irregular plant species distribution, seasonal plant succession, fluctuations in macroinvertebrate food supply, appearance of new macroinvertebrate broods, natural mortality, and occurrence of macroinvertebrates of the same species but of different size (Gaufin et al. 1956; Mracheck 1966; Soszka 1975). This variability makes replication important, especially

when population densities are low or a small sampler is being used (Resh 1979; Downing and Cyr 1985). Although estimates of statistical power in ecological studies have been reported in some recent studies (e.g. Chick and McIvor 1994; Carpenter et al. 1995a; Johnson 1998), these important and biologically relevant statistics are still too seldom calculated and, in particular, have not been examined for studies of epiphytic macroinvertebrates.

Eurasian water milfoil

Eurasian water milfoil (hereafter milfoil, *Myriophyllum spicatum L.*) is an exotic submerged macrophyte found in much of temperate North America. Milfoil was introduced to North America prior to 1950 from Europe and by 1985 was reported in 33 states, the District of Columbia, and the Canadian Provinces of British Columbia, Ontario, and Quebec (Couch and Nelson 1985). Milfoil forms dense surface mats, or canopies, that suppress native plant growth, and lead to homogeneous macrophyte beds (Aiken et al. 1979; Madsen et al. 1988), in addition to interfering with recreational swimming and boating (Newroth 1985). Because milfoil has three mechanisms of propagation, (seed production, stolon formation, and fragmentation; Madsen and Smith 1997) and can grow in water from 1 - 10 m deep, it has spread rapidly throughout North America (Aiken et al. 1979). Seeds serve as long-term mechanisms of reproduction, enabling the species to survive protracted periods of dormancy (Madsen 1991). Stolons (stems that form adventitious roots) extend outward from the parent plant and produce new plants in the immediate area, thus allowing populations to disperse locally over distances of a few meters or less (Madsen et al. 1988; Madsen and Smith 1997). Fragmentation, another type of vegetative clonal propagation, is the predominant means

of dispersal over longer distances (Madsen et al. 1988). The two types of fragmentation that milfoil exhibit are 1) autofragmentation - self-induced abscission of shoot apices, generally after attaining peak biomass, and 2) allofragmentation - mechanical breakage of the plant stem by disturbances in the water, such as those generated by mechanical harvesters, boats, swimmers, animals, and wave action (Madsen and Smith 1997). These three mechanisms of propagation allow milfoil to spread quickly.

Because macrophyte structural complexity is species-specific, certain species provide more substrate for macroinvertebrates and cover for fish (Cyr and Downing 1988a). Milfoil is a dissected-leaf plant, and dissected-leaf plants usually have higher macroinvertebrate densities associated with them (Krecker 1939; Andrews and Hasler 1943; Gerking 1957; Mrachek 1966; Gerrish and Bristow 1979; Cattaneo and Kalff 1980; Dvorak and Best 1982). For the same unit of biomass, milfoil also has a higher surface area than four other native plant species (*N. obtuse, P. lucens, P. perfoliatus, P. pectinatus*; Sher-Kaul et al. 1995), and a low frequency of interstices (Dibble et al. 1996). However, contrary to these findings, milfoil has been found to support fewer invertebrates than native plant species (Soszka 1975; Keast 1984; Cattaneo et al.1998). Even within a milfoil bed, macroinvertebrate density differs. Macroinvertebrate density, biomass, and taxa richness is higher in the upper and edge areas than lower and center areas (Sloey et al. 1997). Low macroinvertebrate densities associated with milfoil may be because milfoil forms dense, homogeneous vegetation beds, which have been shown to support lower densities of epiphytic macroinvertebrates (Brown et al. 1988). Dense, mat-forming, homogeneous milfoil beds may also reduce diurnal and seasonal fish movement by acting as a barrier (Crowder and Cooper 1982; Keast 1984; Trebitz et al.

1996). In fact, Lyons (1989) has attributed a decline in small littoral zone fish species diversity in Lake Mendota in part due to the invasion of milfoil. Thus, excessive milfoil growth affects both the fish forage base and habitat, which can result in large disruptions in littoral zone food webs.

There have been some reports of natural milfoil declines (Lake Wingra and southern Ontario lakes; Carpenter 1980; Painter and McCabe 1988; Trebitz et al. 1993), but the continued spread of this exotic species, and the possible recreational and ecological ramifications of its spread, have prompted much research into milfoil ecology, biology, and management (e.g., Keast 1984; Madsen et al. 1988; Smith and Barko 1990; Chilton 1990; Trebitz et al. 1993; Madsen and Smith 1997). For example, there have been many studies on the relative importance of milfoil's various methods of reproduction to its regional expansion and the implications of those reproductive strategies for milfoil management (Madsen et al. 1988; Madsen and Smith 1997). Due to its multiple propagation mechanisms, traditional management tools such as harvesting without plant removal, derooting, dredging, and drawdown can actually promote expansion of milfoil (Cooke et al. 1990; Smith and Barko 1990). To date, studies have not provided managers with a clear framework for managing milfoil for the combined purposes of fisheries, recreation, and water quality, all of which are negatively impacted by milfoil invasions (Keast 1984; Newroth 1985; Carpenter and Lodge 1986).

A potential management option for controlling milfoil is the use of an aquatic herbicide that is selective for milfoil. Sonar® (active ingredient fluridone, SePRO Corporation, Indianapolis, IN) is a candidate for such an approach. Relative to most native aquatic plant species, milfoil is highly susceptible to low concentrations of

fluridone, increasing the potential for selective plant control (Netherland and Getsinger 1993). Sonar® is relatively non-toxic but must be applied to the whole lake. However, little is known about the direct and indirect effects of this type of whole lake herbicide treatment on the native macrophyte communities, the associated macroinvertebrate communities, and the subsequent effects on fish populations. Past studies of the indirect effects of Sonar® in two Minnesota lakes reported negative impacts on water quality, macroinvertebrates (Delong and Mundahl 1996), and small littoral zone fish diversity, but positive effects on larger fish growth (Pothoven 1996; Pothoven 1999).

As a result of remaining questions and insufficient data regarding the direct and indirect effects of Sonar® treatments, many states, including Michigan, have restricted Sonar® use. In May 1997, the Michigan Department of Environmental Quality (DEQ), the U.S. Army Corps of Engineers (USAE), Michigan State University (MSU), two private environmental consulting firms, and a lake management interest group began a study to determine the direct and indirect effects of whole-lake, low-dose Sonar® treatments (5 ppb) on plant, fish, and invertebrate communities. The USAE examined the direct effects of Sonar® treatments on macrophytes, while the MSU research group continues to examine the indirect effects of Sonar® on invertebrate and fish populations.

A whole-lake ecosystem experiment

An ecosystem approach is most relevant to study the inherently complex linkages between macrophytes, invertebrates and fish. In the past, there have been many studies of particular macrophyte-mediated processes conducted at scales less than whole-lake (Nichols and Keeney 1973; Dale and Gillespie 1977; Carpenter and Adams 1979), small-scale studies of the consequences of macrophyte management, especially by herbicides

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(Sheldon 1986; Netherland and Getsinger 1993), and modeling exercises examining ecosystem responses to macrophyte manipulations (Mittelbach 1981b; Trebitz and Nibbelink 1996). Although many important hypotheses have emerged from these studies, the interactions among macrophytes and their management, macroinvertebrates, and fish cannot be fully understood without whole-lake experiments in which macrophytes are manipulated and the response of the ecosystem is measured (Carpenter and Lodge 1986, Oslon et al. 1998). The Michigan Sonar® project presented a unique opportunity to participate in such an experiment, using multiple treatment and reference lakes to examine the direct and indirect effects of an herbicide treatment on multiple lake trophic levels.

Whereas ecosystem studies provide the opportunity to study real systems with all of their intrinsic complexity under realistic spatial and temporal scales (Carpenter et al. 1995b; Carpenter 1996), that same complexity means all of the important processes may not be measured or even detected. This complication can make the interpretation of ecosystem study results difficult, unless all competing hypotheses have been identified and tested separately. In many cases, conclusions are based on inference and the experiment may not conclusively show that a particular process or mechanism is responsible. Another drawback of ecosystem experiments is that it is often too costly to replicate these studies and rigorous controls may not exist. The experiments are also subject to variability beyond the control of the experimenter, such as the effects of variable weather, which can complicate the interpretation of results (Carpenter 1989).

Because of these problems, ecosystem experiments do not have the same level of sensitivity and precision of lab experiments, and often only a large response to a

treatment can be detected over natural variability (Carpenter 1989). Despite these inherent drawbacks, freshwater ecosystem experiments have successfully been used to address the responses of both communities and biogeochemical processes to a variety of stresses (Carpenter et al. 1995b). Most recently, Olson et al. (1998) used a multi-lake experiment to study the value of managing macrophytes to improve fish growth.

I designed my study on epiphytic macroinvertebrates keeping these potential drawbacks of ecosystem experiments in mind. Using data from one lake sampled in summer 1998, I estimated the statistical power and sample size necessary to detect differences in macroinvertebrate density and biomass among plant species and architectures. During summer 1999, I sampled six lakes, took approximately 75 replicate samples within lakes, and pooled macroinvertebrate samples within plant species in hopes of decreasing plant-to-plant variability so that I might better detect lake-to-lake variability. I also recognized the potential confounding factors inherent in my study. For example, treatment lakes in my study were subjected to additional plant management strategies by riparian lake owners, such as other herbicide applications and mechanical harvesting. Therefore, I cannot be certain that differences between reference and treatment lakes are due to the Sonar® treatments alone. Thus, I study the relationships and patterns within and among trophic levels along a gradient of percent milfoil cover, with lakes low on the gradient as a result of Sonar® treatments. By recognizing and compensating for some of the potential drawbacks of ecosystem experiments, I hope to further explain the relationship between macroinvertebrates and macrophytes.

Many questions have yet to be answered regarding the interactions between macrophytes and macroinvertebrates. We also know little about how the spread of the

exotic milfoil and our subsequent management actions affect those interactions. To address some of these questions, I had the following five objectives:

1. Design a sampler to sample macroinvertebrates associated with submerged plants (Chapter 1).
2. Assess the sample size and statistical power to detect differences in macroinvertebrate density and biomass among species of plants from undissected and dissected plant architecture types using samples taken from a single lake in August 1998 (Chapter 1).
3. Examine patterns between macroinvertebrate density and biomass and plant species and architecture using samples taken from six lakes during the summer of 1999 (Chapter 2).
4. Use meta-analysis to quantitatively synthesize the published literature on the relationship between macroinvertebrates and plant architecture (Chapter 2).
5. Examine patterns between macroinvertebrate density and biomass and the percent cover of milfoil using samples taken from six lakes during the summer of 1999 (Chapter 2).

Chapter 1: Macroinvertebrates associated with submerged macrophytes: Sample size and power to detect effects

Introduction

When planning and conducting ecological experiments, it is important to consider how many samples are necessary to detect differences among treatments with acceptably high statistical power. Clearly, the goal is to maximize power (1 – Beta, the probability of correctly rejecting the null hypothesis) by minimizing beta (the probability of making a type II error or failing to reject a false null hypothesis) (Peterman 1990a). Thus, for an experiment with low power, little confidence can be placed in a conclusion based on the failure to reject a null hypothesis. Power can be calculated for different assumed effect sizes (the magnitude of the change in the parameter of interest that can be detected by an experiment calculated as the arithmetic difference between the expected value and the observed value for the parameter of interest) (Cohen 1988). The experiment should not be performed if the detectable effect size is larger than the effect size that is biologically or economically important (Rotenberry and Wiens 1985). Through these calculations of power, a researcher can determine the feasibility of a study and anticipate how many samples are necessary to detect differences among treatments with various levels of power, thus facilitating better experimental design.

Although estimates of statistical power in ecological studies have been reported in some recent studies (e.g. Carpenter et al. 1995a; Johnson 1998), these important and biologically relevant statistics are still too seldom calculated and, in particular, have not been examined for studies of epiphytic macroinvertebrates. An analysis of statistical

power is especially important when studying epiphytic macroinvertebrates because these organisms exhibit large plant-to-plant variability due to predation, periodic macroinvertebrate emergence, fluctuations in macroinvertebrate food supply, appearance of new macroinvertebrate broods, natural mortality, and the occurrence of macroinvertebrates of the same species but of different size (Gaufin et al. 1956; Mrachek 1966; Soszka 1975).

Epiphytic macroinvertebrates and the macrophytes they colonize are ecologically important components of lake ecosystems. In particular, 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 (Diehl and Kornijow 1998). However, macrophytes are diverse in shape and form, and the morphology of the plants themselves has been suggested to influence the importance and colonization of epiphytic macroinvertebrates (Jackson 1997). Submerged macrophytes can be grouped according to architecture based on plant morphology (the number, morphometry, and arrangement of stems, branches and leaves) (Lillie and Budd 1992). Macrophyte architecture type has been found to explain some of the variation in the density of macroinvertebrates, with plants having finely dissected leaves supporting more macroinvertebrates than plants with broader, undissected leaves (Krecker 1939; Andrews and Hasler 1943; Gerking 1957; Mrachek 1966; Gerrish and Bristow 1979; Kershner and Lodge 1990; Jeffries 1993). It has been suggested that this pattern occurs because most dissected-leaf plants provide more habitat for colonization, more epiphyton for grazing macroinvertebrates, or additional complexity that offers better refuge from predators. However, a more recent study found

that macroinvertebrate density did not vary predictably with leaf dissection across multiple lakes (Cyr and Downing 1988a).

The patterns of epiphytic macroinvertebrate communities and their role in lentic food webs have been difficult to quantify, partly because sampling macroinvertebrates on submerged plants is difficult and past studies have not used comparable methods to sample, process, analyze, and report data (Downing and Cyr 1985; Jackson 1997). In addition, power analyses have not been conducted in any study examining the patterns of epiphytic macroinvertebrates. Thus, questions remain about the relationship between epiphytic macroinvertebrates and macrophytes, and whether these organisms are too variable to discern patterns of density and biomass.

To address these questions, I designed a mesh bag sampler that is a modification of the folding quadrat sampler (Welch 1948) to sample macroinvertebrates associated with submerged plants. I assessed the sample size and statistical power to detect differences in macroinvertebrate density and biomass among species of plants from broad and dissected plant architecture types. I also examined patterns between macroinvertebrate density and biomass and plant species and architecture types. I hypothesized that broad-leaf plants would harbor fewer macroinvertebrates than dissected-leaf plants.

Materials and Methods

Study Site

I sampled epiphytic macroinvertebrates on August 4 and 5, 1998 in Heron Lake, located in Seven Lakes State Park in S.E. Michigan, U.S.A (42.81N, 83.52W). The lake

has an extensive forested riparian zone and undergoes very little plant management, except for occasional mechanical harvesting in localized areas surrounding the public boat launch and beach. The surface area of Heron Lake is 53 ha and the mean depth is 3.5 m. Nearly 65% of the lake is littoral (littoral zone defined as average depth beyond which no plant growth is observed; ~4.6 m). Nineteen plant species were recorded during macrophyte surveys performed in August of 1998 (J.D. Madsen *unpublished data*).

Sampling

Sampler Description: I sampled individual plant stems with a mesh bag sampler that is a modification of the folding quadrat sampler (Welch 1948) (Figure 1). It is constructed of 200 and 500 μm mesh, thus the sampler collects organisms > 500 μm. The sides are constructed of 200 μm mesh for flexibility, ease of construction, and sampler deployment. Two brass rings provide structure to the mesh bag (the top ring is smaller than the bottom ring for easy inversion of the sampler). All seams are on the outside of the sampler, allowing for a smooth inner surface. The sampler is 65 cm long and 24 cm in diameter. It has a drawstring at the bottom to close the sampler and trap the sampled macrophyte and its associated macroinvertebrates. A crew of three people performs the sampling: one snorkeller collects samples and two people process the samples in a boat. The snorkeller positions the sampler above a randomly chosen plant and slowly (to limit disruption and subsequent loss of organisms) lowers it down until the desired plant length is inside the sampler. Then the drawstring is pulled taut, the plant stem is broken off at its base, and the sampler is brought to the surface. The processors in the boat cut off any additional plant material extending beyond the sampler. The sampler

is then inverted and rinsed, and the contents (macrophyte, macroinvertebrates, and water) are stored in a sealed plastic bag. Samples are kept cool and dark for further processing.

Sample Protocol: I sampled five common plant species that fit into the two plant architecture groups. Two species were classified as undissected, or broad-leafed plants: *Potamogeton richardsonii* Benn. (clasping-leaf pondweed), and *Potamogeton illinoensis* Morong. (Illinois pondweed); and three as dissected-leafed: *Ranunculus sp.* (water crowfoot), *Potamogeton pectinatus* L. (sago pondweed), and *Myriophyllum spicatum* L. (Eurasian water milfoil) (Figure 2). I sampled epiphytic macroinvertebrates at three sites separated by greater than 100 m. Each site was approximately 2 m deep (average depth of littoral zone) and contained each of the five plant species. I randomly sampled five macrophytes of each species from approximately a 10 m radius around an anchored boat at each site, resulting in 15 individuals of each plant species totaling 75 samples. I chose these numbers of plant species and replicates based on comparisons with previous studies (Table 1).

Sample Processing: In the lab, I rinsed all individual macrophyte samples with water to detach insects, then dried the plants at 105 °C for 48 hours and weighed them to estimate plant biomass. Macroinvertebrates were preserved in 95% ethanol, counted, and identified to the lowest taxonomic level possible (usually genus). Length-weight equations from the literature were used to estimate macroinvertebrate biomass from body lengths measured using an ocular micrometer (Rogers et al. 1977; Smock 1980; Meyer 1989; Burgherr and Meyer 1997; G.G. Mittelbach *unpublished data*).

Data Analysis

For all analyses, I standardized macroinvertebrate density and biomass (expressed as numbers and mg of animals) by plant dry weight, which allows for the comparison of macroinvertebrate density and biomass among different plant species and architecture types. I conducted sample size and power analyses using PASS 6.0 software (NCSS Statistical Software 1998). I calculated the power to detect differences in macroinvertebrate density and biomass among the five plant species and two architecture types given the number of samples taken. Using one-way ANOVAs and setting alpha = 0.05, I estimated the number of samples necessary to detect differences in macroinvertebrate density and biomass between the five plant species and two architecture types at different levels of power and a fixed effect size. I also calculated the number of samples necessary to detect differences in macroinvertebrate density and biomass among the five plant species and two architecture types with a fixed power level and various effect sizes. Finally, I performed ANOVA tests to determine if macroinvertebrate density and biomass varied predictably by plant species or architecture.

Results

Using power analysis, I found that by taking an average of 36 samples per architecture type, I had a power of 1.000 to detect the difference present between the two plant types (effect size = 0.872). In fact, it would have taken just 7-14 samples within each architecture type to detect this large difference with a power of 0.85-0.99 (Figure 3). However, to detect very small differences between the two architecture types (effect sizes

= 0.1-0.3) I determined that 60-527 samples were necessary to achieve similar power (Figure 4a). However, intermediate effect sizes (0.6-0.4) could be reasonably achieved with 16-34 samples (power = 0.9) (Figure 4a).

For the same analysis of macroinvertebrate density and biomass by plant species, I found that with our sample protocol (average of 14 replicates per plant species), I had a power of 0.994 to detect the differences present between the five plant species (effect size = 0.646). I could have taken just 7-14 samples within each plant species to detect these differences with a power of 0.820-0.994 (Figure 3). Similar to the analysis for plant architecture, I determined that 36-310 samples were necessary to detect very small differences between plant species (effect sizes = 0.3-0.1) and intermediate effect sizes (0.6-0.4) could be reasonably achieved with 10-21 samples (Figure 4b).

My results suggest that macroinvertebrate density and biomass are significantly related to leaf dissection (Figure 5). Dissected-leaf plants (*M. spicatum*, *P. pectinatus*, and *Ranunculus sp.*) harbored higher densities and biomass of macroinvertebrates than undissected, broad-leaf plants (*P. illinoensis* and *P. richardsonii*) (ANOVA, density P = .001, biomass $p < 0.001$). There were no significant differences in macroinvertebrate density or biomass among plant species within the same architecture type.

Discussion and Conclusion

When planning and conducting ecological experiments, power analysis can lend insight into how many samples will be necessary to detect differences among treatments with acceptably high power. I performed these analyses on lentic, epiphytic macroinvertebrates collected with a mesh bag sampler. I found that I had extremely high

power to detect the large differences in macroinvertebrate density and biomass between the five plant species and two plant architectures (power = 1.000 and 0.994, respectively). A 'conservative' estimate of the number of samples necessary to detect effects would allow alpha and beta to be set at a level of 0.05, whereas a more 'liberal' estimate would allow alpha to equal 0.05 and beta to equal 0.20 (Peterman 1990b). Choosing an intermediate of these two (alpha = 0.05, beta < 0.1, resulting in power > 0.9), I determined that far fewer samples could have been taken within each species or architecture (9-14), thus allowing time for sampling additional species. I also found that we could reasonably take sufficient samples to detect intermediate differences among species or between architectures (10-21 and 16-34 samples, respectively, effect sizes 0.6-0.4). This knowledge will allow ecologists to better design further studies of epiphytic macroinvertebrates.

Epiphytic macroinvertebrates and the macrophytes they colonize are ecologically important components of lake ecosystems. Our results indicate that dissected-leaf plants harbored higher densities and biomass of macroinvertebrates than undissected, broad-leaf plants. In Table 1, I summarize some of the past research studying epiphytic macroinvertebrates in single lakes. These studies sampled from 3-8 plant species, took 2-85 replicates of each species, and, similar to this study, found that dissected-leaf plants harbored more macroinvertebrates than other plant types. I had enough information to calculate power for the study by Gerrish and Bristow (1979). With an alpha of 0.05 and an N of 10, they had a power of 1.000 to detect the very large differences found between the three plant species sampled on June 18, 1974 (effect size = 1.87). In fact, the authors could have detected smaller differences (effect size = 0.5) by taking only 18 samples of

each plant species and they could have taken just 3 samples to detect the differences present (power > 0.9). Knowing this, more time could have been spent sampling additional plant species rather than replicates within plant species, resulting in more information about the relationship between macroinvertebrate density and biomass and plant architecture.

The management of aquatic plants typically involves the removal of plant biomass either selectively by species or nonselectively. Thus, plant management affects the abundance and community composition of macrophytes and, consequently, epiphytic macroinvertebrates. Because these macroinvertebrates are an important source of food for many species of juvenile fish, an important component of lake food webs, it is important that ecologists understand the relationship between macrophytes and macroinvertebrates so that humans may better manage lakes for both plants and fish. With the knowledge I have gained in this study, I am better prepared to answer questions such as: Are the patterns seen here between macroinvertebrate density and biomass and plant architecture common among lakes (Chapter 2)? and, How do macroinvertebrates respond to changes in macrophyte communities (Chapter 2)?

Chapter 2: The interactions between plant architecture and epiphytic macroinvertebrates and the effects of Eurasian water milfoil invasion

Introduction

The relationship between macroinvertebrates and submerged macrophytes is partly explained by macrophyte physical structure, also known as architecture. Submerged macrophytes can be grouped according to architecture based on the number, morphometry, and arrangement of stems, branches, and leaves (Lillie and Budd 1992). Macrophytes are diverse in shape and form, and the architecture of plants has been suggested to influence the colonization of epiphytic macroinvertebrates by providing macroinvertebrates varying amounts of substrate and cover from predators (Cyr and Downing 1988a; Jackson 1997). Similarly, macroinvertebrates can be grouped according to functional feeding groups based on morphological and behavioral adaptations for food resource acquisition (Merritt and Cummins 1996; Merritt et al. 1996). Although macroinvertebrate functional feeding groups have been used extensively in lotic systems (e.g. Vannote et al. 1980; Gregg and Rose 1985; Merritt et al. 1996), the use of these groups is much less common in lakes (but see Chilton 1990), and subsequently much less is known about the relationship between these macroinvertebrate groups and plants in lakes.

Using functional groups such as macroinvertebrate feeding groups and plant architecture may help us find and explain patterns between epiphytic macroinvertebrates and macrophytes. In fact, many studies of plant architecture have found that macroinvertebrate density is higher on dissected-leaf plants than undissected-leaf plants (Krecker 1939; Andrews and Hasler 1943; Gerking 1957; Mrachek 1966; Gerrish and

Bristow 1979; Cattaneo and Kalff 1980; Dvorak and Best 1982). It has been postulated that this result is because dissected-leaf plants have a higher surface area to plant weight ratio and therefore provide more habitat for macroinvertebrate colonization, more food for grazing macroinvertebrates in the form of periphyton, or additional complexity which offers better refuge from predators (Krull 1970; Pardue 1973; Dvorak and Best 1982; Gilinsky 1984; Jackson 1997). However, a more recent study found that macroinvertebrate density did not vary predictably with leaf dissection (Cyr and Downing 1988a and b). Instead, macroinvertebrate density was plant-species specific (Cyr and Downing 1988a and b). In addition to surface area to plant weight ratio, other factors have been suggested to drive macroinvertebrate colonization. In a study of dissected and thinly leafed plants (all with large surface areas per unit weight), Parsons and Matthews (1995) suggest that the nature of the colonizable surface (soft or hard stems, brittle or pliable leaves, whorled or non-whorled leaves) is at least as important as the surface area. Also, a study relating biomass and surface area of six submerged plants actually found that all dissected-leaf plants did not have higher surface areas than plants with undissected leaves (Sher-Kaul et al. 1995). Instead, a dissected and an undissected species (*Myriophyllum spicatum L.* and *Elodea canadensis* Michx.) were found to have higher surface areas than three undissected species (*Nitellopsis obtuse* Desv., *Potamogeton lucens* L., and *Potamogeton perfoliatus* L.), and one dissected species *(Potamogeton pectinatus* L.*)*. Therefore, the architecture of the plant may not completely explain differences in surface area (Sher-Kaul et al. 1995). Although the relationship between surface area and plant architecture and biomass is not straightforward, because

surface area is difficult to measure directly, surrogates such as biomass or architecture type are often used instead.

Leaf dissection, or plant architecture, may become important at the whole-lake scale when the macrophyte community becomes dominated by a single type of plant. One such plant is *Myriophyllum spicatum* (hereafter milfoil), an exotic, submerged, dissected-leaf macrophyte found in much of temperate North America. This exotic was introduced to North America prior to 1950 from Europe, and by 1985 was reported in 33 states, the District of Columbia, and the Canadian Provinces of British Columbia, Ontario, and Quebec (Couch and Nelson 1985). Because milfoil has three mechanisms of propagation (seed production, stolon formation, and fragmentation; Madsen and Smith 1997) and can grow in water from 1 - 10 m deep, it has spread rapidly throughout North America (Aiken et al. 1979; Couch and Nelson 1985). Milfoil typically forms dense surface mats or canopies that suppress native plant growth and result in homogeneous macrophyte beds (Aiken et al. 1979; Madsen at al. 1991). The continued spread of this exotic species has recreational and ecological ramifications that have prompted much research into milfoil ecology, biology, and management (Keast 1984; Madsen et al. 1988; Smith and Barko 1990; Chilton 1990; Trebitz et al. 1993; Madsen and Smith 1997).

Milfoil, a dissected-leaf plant, has a higher surface area for the same unit of biomass than four other native plant species (undissected: *N. obtuse, P. lucens, P. perfoliatus, and* dissected: *P. pectinatus*; Sher-Kaul et al. 1995). This result would suggest that milfoil should have high rates of macroinvertebrate colonization. However, other studies have shown that milfoil actually supports fewer macroinvertebrates than native plant species (Soszka 1975; Dvorak and Best 1982; Keast 1984; Cattaneo et al.

1998). These low macroinvertebrate densities on milfoil may be because milfoil forms dense homogeneous vegetation beds which, in general, have been shown to support lower densities of epiphytic macroinvertebrates (Brown et al. 1988). Spatial complexity may also explain low macroinvertebrate densities associated with milfoil. Dibble et al. (1996) measured frequency of interstices (gaps among stems and leaves) and found that milfoil had lower spatial complexity than six other plant species (undissected: *Egeria densa*, *Hydrilla verticillata*, *Potamogeton nodosus* Poir., *Vallisneria americana* Michx., *Zosterella dubia* L., and dissected: *P. pectinatus*).

I developed a multi-lake study to answer a few key questions regarding the relationship between macrophytes and macroinvertebrates, and in particular, how the spread of the exotic milfoil might affect that relationship. My objectives were: 1) to document and examine patterns among macroinvertebrates, macroinvertebrate functional feeding groups, plant species, and plant architectures at a range of scales (within individual lakes, across six lakes, and for six lakes pooled), 2) to quantitatively synthesize the published literature on the relationship between macroinvertebrates and plant architecture, and 3) to examine patterns between macroinvertebrates and the percent cover of milfoil across six lakes. I hypothesized that 1) macroinvertebrate density and biomass is related to plant architecture, with dissected plants harboring higher macroinvertebrate densities and biomass than undissected plants, and 2) because dense homogeneous macrophyte beds may support fewer macroinvertebrates, overall macroinvertebrate density and biomass will decrease as percent milfoil cover increases across lakes, even though milfoil is a dissected plant.

Materials and Methods

Study Area

Epiphytic macroinvertebrates were sampled from six lakes in southern Michigan during July and August 1999 (Figure 1). The lakes fall along a gradient of percent milfoil cover (Table 1, see explanations of calculations below). The three lakes low on the gradient (Camp, Big Crooked, and Lobdell) were treated in May 1997 with 5 - 7 ppb Sonar® and are part of a study examining the direct and indirect effects of whole-lake Sonar® treatments on plants, fish, and invertebrates. The three reference lakes were chosen because they had high percent milfoil cover and have undergone very little plant management. Two of the three reference lakes (Big Seven and Heron Lakes) are located in State Recreational and State Park Areas.

Sampling

Macrophytes: Plants were sampled in August of 1999 in the six lakes by the U.S. Army Engineer Research and Development Center using the point intercept method (Madsen 1999). 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). Points were located with a global positioning system. At each survey point, water depth was measured, a two-sided rake was thrown, and plant species presence/absence was recorded (J.D. Madsen *unpublished data*).

Lake Characteristics: To account for inherent differences among lakes, monthly water quality samples were taken from the deepest area of each lake for nutrients, chlorophyll, and Secchi depth. The depth of the epilimnion was estimated from temperature profiles taken each sampling date. A tube sampler was used to take

integrated epilimnetic samples for total phosphorus, total nitrogen and chlorophyll *a* concentrations. For chlorophyll analysis, water was filtered on site through a glass fiber filter (Whatman GF-C) and stored in the dark until being returned to the lab and frozen. Chlorophyll *a* concentrations were determined fluorometrically with phaeopigment correction following 24 hour extraction in methanol (Nusch 1980). Total nitrogen was determined using a persulfate digestion followed by second derivative spectroscopy (Crumpton et al. 1992). Total phosphorus was determined using a persulfate digestion (Menzel and Corwin 1965) followed by standard colorimetry (Murphy and Riley 1962). Secchi disk depth was measured for each lake off of the shady side of the boat.

Macroinvertebrates: Using August 1998 vegetation survey results conducted for the six lakes (J.D. Madsen *unpublished data*), the five most common submerged plant species for each lake were selected for epiphytic invertebrate sampling in summer 1999. Less common species were sampled in a few cases in order to collect at least two species within each plant architecture type (dissected and undissected) and to include milfoil in each lake. I adapted the final list on-site for seasonal and interannual changes that may have occurred from 1998 to 1999. Each lake was sampled for macroinvertebrates twice during summer 1999 (June 28 - July 7 and August 16 - August 24). To sample epiphytic macroinvertebrates, a snorkeller sampled individual plant stems with a 500 μm mesh bag sampler measuring 65 cm long by 24 cm in diameter (Chapter 1). For each lake, epiphytic macroinvertebrates were sampled at 3 - 5 sites separated by greater than 100 m. Each site was approximately 2 m deep and consisted of heterogeneous macrophyte beds. Based on power and sample size analyses from data collected in Heron Lake in August 1998 (Chapter 1), 2 - 4 stems from each of the five macrophyte species were randomly

sampled from approximately a 10 m radius around an anchored boat at each site, resulting in 13 individuals of each plant species, or 65 samples per lake per date (except Camp Lake in July when only four plant species were sampled), totaling ~800 samples. Individual samples (macrophyte stem, associated macroinvertebrates, and water) were stored in a sealed plastic bag and kept cool and dark until further processing.

In the lab, individual macrophyte stems were rinsed with water to detach macroinvertebrates; the plants were dried at 105 °C for 48 hours and weighed to estimate plant biomass. Macroinvertebrates were preserved in 95% ethanol. For each lake, the 13 macroinvertebrate replicates from each plant species were pooled and subsampled using methods developed by Waters (1969). Subsamples were counted until at least 140 individuals had been counted, which resulted in estimates within 20% of the mean. Macroinvertebrates were identified to the lowest taxonomic level necessary to be placed into functional feeding groups (scraper, gathering collector, filtering collector, plant piercer, predator, and shredder; Merritt and Cummins 1996; Merritt et al. 1996). Each individual was measured to the nearest μm using a drawing tube and digitizing tablet. Macroinvertebrate biomass was estimated from body lengths using length-dry weight regressions from the literature (Rogers et al. 1977; Smock 1980; Meyer 1989; Burgherr and Meyer 1997; G.G. Mittelbach *unpublished data*)

Data Analysis

Macrophytes: Using macrophyte data collected in 1999, I calculated two milfoil gradients, a non-weighted and a weighted gradient. To develop the gradients, I included all submerged macrophytes except the macro-alga *Chara sp.*, thus excluding emergent, free-floating, and floating-leaf plants. For each lake, the littoral zone was defined as the

zone from shore to the deepest point at which plants consistently occurred. Within the littoral zone, I calculated the percent of sites that were vegetated. To calculate the non-weighted gradient for each lake, I calculated the percent of the vegetated littoral zone that had milfoil present (number of points with milfoil present divided by the number of vegetated sites in the littoral zone multiplied by 100). This non-weighted gradient does not make any assumptions about the relative density within a grid, only species presence, so is likely a liberal estimate of percent milfoil cover. I tried to estimate a more realistic gradient by calculating a weighted milfoil gradient in which I assumed that 1) the number of plant species found at a single point was representative of species composition for the entire grid cell, and 2) that each plant species was found at equal densities within the grid cell. Therefore, each milfoil presence count was weighted by the reciprocal of the number of other species found at that site. I then calculated the percent of the vegetated littoral zone that had milfoil present (sum of weighted milfoil points divided by the number of vegetated sites in the littoral zone multiplied by 100). Because the point intercept sampling method does not assess plant biomass or density, the weighted gradient was an attempt to approximate the relative milfoil biomass or density within a grid, and is likely a conservative estimate. The weighted gradient resulted in a lower milfoil gradient overall; however, the order of the lakes along the gradient did not differ between the two gradients. The actual percent milfoil cover for each lake is likely somewhere between these two gradients (non-weighted and weighted). I present results for the weighted percent milfoil gradient only because regression analyses along both gradients gave similar results and I felt that, because it considers other plant species presence, the weighted gradient was more realistic.

Macroinvertebrates: For all analyses, macroinvertebrates were standardized by plant dry weight (g), which allows for the comparison of macroinvertebrates among different plant species and architecture types. So as to not lose information, I report results for July and August separately rather than as an average because macroinvertebrate life cycles are short and periodic, thus density, biomass, and species composition changes throughout the summer (Gaufin et al. 1956; Mracheck 1966; Soszka 1975; Merritt and Cummins 1996). Macroinvertebrates (expressed as either density (#) of individuals per gram plant biomass or biomass (mg) per gram plant biomass) were $\log_{10}$ transformed to meet statistical assumptions.

I tested whether macroinvertebrate density and biomass varied predictably by plant species, plant architecture, and macroinvertebrate functional feeding group at different scales (within and across the six lakes and pooled lakes) using ANOVA and adjusted Bonferroni post-hoc comparisons. 'Within-lake' analyses refer to macroinvertebrates in each of the individual six lakes; 'across-lake' analyses make comparisons across the six lakes using the within-lake results; 'pooled-lake' analyses combine data from all six lakes. I also calculated post-hoc power analyses to determine whether I sampled sufficiently to detect differences in macroinvertebrate density and biomass among the plant species and architecture types within lakes and with the six lakes pooled. These post-hoc sample size and power analyses were conducted using PASS 6.0 software (NCSS Statistical Software 1998). Using one-way ANOVAs and setting alpha = 0.05, the number of samples that would have been necessary to detect differences in macroinvertebrate density and biomass between the plant species and architecture types was estimated at different levels of power and a fixed effect size (the

arithmetic difference between the expected value and the observed value for the parameter of interest).

Regression analyses were performed to determine if macroinvertebrate density and biomass were related to the percent cover of milfoil. To extrapolate macroinvertebrate density and biomass to the whole-lake scale, a weighted percent macrophyte presence was calculated for each plant species from which I sampled epiphytic macroinvertebrates (the same calculations as for the weighted milfoil gradient in the macrophyte section above). These numbers were multiplied by the grid cell area (40-100 m^2, depending on lake area) and then by macroinvertebrates per m^2 sampler area to get macroinvertebrate density and biomass per vegetated littoral zone (for that plant species sampled). For the one case in which I sampled macroinvertebrates from a species that was not recorded as present at any sites in the plant survey, this plant was given the lowest experienced occurrence (0.125, or found at one site with eight other species).

Meta-analysis

I used meta-analysis to quantitatively synthesize the published studies on the relationship between epiphytic macroinvertebrates and plant architecture. In order to keep personal bias low I did not include selection criteria based on study quality (Englund et al. 1999). Instead, I included all field studies in which lentic, epiphytic macroinvertebrates were sampled from submerged plants within the two architecture groups of dissected and undissected leaves. Although the sampling methods differed among studies, results from the studies can be compared by calculating a dimensionless overall effect size by architecture group within each individual study (the ratio of the means of the two architecture types). Because each study is compared only to itself, the

different sampling methods and different approaches should not confound comparisons (Fernandez-Duque and Valeggia 1993; Gurevitch and Hedges 1999).

The published articles I included in these analyses were found using computer databases: Aquatic Sciences and Fisheries Abstracts (Cambridge Scientific Abstracts), Biological Abstracts, and ISI Citation Databases (Institute for Scientific Information Science Citation Index Expanded). Keywords and combinations of keywords included macroinvertebrate, invertebrate, macrophyte, plant, plant architecture, lake, and lentic. Older articles not included in these databases were identified and collected from the reference sections of the more recent articles. Although these extensive searches resulted in over 75 articles, only 13 articles were included in my final analysis (Table 2). Articles were eliminated that: 1) did not report/collect quantitative data, 2) did not express data as numbers of macroinvertebrates per unit of plant biomass, 3) combined benthic and epiphytic samples, 4) contained data already reported in another article, or 5) aggregated samples across plant species from different architectures. In addition, of the remaining 13 articles, many did not include all the necessary information (variance) to perform a weighted meta-analysis, so I performed both weighted and unweighted analyses (see below). For one of the articles included in the analyses, (Cyr and Downing 1988a) I obtained raw data from the authors. Because all other studies did not include zooplankton in analyses, I removed zooplankton from the Cyr and Downing dataset. I also eliminated samples from their data that aggregated macroinvertebrate samples across macrophyte species in different architecture groups. Therefore, my conclusions may differ from Cyr and Downing's (1988a and b) published conclusions.

Several of the 13 articles included results from more than one lake (Krull 1970; Cyr and Downing 1988a; Kornijow 1989), resulting in 18 lakes as independent observations (hereafter referred to as studies). For each study, I recorded the number of times macroinvertebrates were sampled, the decade of sampling, the study location, the number of species of macrophytes sampled, the number of plants sampled within each species, the sampler used, the organisms sampled, and the macroinvertebrate density and variance estimate for each plant architecture group (Table 2). Two studies averaged macroinvertebrate density across multiple lakes. Because these means included among-lake variability, meta-analysis was performed with and without these two studies. For articles that reported data in figure form only (Pip and Stewart 1976; Gerrish and Bristow 1979; Kornijow 1989; Chilton 1990), I scanned the graphs and interpolated the values using Scion Image software (Scion Corporation 1998). For papers that reported multiple estimates within a season (May-October), densities were averaged across the season (Pip and Stewart 1976; Gerrish and Bristow 1979; Keast 1984; Chilton 1990). For the two articles that reported multiple years of data (Soszka 1975; Kornijow 1989), only the final year of data was used to be consistent with all other studies that only had one year of data. Four studies reported macroinvertebrate density from one sample date only (Andrews and Hasler 1943; Cyr and Downing 1988a; Chapter 1) and the remaining studies presented single mean density estimates for the summer season.

I performed two types of meta-analyses: weighted and unweighted. Weighted meta-analysis incorporates sample variance into the overall effect size (using the variance as the weighting variable), whereas unweighted meta-analysis does not. Because not all of the studies included in my meta-analysis provided variance estimates, it was necessary

to conduct two meta-analyses: 1) unweighted using all 18 published studies and 2) weighted using the previous seven published studies (except Heron Lake 1998 to be consistent with my methods of only using a single year of data when multiple years were reported) and the six individual lakes in this chapter after averaging across months to be consistent with all other studies. Three of the studies included in the weighted analysis (published studies only) reported variance estimates directly (Cyr and Downing 1988a; Chapter 1). For the other studies, I calculated variance by averaging macroinvertebrate density across two or more plant species within each architecture group (viewing plant species as replicates within architecture groups as I do in this chapter; Krull 1970; Andrews and Hasler 1943; Mrachek 1966; Kornijow1989).

For both the weighted and unweighted meta-analyses,

$$\text{effect size} = \ln\left[\frac{\text{average macroinvertebrate density per plant biomass on dissected plants}}{\text{average macroinvertebrate density per plant biomass on undissected plants}}\right]$$

(Cooper and Hedges 1994; Hedges et al. 1999). The natural log response ratio is centered around zero (Cooper and Hedges 1994; Hedges et al. 1999). Thus, values greater than zero indicate that dissected plants have higher densities of macroinvertebrates than undissected plants.

The weighted meta-analysis was performed with MetaWin (Rosenberg et al. 1997). 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 studies included estimates of variance calculated different ways, and six studies performed by one author (Chapter 2), I grouped studies according to author and type of variance estimate and tested for differences between groups using chi-square tests. Mean effect size (natural log response ratio) and 95% confidence intervals were calculated for

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the unweighted meta-analysis. ANOVA tests were performed to examine whether mean effect size differed among groups according to the number of lakes sampled (one or multiple), study area (North America or elsewhere), number of plant species sampled, number of dates sampled (once, multiple, unknown), organisms sampled (all macroinvertebrates, snails only, chrionomids only), whether or not milfoil was sampled (N. American studies only where milfoil is exotic), or decade sampled.

Results

Lake Characteristics

Macrophyte surveys of the six lakes resulted in a non-weighted gradient of percent milfoil ranging from 21% - 95% and a weighted gradient of percent milfoil ranging from 4% - 41% of the vegetated littoral zone (Table 1). Each lake had different plant assemblages, with a range of 10 - 18 submerged plant species in the vegetated littoral zones and 26 species total across lakes (Figure 2). The percent of the littoral zone covered with the plant species that were sampled for epiphytic macroinvertebrates ranged from 56 - 95% (Table 1). The six lakes had similar summer mean Secchi disk depth ranges of 3.3 - 3.7 m, with corresponding photic depth ranges of 8.9 – 10.0 m, and epilimnion depth ranges of 4.0 - 5.0 m (Table 3). Total nitrogen and total phosphorous concentrations ranged from 403 - 544 and 15 - 32 μg/L, respectively, in the six lakes (Table 3).

Macroinvertebrates, plant species, and plant architecture

Pooled lakes: In general, the six lakes had similar dominant epiphytic macroinvertebrate taxa and functional feeding groups (Tables 4 and Figure 3). Thirty-two total taxa were identified across the six lakes (see Appendix 3), but most taxa were uncommon (averaging < 1% of total macroinvertebrate density or biomass). After pooling lakes, I found few patterns when I analyzed macroinvertebrate density by functional feeding groups (ANOVA, Figure 4a and b). In July, I found that no functional feeding groups were statistically different (Figure 4a, $p = 0.15$). In August, the density of predators was significantly higher than gathering collectors, plant piercers, and scrapers (Figure 4b, $p = 0.000, 0.013, 0.039$, respectively), and I found a significantly higher density of shredders than gathering collectors (Figure 4b, $p = 0.027$). Upon examining macroinvertebrate biomass, I found that scrapers and shredders generally exhibited higher biomass than other functional feeding groups (Figure 4c and d). Specifically, in July, scraper biomass was significantly greater than predator biomass (Figure 4c, ANOVA $p = 0.007$) and in August, scraper biomass was significantly greater than filtering and gathering collector, plant piercer, and predator biomass (Figure 4d, $p = 0.01, 0.028, 0.006, 0.000$, respectively) while shredder biomass was significantly greater than predator biomass (Figure 4d, $p = 0.027$).

I also examined patterns among the four plant species that were sampled in at least three of the six lakes. I found no difference in macroinvertebrate density or biomass (Figure 5, $p > 0.273$). However, after aggregating all plant species sampled into the two plant architecture groups (dissected and undissected), I found higher macroinvertebrate density and biomass on dissected plants than undissected plants (Figure 6 and Table 5

last row). Post-hoc power analyses indicated that for analyses that were not statistically significant at alpha < 0.05, I may have lacked the necessary power to detect differences between the two plant architectures (Table 5 last row).

Within and across lakes: Unlike the analyses done by pooling lakes, when I analyzed macroinvertebrate functional feeding groups within individual lakes, I found that functional feeding groups did not significantly differ ($p > 0.1$). Similarly, there was no discernible pattern between average macroinvertebrate density or biomass and particular plant species within lakes. However, after aggregating all plant species sampled within single lakes into the two plant architectures, I found patterns of higher macroinvertebrate density and biomass on dissected compared to undissected-leaf plants in both July and August, although not all comparisons were significant (Table 5). Post-hoc power analyses indicated that for analyses that were not statistically significant at alpha < 0.05, I may have lacked the necessary power to detect the differences between the two plant architectures (Table 5). In July and August, average macroinvertebrate density and biomass on dissected versus undissected plants were significantly different across some of the six lakes (ANOVA; Tables 6 and 7).

Meta-analysis: My meta-analyses corroborate the hypothesis that dissected plants harbor more macroinvertebrates than undissected plants (Figure 7a). In fact, the weighted meta-analysis showed that dissected plants have almost twice as many macroinvertebrates than undissected plants (Figure 7b). I found that studies grouped according to the number of plant species sampled, the number of times sampling occurred within a season (once, multiple, unknown), the decade, the organisms sampled (all macroinvertebrates, chironomids only, snails only), and whether or not milfoil was

sampled (N. American studies only where milfoil is exotic) were not significantly different from one another ($p > 0.11$). In addition, for the weighted meta-analysis, there were no differences between the two methods of estimating variance (with raw data or averaging across plant species within architecture groups, $p > 0.343$) or between studies conducted by myself versus other authors ($p > 0.825$). However, the four studies conducted outside of N. America (Soszka 1975; Dejoux 1983; Kornijow 1989) had significantly lower mean effect sizes than the 14 N. American studies ($p = 0.017$) and the two multiple lake studies had significantly lower mean effect sizes than the other 16 studies ($p = 0.091$) (Krull 1970; Cyr and Downing 1988a).

Macroinvertebrates along a percent milfoil gradient

Along the percent milfoil cover gradient (across the six lakes), I found that the proportion of dissected plants present significantly increased (Figure 8). If I consider the relationship between macroinvertebrates and plant architecture alone, then as the proportion of dissected species increases with increasing percent milfoil cover, I might expect macroinvertebrates to increase as well. However, when I regressed average macroinvertebrate biomass and density against the percent milfoil gradient, I actually found decreasing macroinvertebrates with increasing percent milfoil cover in July, but not in August (Figure 9). I also examined whole-lake macroinvertebrate density and biomass using the extrapolated data (whole-lake scale). Although trends were similar (macroinvertebrate density and biomass decreased with increasing percent milfoil except for August density), I did not find a significant influence of percent milfoil cover on macroinvertebrate density and biomass per m^2 of the vegetated littoral zone ($p > 0.172$).

Discussion and Conclusion

Using data from my six study lakes, I found that lakes had similar dominant epiphytic macroinvertebrate taxa and functional feeding groups. Scrapers and shredders generally exhibited higher biomass than other functional feeding groups, especially in August. I would expect this result because scrapers and shredders use the plant material and the periphyton that macrophytes provide, and macrophyte senescence in late summer increases the availability of some of these resources. I also found that higher densities and biomass of macroinvertebrates were associated with dissected plants than undissected plants both within lakes and with lakes pooled, although not all relationships were significant. However, using meta-analysis across a large number of similar studies, I found very strong patterns that showed that dissected plants had almost twice as many macroinvertebrates than undissected plants, even when the six lakes from my study were included. I also found a pattern of decreasing macroinvertebrates with increasing percent milfoil cover, although the results were not conclusive. Below, I explore the relationships between plant architecture and macroinvertebrate colonizations, and some reasons for the equivocal relationships between milfoil and macroinvertebrate patterns.

Macroinvertebrates, plant species, and plant architecture

I hypothesized that plant architecture would be related to macroinvertebrate density and biomass, with dissected plants harboring higher macroinvertebrate density and biomass than undissected plants. At multiple scales (within lakes and after pooling lakes), I found that, although dissected plants exhibited higher densities and biomass of macroinvertebrates than undissected plants, the patterns were not statistically significant

within most individual lakes. Results of post-hoc power analyses indicate that this lack of significance may have been due to low power.

When designing my study I recognized the high natural variability associated with macroinvertebrates and tried to maximize statistical power to detect differences between architecture groups. In each lake, I based my sample sizes on a study conducted in Heron Lake in 1998 (Chapter 1). A-priori power analyses of Heron Lake 1998 macroinvertebrate data indicated that 9 - 14 samples of each plant species would provide us with power > 0.9 (alpha = 0.05) to detect differences between plant species and architecture groups (effect size, the difference between the expected and observed value of the parameter of interest, > 0.6). To detect smaller differences between plant species or architectures, I would have needed to take 10 - 21 and 16 - 34 samples per plant species or architecture, respectively (effect sizes 0.6 - 0.4) (Chapter 1). Because ecologists do not know what effect sizes are ecologically relevant for littoral zone food webs, I chose an intermediate 13 replicates per plant species that resulted in statistically significant differences in Heron Lake in 1998. Contrary to these results, post-hoc power analyses on the six lakes sampled in 1999 demonstrated that epiphytic macroinvertebrate density and biomass is extremely variable both across lakes and years. For example, in Heron Lake 1999, no results were statistically significant at alpha = 0.05, even though in 1998 I had high power to detect differences between the two plant architecture groups in that lake (Chapter 1). The high variability in Heron Lake may be related to the relatively large natural decrease in percent milfoil cover Heron Lake experienced between 1997 and 1999 (31%; J.D. Madsen *unpublished data*). Although the causes are still uncertain,

natural milfoil decreases have been documented in other lakes (e.g. Lake Wingra and southern Ontario lakes; Carpenter 1980; Painter and McCabe 1988; Trebitz et al. 1993).

Although many of the macroinvertebrate/ architecture comparisons in my six study lakes were not statistically significant (Table 5), the results of my meta-analyses strongly suggest that dissected plants harbor more macroinvertebrates than undissected plants. Despite some significant differences among study groups (i.e. studies in N. American vs. elsewhere), in no analysis did the non-logged 95% confidence interval overlap zero (which would indicate no difference between dissected and undissected species) and the weighted analysis indicated that dissected plants harbor almost twice as many macroinvertebrates as undissected plants. I do not know what is driving patterns of high macroinvertebrate densities and biomass on dissected plants (e.g. surface area to volume ratio or structural complexity). However, when I grouped plants into these two architecture groups, which is much easier to do than measure surface area, I found differences in macroinvertebrate density and biomass. Therefore, using plant architecture groups as an alternative to measuring surface area may be an appropriate way to characterize macroinvertebrate density and biomass.

I stated earlier that the four studies conducted outside of North America (Soszka 1975; Dejoux 1983; Kornijow 1989) and the two multiple lake studies (Krull 1970; Cyr and Downing 1988a) had significantly lower mean effect sizes than the rest of the studies. Upon removing these six studies, the mean effect size increased from 0.30 (95% CI 0.01 – 0.59) to 0.55 (95% CI 0.22 – 0.89). In contrast, when I calculated the pooled effect size for the six lakes in this chapter, the mean effect size falls within the weighted 95% confidence interval and supports the hypothesis that dissected plants exhibit higher

macroinvertebrate density than undissected plants (Figure 7b). The other two multi-lake studies may have had low power because there was little replication within architecture groups and individual lakes. For example, in Cyr and Downing (1988a) only one plant architecture was sampled in five of the eight lakes. This sample design introduces a high amount of among-lake variability that may have resulted in low power to detect differences between the two architecture groups. Although there seems to be no clear answer for why the four studies performed outside of N. America (Dejoux 1983; Soszka 1975; Kornijow 1989) were significantly different from the rest, I offer a few possibilities: differences in climate (e.g., Africa compared to N. America), differences in plant species sampled (e.g., *P. schweinfurthi* is not found in N. America), or differences in macroinvertebrate populations between regions.

In my study, although I found that dissected plants had higher densities and biomass of macroinvertebrates than undissected plants, only one lake and two of the four pooled-lake analyses had statistically significant differences between the two plant architecture groups. However, when I included these six lakes in the weighted meta-analysis, I found that all effect sizes were greater than zero and the confidence interval did not overlap zero. Thus, I conclude that higher macroinvertebrate density is associated with dissected plants than undissected plants. This result also demonstrates the utility of meta-analysis to increase power to detect effects and quantitatively synthesize results across studies.

Macroinvertebrates along a percent milfoil gradient

I found that dissected plants had higher macroinvertebrate densities and biomass than undissected plants and that the proportion of dissected plants increased across lakes

along the percent milfoil gradient. Based on these relationships, I might expect higher macroinvertebrate densities and biomass in lakes high on the percent milfoil gradient. However, other studies have suggested that milfoil actually harbors fewer macroinvertebrates than other dissected plants (Soszka 1975; Dvorak and Best 1982; Keast 1984; Cattaneo et al. 1989). To ensure that any pattern along the milfoil gradient was not a result of my sampling scheme, I looked more closely at the proportion of dissected plants sampled for epiphytic macroinvertebrates in each lake. If the proportion decreased along the percent milfoil gradient, then my sampling strategy alone might have influenced the results along the milfoil gradient. However, I found similar proportions of dissected plants sampled for epiphytic macroinvertebrates across lakes along the percent milfoil gradient (Table 1).

I hypothesized that because dense homogeneous macrophyte beds, such as those produced in high-milfoil lakes, support fewer macroinvertebrates (Brown et al. 1988), macroinvertebrate density and biomass should decrease as percent milfoil cover increases in lakes. My results in July support this hypothesis as macroinvertebrate density and biomass significantly decreased with increasing percent milfoil cover. However, in August, these patterns were not evident and after extrapolating my samples to the whole-lake scale, percent milfoil cover had no significant effect on total lake macroinvertebrate density and biomass. Epiphytic macroinvertebrates exhibit high natural variability, which may have contributed to the lack of pattern I found in some cases. For example, the lake lowest on the milfoil gradient (Camp Lake) was the only lake that experienced a decrease in macroinvertebrate densities and biomass from July to August. Upon examining Camp Lake macroinvertebrates in more detail, I found significantly different

insect taxa densities and biomass between the two months ($p < 0.000$; Figure 9), probably due to odonate and chironomid emergences between July and August (Figure 10). Across all lakes in August, these two insect taxa account for approximately 50% and 20% of the total macroinvertebrate density and biomass, respectively. Although the patterns were not significant ($p = 0.075$), the August regressions without Camp Lake were quite different from those that include Camp Lake and, similar to July, decreased with increasing percent milfoil cover (Figure 11 versus Figure 9b and d). Thus, odonate and chironomid emergences may have contributed to my inability to detect a pattern between macroinvertebrates and percent milfoil cover across the six lakes in August.

To better understand the factors driving the patterns of decreasing macroinvertebrate density and biomass with increasing percent milfoil cover, I examined macroinvertebrates on milfoil alone. Figure 5 demonstrates that with the six lakes pooled, on average, milfoil had similar macroinvertebrate densities and biomass as *C. demersum*, *P. zosteriformis*, and *P. illinoensis*. However, macroinvertebrate density and biomass on milfoil may be related to the percent cover of milfoil. In general, I found that macroinvertebrate density and biomass on milfoil decreased as percent milfoil cover increased, although not significantly (Figure 12). This pattern of decreasing macroinvertebrate density and biomass as percent milfoil cover increased was not consistent for the other three plant species, suggesting that as milfoil becomes more dense along the gradient and throughout the summer, colonizable area on milfoil decreases, and only smaller macroinvertebrates may be able to use the milfoil habitat.

Because juvenile bluegill (*Lepomis macrochirus*) feed on epiphytic macroinvertebrates within the vegetated littoral zone (Werner and Hall 1988; Olson et al.

1995), I also considered juvenile bluegill densities as a potential driver of macroinvertebrate density and biomass. If fish densities were driving macroinvertebrate densities and biomass rather than percent milfoil cover, I would expect to see an increase in juvenile fish density with increasing percent milfoil cover (and decreasing macroinvertebrate densities and biomass). However, juvenile bluegill density and percent milfoil cover were not related (Figure 13; R.D. Valley *unpublished data*), thus bluegill densities were not the main factor driving macroinvertebrate densities and biomass.

Because my expectation of fewer macroinvertebrates existing on plants in high percent milfoil lakes was not consistently proven and could not be explained by bluegill densities, I considered additional factors that may have confounded the results. For example, the two lakes lowest on the percent milfoil gradient (Camp and Big Crooked Lakes) had considerably smaller percent littoral zones and greater mean depths than the rest of the lakes (Table 3). Although I standardized analyses by the vegetated littoral zone area when I estimated total macroinvertebrate density and biomass for each lake (see methods), these morphological differences among lakes may play a role in my observed patterns. In addition, macrophyte senescence, which starts in late summer for some plants, may have affected macroinvertebrate density and biomass and confounded my ability to detect patterns in August. Thus, inherent lake and plant features may have affected my attempts to relate macroinvertebrates to percent milfoil cover at the whole-lake scale.

It is important to recognize the limitations of whole-lake ecosystem experimental designs. For example, Carpenter (1995b) states that for a given experiment, the number

of lakes you must sample in order to detect differences depends on the magnitude of the response factor that is considered significant from biological or management perspectives. My weighted milfoil gradient ranged from 4 - 41%. From the highest percent lake to the lowest, this is a difference of only 37%, with the average between any two lakes along the gradients of only 6%. It is possible that natural inter-lake variation masked differences caused by such small changes in percent milfoil cover.

Another potential reason I failed to see strong relationships between macroinvertebrate density and biomass and percent milfoil cover may be found in my sampling technique. I sampled epiphytic macroinvertebrates from plants in relatively heterogeneous macrophyte beds. However, milfoil forms dense homogeneous beds within which macroinvertebrate density, biomass, and taxa richness is higher in the upper and edge areas than lower and center areas (Sloey et al. 1997). Therefore, I may have been masking the effects of milfoil by sampling plants from heterogeneous rather than homogeneous macrophyte beds. Thus, if anything, my results should be conservative and had I sampled the characteristic dense mats of milfoil, I might have seen stronger negative relationships between macroinvertebrates and percent milfoil cover.

This study showed that 1) higher macroinvertebrate density and biomass is, in fact, associated with dissected plants and 2) macroinvertebrate density and biomass may decrease with increasing percent milfoil. Both of these results have implications for lake food webs and lake management because macroinvertebrates are an integral component linking macrophytes, macroinvertebrate-eating fish, and piscivorous fish. Research on these important food web effects of milfoil on multiple trophic levels and water quality parameters should improve holistic lake management. However, additional research is

needed to further examine the relationship between macroinvertebrates and percent milfoil cover because my results were equivocal. Based on my findings, I would recommend a study design that includes multiple lakes with larger differences in percent milfoil, a sampling scheme that includes sampling milfoil from more characteristic dense homogeneous macrophyte beds, and that include whole-lake macrophyte biomass or density estimates.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

I set out on this research project to address some of the many ecological questions that have yet to be answered regarding the interactions between macrophytes and macroinvertebrates. I also wanted to explore how the spread of milfoil, an exotic macrophyte, and our subsequent management actions to control milfoil might affect these relationships . My primary conclusions are:

1. The mesh bag sampler I designed to sample macroinvertebrates associated with submerged plants was relatively easy to use, inexpensive to produce, and had high statistical power (although power was variable both across lakes and years; Chapters 1 and 2).
2. Using meta-analysis and data from six lakes, I found that dissected plants exhibited higher macroinvertebrate density and biomass than undissected plants (Chapter 2).
3. Macroinvertebrate density and biomass decreased as percent cover of milfoil increased across six lakes (Chapter 2).

Below I explore how my results can be applied to improve lake management.

The mesh-bag sampler I designed could be used effectively by others to sample macroinvertebrates associated with submerged plants. This sampler may be a useful management tool for assessing lake biological integrity as well as a useful scientific tool for research studies. I hope this sampler will promote further study of epiphytic macroinvertebrates on submerged plants in lakes.

The three lakes low on the milfoil gradient (Camp, Big Crooked, and Lobdell Lakes), were the result of Sonar® treatments in May 1997. Because I had no control over management actions taken in these lakes, and each lake was subjected to additional plant management strategies such as other herbicide applications and mechanical harvesting, I cannot be certain that differences between reference and treatment lakes were caused by the Sonar® treatments. Therefore, in chapter 2, I analyzed macroinvertebrate density and biomass along a gradient of percent milfoil cover. Here, however, I look for differences between reference and treatment lakes. In July, macroinvertebrate density and biomass was significantly higher in treatment lakes than in reference lakes (Figure 1a and d, $p < 0.002$). Similar to the patterns I saw when looking at macroinvertebrates along the percent milfoil gradient, macroinvertebrate density and biomass in August were not significantly different between reference and treatment lakes (Figure 1b and d, $p > 0.511$). Recall that there were large odonate and chironomid emergences in Camp Lake between July and August (Figures 9 and 10). Similar to analyses in Chapter 2, I removed Camp Lake from the August data and performed another ANOVA. However, macroinvertebrate density and biomass remained insignificantly different between reference and treatment lakes (Figure 1c and f, $p > 0.496$).

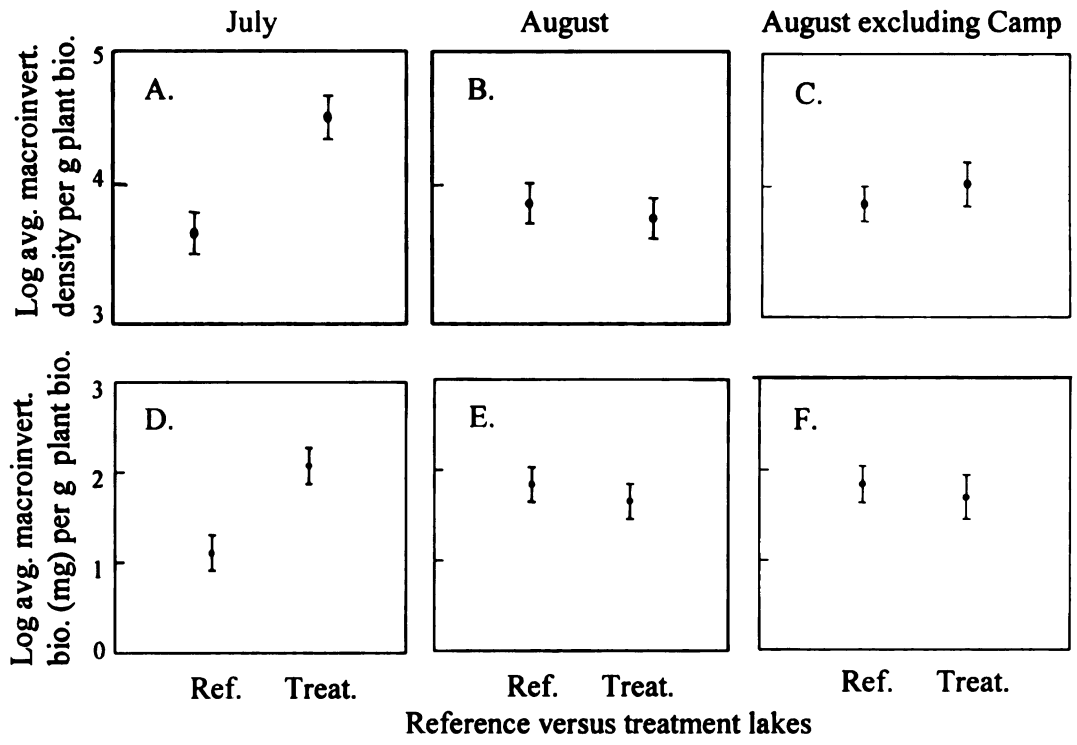

Figure 1. Average macroinvertebrate density (#) and biomass (mg) per g plant biomass in reference and treatment lakes during July (A and D), August (B and E), and August excluding Camp Lake (C and F).

Other studies have examined the direct toxic effects and the indirect effects of Sonar® on benthic macroinvertebrates. In general, direct toxic effects of fluridone on benthic macroinvertebrates have been negligible. Two studies of *Chironomus tentans* larvae found that interactions of fluridone (Sonar® active ingredient) with suspended solids or sediment had relatively little effect on herbicide accumulation (Muir et al. 1982) and that fluridone assimilation by these larvae from ingested sediments was negligible (Muir et al. 1983). Hamelink et al. (1986) found that at the Sonar® label rate (100 ppb) there was a favorable safety margin between the concentration that affects *Gammarus pseudilimnaeus* and *Chironomus pulmosus*. The only study that found some direct toxic effects of fluridone on macroinvertebrates (fly larvae; *Hydrellia*) used fluridone at concentrations of 4600-9200 ppb. Therefore, although studies have looked only at a few

taxa, it appears that there are minimal direct toxic effects of Sonar® on macroinvertebrates.

Although I cannot attribute the difference between reference and treatment lakes to Sonar® applications alone, the results of this study indicate potential positive indirect effects of Sonar® treatments on macroinvertebrate density and biomass. The only previous study that examined the indirect effects of Sonar® on macroinvertebrates found that, contrary to the results of this study, fluridone applications resulted in decreased macroinvertebrate density and diversity (Delong and Mundahl 1996). However, Sonar® was applied at a much higher concentration of 23 ppb as compared to 5 - 7 ppb in this study, and there was no replication of treatment lakes (Delong and Mundahl 1996). In addition, Delong and Mundahl (1996) sampled during the year of treatment and one year after treatment, during which time there may have been more transient effects of the treatment present. However, with more replication (three Sonar® lakes) and lower concentrations of fluridone (5-7 ppb), this study found adequate milfoil control (J.D. Madsen *unpublished data*) and potentially positive indirect effects on macroinvertebrates (Chapter 2).

At the beginning of this study, insufficient data regarding the direct and indirect effects of Sonar® had not been collected and synthesized. Therefore, Sonar® use in Michigan had been restricted and debated for nearly a decade. Now, with our collaborative study nearing conclusion, it appears that Sonar® may be a useful management tool for lake management of both macrophytes and fish. In fact, at the time of this writing, the state of Michigan has decided to allow Sonar® use at low concentrations ($\leq$6 ppb) as a milfoil management tool (Batterson 2000). Based on the

conflicting conclusions of the two studies examining the indirect effects of Sonar® on macroinvertebrates (Delong and Mundahl 1996; Chapter 2), it is difficult to conclude whether Sonar® use has indirect effects (positive or negative) on macroinvertebrates. Therefore, the indirect effects should continue to be monitored, and management plans should be adapted as new data are gathered and analyzed.

I have an additional recommendation for managers faced with decisions such as how to control macrophytes such as milfoil: because I have shown that dissected plants exhibit higher macroinvertebrate densities and biomass than undissected plants, managers may wish to monitor native plant species composition to be sure that after removing milfoil, dissected plants remain in the lake. 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 Kornijow1998; Persson and Crowder 1998). Thus, a low proportion of dissected plants may cause repercussions through the lake foodweb from macrophytes to macroinvertebrates to fish.

APPENDICES

APPENDIX 1

Chapter 1 Tables and Figures

Table 1. Examples of previous studies examining epiphytic macroinvertebrates in individual lakes.

Citation	Number of plant species	Number of replicates taken per plant species[1]
Andrews & Hasler 1943	8	17
Gerking 1957	3	2
Gerrish & Bristow 1979	3	10
Krecker 1939	7	Variable[2]
Mrachek 1966	8	Variable[3]
This study	5	14

[1] Number of replicates taken per plant species for a single sampling period

[2] Number of plants sampled not reported, expressed as length of plant sampled

[3] Number of samples reported as total for entire summer only (25-85 per plant species, number of times sampled not specified)

FIGURE LEGENDS

Figure 1. Epiphytic macroinvertebrate mesh bag sampler that is a modification of the folding quadrat sampler (Welch 1948). The sampler has the dimensions of 65 X 24 cm and is constructed from 200 μm and 500 μm mesh, 2 steel rings, and canvas. It is closed at the bottom by a drawstring.

Figure 2. Five common macrophyte species of Heron Lake, MI, USA. Undissected: a) *P. illinoensis* and b) *P. richardsonii*; Dissected: c) *P. pectinatus*, d) *M. spicatum*, and e) *Ranunculus sp.* Adapted from Fassett (1957).

Figure 3. The relationship between the number of samples and power at alpha = 0.05 and effect size = 0.872. The number of samples necessary are indicated by circles for plant architecture and triangles are for plant species.

Figure 4. The relationship between the number of samples and effect size for a) plant species and b) plant architecture (alpha = 0.05). Power levels shown are 0.9 (circles), 0.8 (triangles), and 0.5 (squares). For comparison, the lower two graphs show the enlarged region of 0-50 samples.

Figure 5. Macroinvertebrate a) density and b) biomass by plant species and architecture. Plant species are abbreviated as: Ill (*P. illinoensis),* Ric (*P. richardsonii),* Pec (*P. pectinatus)*, Spi (*M. spicatum)*, and Ran (*Ranunculus sp.).* Bars represent the standard error for each plant species.

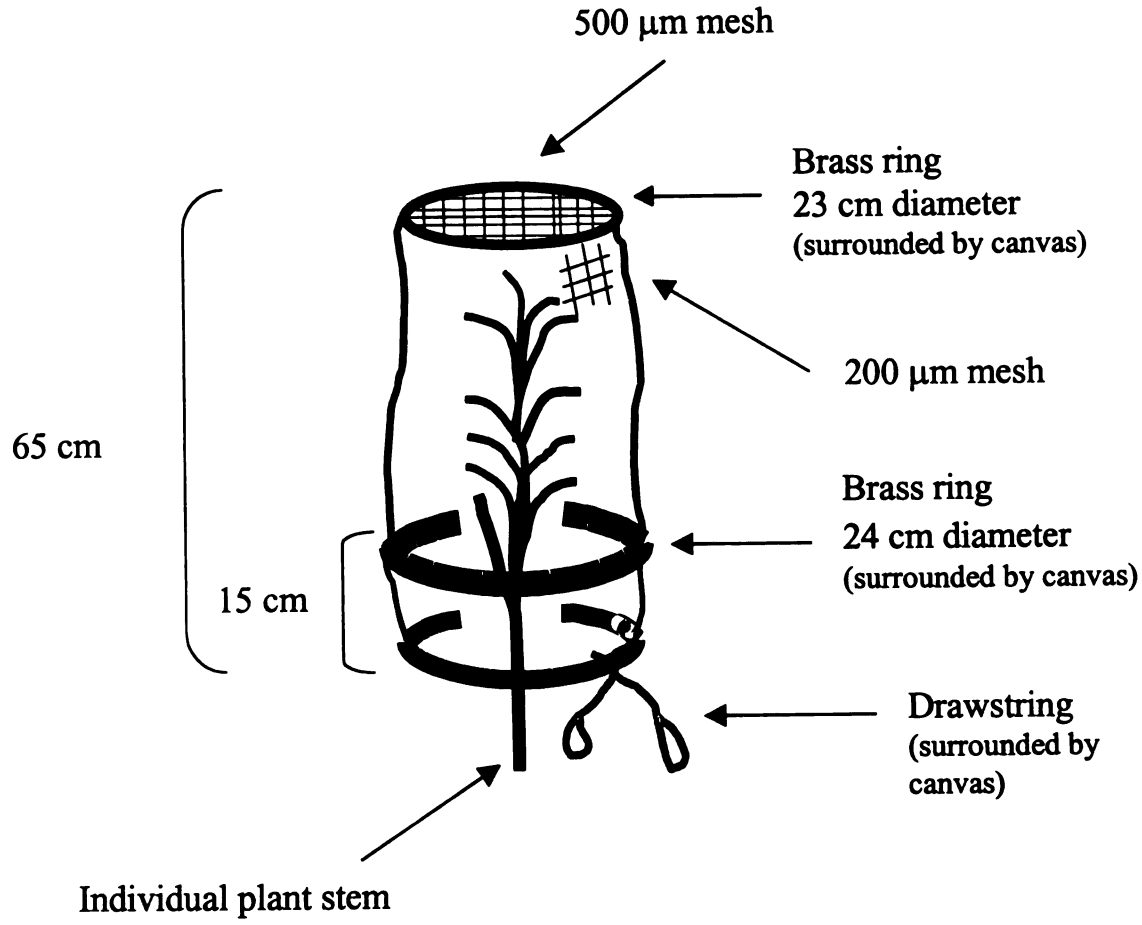
500 µm mesh
Brass ring
23 cm diameter
(surrounded by canvas)
200 µm mesh
65 cm
Brass ring
24 cm diameter
(surrounded by canvas)
15 cm
Drawstring
(surrounded by
canvas)
Individual plant stem

Figure 1

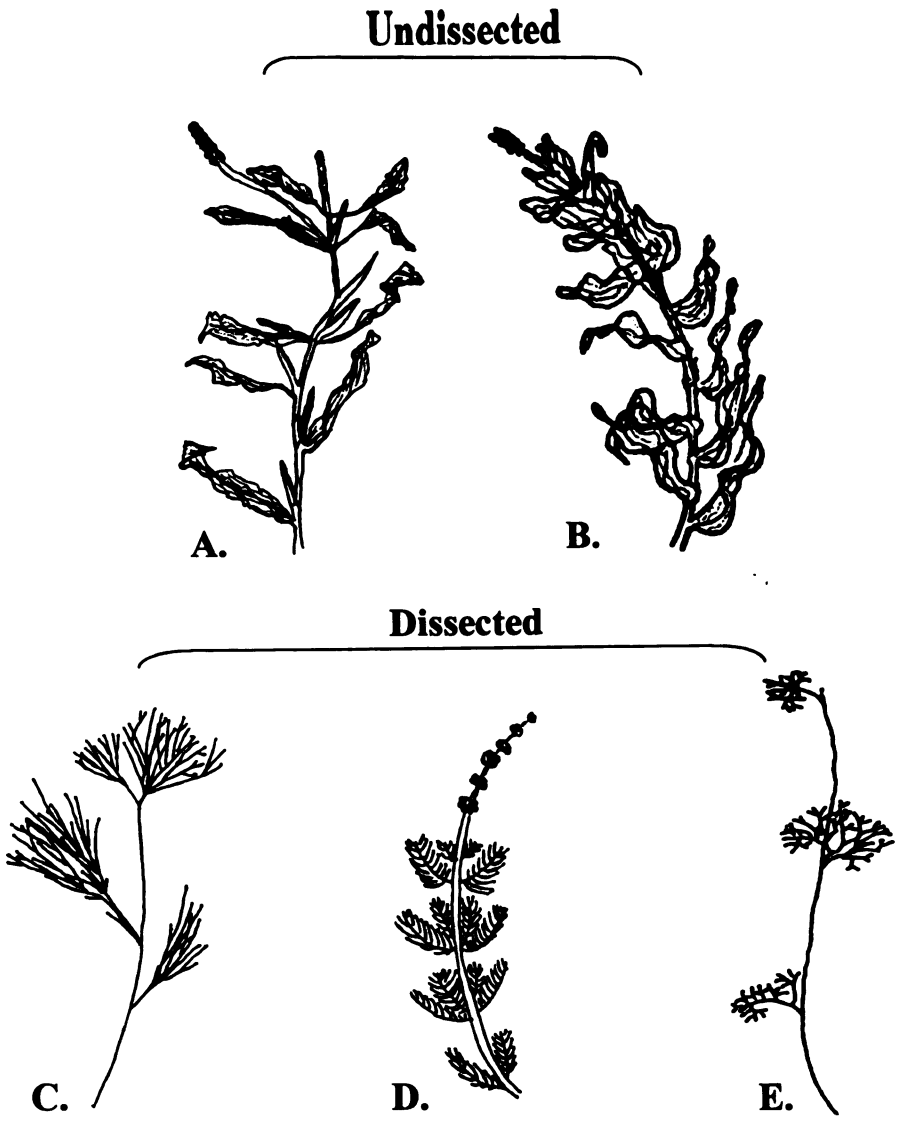

Figure 2

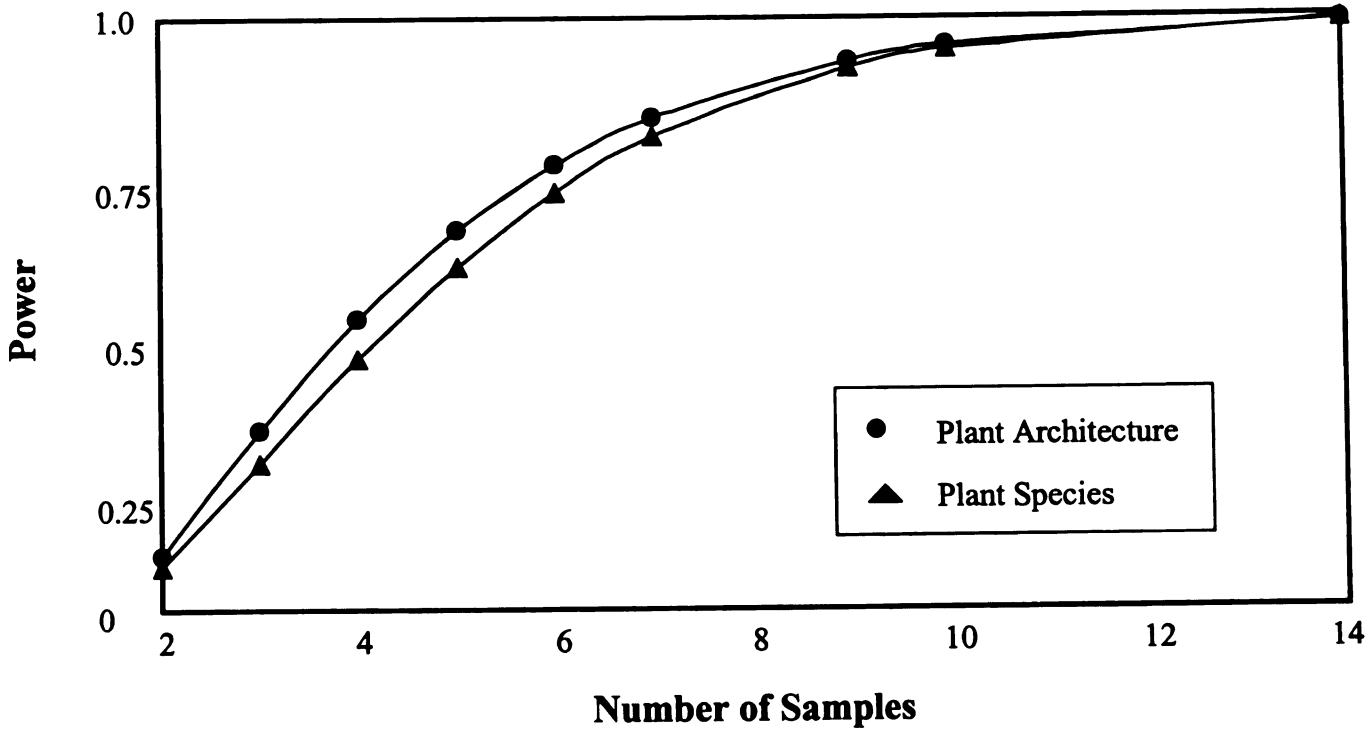
1.0
0.75
0.5
0.25
0
Power
2
4
6
8
10
12
14
Number of Samples
Plant Architecture
Plant Species

Figure 3

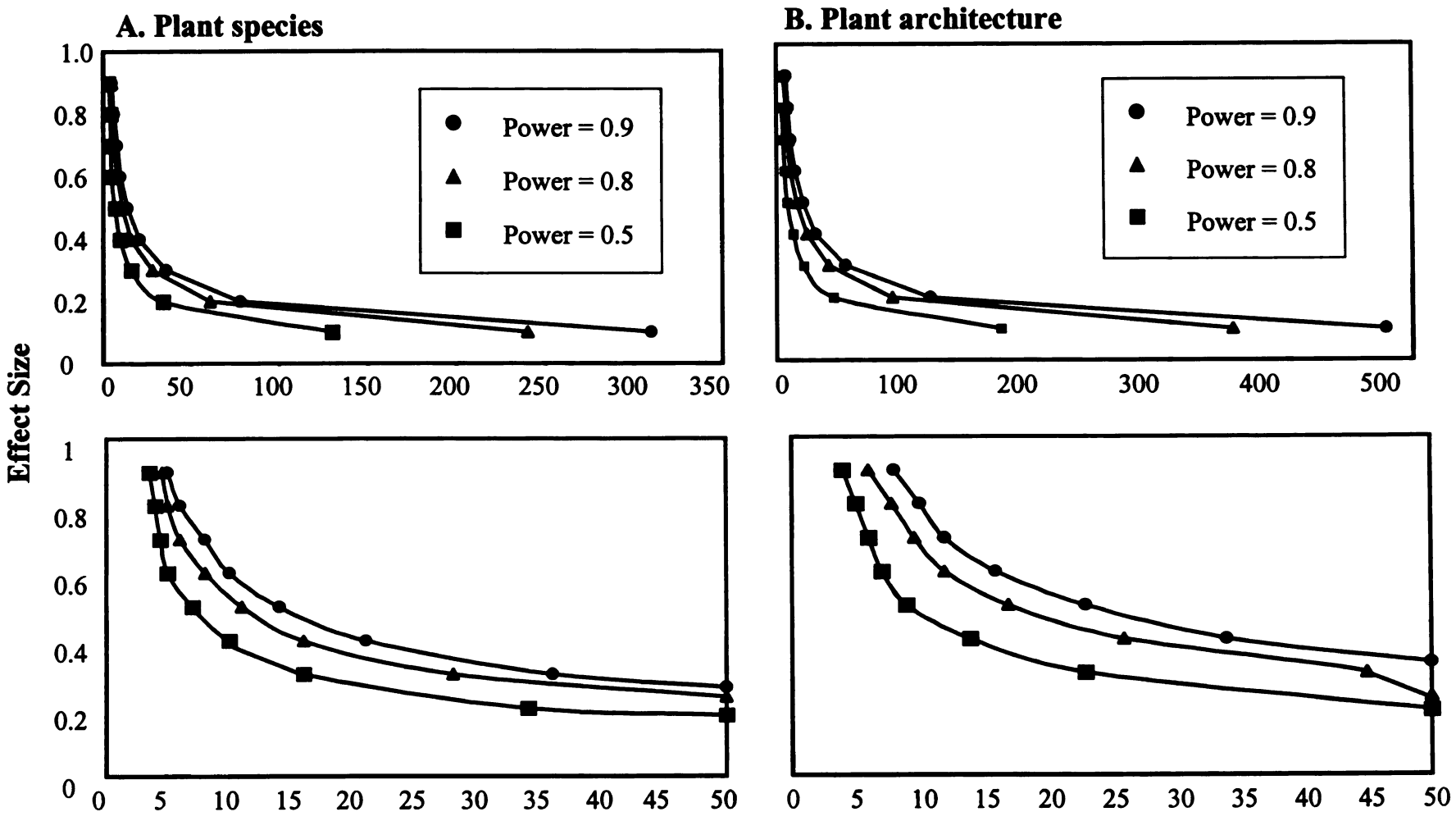
A. Plant species
B. Plant architecture
Power = 0.9
Power = 0.8
Power = 0.5
Effect Size
Number of Samples
1.0
0.8
0.6
0.4
0.2
0
1
0 50 100 150 200 250 300 350
0 100 200 300 400 500
0 5 10 15 20 25 30 35 40 45 50

Figure 4

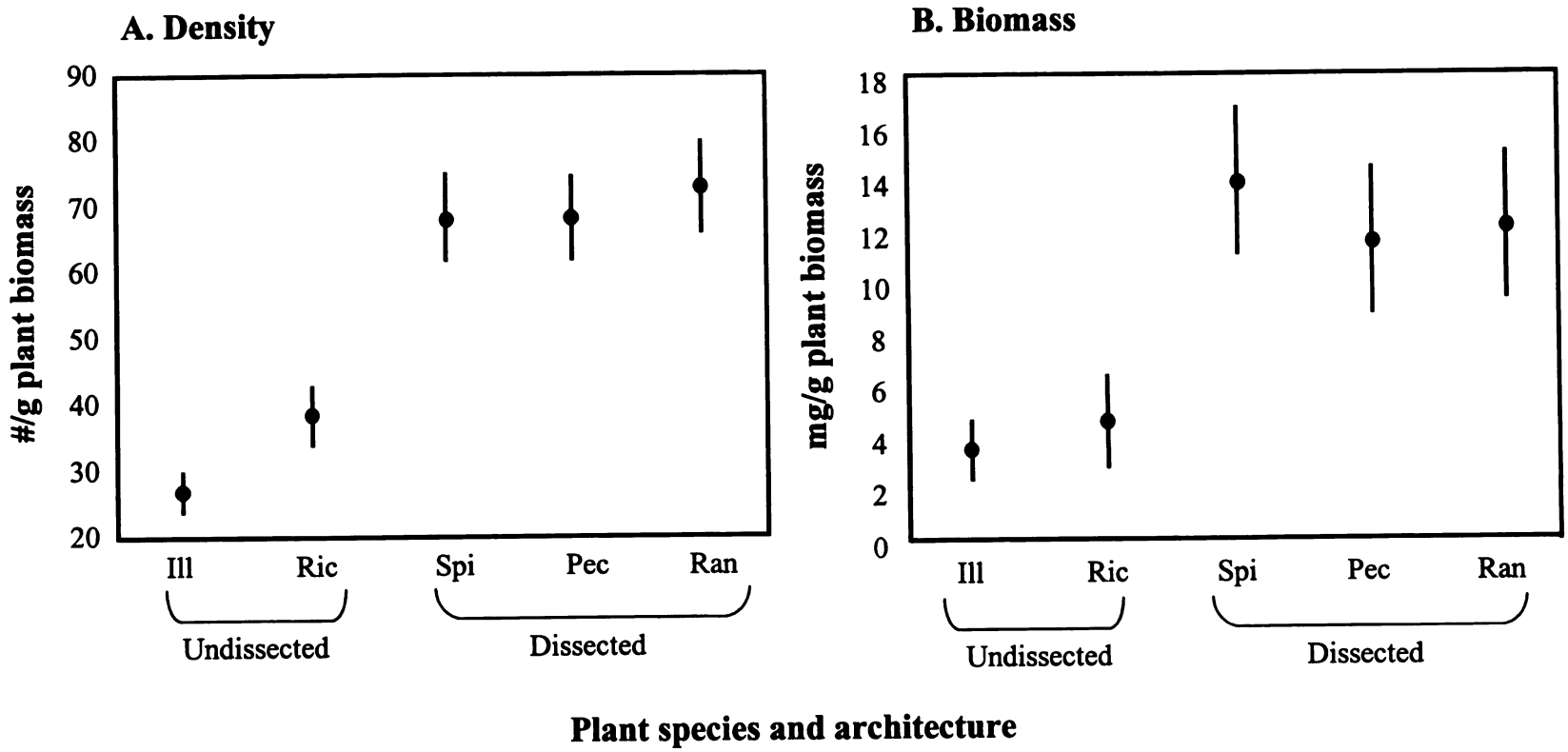
A. Density
#/g plant biomass
90
80
70
60
50
40
30
20
Ill
Ric
Spi
Pec
Ran
Undissected
Dissected
B. Biomass
mg/g plant biomass
18
16
14
12
10
8
6
4
2
0
Ill
Ric
Spi
Pec
Ran
Undissected
Dissected
Plant species and architecture

Figure 5

APPENDIX 2

Chapter 2 Tables and Figures

Table 1. Lake macrophyte characteristics. The percent-dissected plants sampled indicates the percent of plants sampled for epiphytic macroinvertebrates that had dissected-leaves. Lakes are numbered to correspond with numbers on Figure 1.

Lake	**% milfoil cover weighted (non-weighted)**	**% vegetated littoral zone covered by plants sampled for macroinvertebrates**	**% dissected plants sampled, *July***	**% dissected plants sampled, *August***
1. Camp	4 (21)	66	50	40
2. Big Crooked	8 (27)	75	40	40
3. Lobdell	19 (55)	84	40	60
4. Heron	25 (55)	75	40	40
5. Clear	39 (88)	56	40	40
6. Big Seven	41 (95)	95	60	60

Table 2. Studies included in the meta-anlyses. The number of times sampled is the number of times organisms were sampled within one season. The asterisk (*) indicates that the three ponds included plant species of only one architecture type, so we combined the three lakes for the meta-analyses.

Citation	Lake	Plants sampled	Sampler	# times sampled	State or Province, Country	Organisms sampled
Andrews and Hasler 1943	Mendota	*Ceratophyllum demersum, Potamogeton pectinatus, Myriophyllum spicatum, Vallisneria americana, Potamogeton amplifolius, Potamogeton richardsonii, Potamogeton americanus*	Zippered net	Once	WI, U.S.A.	Macro-invertebrates
Cheruvelil Chapter 1	Heron	*Myriophyllum spicatum, Potamogeton pectinatus, Potamogeton richardsonii, Potamogeton illinoensis, Potamogeton zosteriformis, Ranunculus sp.*	Mesh bag	Once	MI, U.S.A.	Macro-invertebrates
Chilton 1990	Onalaska	*Myriophyllum spicatum, Vallisneria americana, Ceratophyllum demersum*	Mesh bag	Multiple	WI, U.S.A	Macro-invertebrates
Cyr and Downing 1988a	Champlain	*Ceratophyllum demersum, Myriophyllum spicatum, Vallisneria americana, Najas flexilis, Elodea canadensis*	Box sampler	Once	Quebec, Canada	Macro-invertebrates

Cyr and Downing 1988a	Memphremagog	*Myriophyllum spicatum, Vallisneria americana*	Box sampler	Once	Quebec, Canada	Macro-invertebrates
Cyr and Downing 1988a	8 lakes: Brome, Des Isles, Echo, Fournelle, Ludger, Magog, Massawippi, Quenouilles	*Elodea canadensis, Myriophyllum spicatum, Vallisneria americana, Potamogeton robbinsii, Potamogeton amplifolius, Utricularia spp.*	Box sampler	Once	Quebec, Canada	Macro-invertebrates
Dejoux 1983	Chad	*Potamogeton schweinfurthi, Najas spp., Ceratophyllum demersum*	Phyto-isolator	Unknown	5 African countries	Chironomids only
Gerrish and Bristow 1979	Opinicon	*Myriophyllum spicatum, Vallisneria americana, Potamogeton richardsonii*	Plastic bags	Multiple	Ontario, Canada	Macro-invertebrates
Keast 1984	Opinicon	*Myriophyllum spicatum, Vallisneria americana, Potamogeton robbinsii*	Plastic bags	Multiple	Ontario, Canada	Macro-invertebrates
Kornijow 1989	Piaseczno	*Potamogeton praelongus, Myriophyllum alterniflorum, Ceratophyllum demersum, Elodea canadensis*	Self-made apparatus	Multiple	Poland	Macro-invertebrates
Kornijow 1989	Glebokie	*Potamogeton lucens, Myriophyllum spicatum, Ceratophyllum demersum*	Self-made apparatus	Multiple	Poland	Macro-invertebrates

Krull 1970	Montezuma Main Pool	*Ceratophyllum demersum, Potamogeton foliosus, Potamogeton pectinatus, Heteranthera dubia*	Ekman Dredge & Plastic bag	Multiple	NY, U.S.A.	Macro-invertebrates
Krull 1970	Black Duck Pond	*Utricularia vulgaris, Elodea canadensis*	Ekman Dredge & Plastic bag	Multiple	NY, U.S.A.	Macro-invertebrates
Krull 1970	3 ponds*: Montezuma Spring Hole, Reagan Pond, Labrador Pond	*Najas marina, Najas flexilis, Myriophyllum spicatum*	Ekman Dredge and Plastic bag	Multiple	NY, U.S.A.	Macro-invertebrates
Mrachek 1966	Clear Lake	*Ceratophyllum demersum, Potamogeton pectinatus, Najas flexilis, Myriophyllum spicatum, Potamogeton richardsonii, Potamogeton nodosus*	Net	Multiple	IA, U.S.A.	Macro-invertebrates
Parson and Matthews 1995	Cannery Pond	*Ceratophyllum demersum, Potamogeton pusillus, Potamogeton natans*	Net	Multiple	WA, U.S.A.	Macro-invertebrates
Pip and Stewart 1976	Manitoba	*Potamogeton pectinatus, Potamogeton richardsonii*	Box-like sampler	Multiple	Manitoba, Canada	Snails only
Soszka 1975	Mikolajskie	*Elodea canadensis, Myriophyllum spicatum, Potamogeton perfoliatus, Potamogeton lucens*	Plastic bags	Multiple	Poland	Macro-invertebrates

Table 3. Lake characteristics. TP stands for total phosphorous and TN stands for total nitrogen. Lakes are numbered to correspond with numbers on Figure 1 and the littoral zone is defined as the area from shore to the deepest point at which plants consistently occur.

Lake	County	Latitude, Longitude	Lake Area, ha	Mean Depth, m (max)	% Littoral	Secchi depth, m	Epi-limnion depth, m	Pelagic Chl *a*, µg/L	TN, µg/L	TP, µg/L
1. Camp	Kent	43.11 N, 85.40 W	43.5	7.3 (15)	35	3.7	4.6	9.5	478.6	32.3
2. Big Crooked	Kent	43.03 N, 85.23 W	63.9	4.5 (18.3)	54	3.3	4.0	8.0	496.9	25.6
3. Lobdell	Genesee/ Livingston	42.47 N, 83.50 W	196.9	2.7 (21.3)	88	3.4	4.5	3.9	431.4	16.7
4. Heron	Oakland	42.81 N, 83.52 W	53.2	3.3 (12.2)	75	3.7	5.0	5.8	403.7	15.0
5. Clear	Barry	42.30 N, 85.16 W	73.4	2.2 (4.6)	89	3.6	4.2	11.6	543.9	23.0
6. Big Seven	Oakland	42.49 N, 83.40 W	64.2	3.2 (15)	82	3.7	4.3	3.7	421.7	18.2

Table 4. The six most dominant macroinvertebrate taxa (total ≥ 70% of total macroinvertebrate density and biomass) by macroinvertebrate density and biomass and their associated functional feeding group across all 6 lakes. Percentages refer to the percentage those six dominant taxa make up of the total taxa

Taxa, Functional feeding group (by macroinvertebrate density)		**Taxa, Functional feeding group (by macroinvertebrate biomass)**	
July	**August**	**July**	**August**
Chironomidae: Orthocladiinae, Shredder Chironomini, Gathering Collector Oligochaeta: Naididae, Gathering Collector Gastropoda: Hydrobiidae, Scraper Amphipoda: Hyallela, Shredder Turbellaria: Planaridae, Predator	Chironomidae: Tanypodinae, Predator Odonata: Coenagrionidae, Predator Libellulidae, Predator Ostracoda, Filtering Collector Lepidoptera: Pyralidae, Shredder Hydracarina, Predator	Chironomidae: Orthocladiinae, Shredder Oligochaeta: Naididae, Gathering Collector Gastropoda: Physidae, Scraper Hydrobiidae, Scraper Planorbidae, Scraper Amphipoda: Hyallela, Shredder	Chironomidae: Orthocladiinae, Shredder Odonata: Coenagrionidae, Predator Oligochaeta: Naididae, Gathering Collector Gastropoda: Hydrobiidae, Scraper Planorbidae, Scraper Amphipoda: Hyallela, Shredder
79%	70%	75%	78%

Table 5. p-value, power, and number of plant species that needed to be sampled to detect differences between dissected and undissected plants with an alpha of 0.05 within each lake. Numbers in parentheses indicate average number of plant species within architecture groups actually sampled. Bold numbers indicate high power (> 0.7) and asterisks indicate significant differences between dissected and undissected plants at alpha ≤ 0.05. Lakes are numbered to correspond with numbers on Figure 1.

	Macroinvertebrate density		**Macroinvertebrate biomass**	
Lake	**July** p-value, power, N	**August** p-value, power, N	**July** p-value, power, N	**August** p-value, power, N
1. Camp	**0.051, 0.758, 3 (2)**	**0.004, 1.000, 2 (2.5)***	0.114, 0.429, 4 (2)	**0.023, 1.000, 2 (2.5)***
2. Big Crooked	0.155, 0.602, 4 (2.5)	**0.120, 0.857, 3 (2.5)**	0.283, 0.269, 9 (2.5)	0.193, 0.446, 5 (2.5)
3. Lobdell	0.291, 0.210, 12 (2.5)	0.983, 0.057, 225 (2.5)	0.264, 0.270, 9 (2.5)	0.875, 0.050, 34275 (2.5)
4. Heron	0.112, 0.690, 4 (2.5)	0.266, 0.305, 8 (2.5)	**0.599, 0.819, 3 (2.5)**	0.320, 0.334, 7 (2.5)
5. Clear	0.349, 0.303, 8 (2.5)	0.148, 0.678, 4 (2.5)	**0.072, 0.819, 3 (2.5)**	0.540, 0.115, 26 (2.5)
6. Big Seven	0.464, 0.245, 10 (2.5)	0.519, 0.088, 43 (2.5)	0.341, 0.416, 6 (2.5)	0.195, 0.489, 5 (2.5)
Six lakes pooled	**0.269, 0.712, 24 (14.5)**	**0.009, 0.958, 12 (15)***	0.162, 0.658, 27 (14.5)	**0.040, 0.828, 19 (15)***

Table 6. Adjusted Bonferonni p-values from an ANOVA test for differences between mean macroinvertebrate densities on dissected versus undissected plants for all 6 lakes in July and August. Bolded numbers represent values significant at alpha < 0.05. Lakes are numbered to correspond with numbers on Figure 1.

	July						August					
Lake	**Camp**	**Big Crooked**	**Lobdell**	**Heron**	**Clear**	**Big Seven**	**Camp**	**Big Crooked**	**Lobdell**	**Heron**	**Clear**	**Big Seven**
1. Camp	-	-	-	-	-	-	-	-	-	-	-	-
2. Big Crooked	1.000	-	-	-	-	-	0.848	-	-	-	-	-
3. Lobdell	0.273	1.000	-	-	-	-	**0.009**	0.729	-	-	-	-
4. Heron	**0.001**	**0.007**	0.370	-	-	-	**0.000**	**0.026**	1.000	-	-	-
5. Clear	0.907	1.000	1.000	0.094	-	-	0.162	1.000	1.000	0.176	-	-
6. Big Seven	**0.001**	**0.006**	0.292	1.000	0.073	-	**0.000**	**0.002**	0.278	1.000	**0.014**	-

Table 7. Adjusted Bonferonni p-values from an ANOVA test for differences between mean macroinvertebrate biomass on dissected versus undissected plants for all 6 lakes in July and August. Bolded numbers represent values significant at alpha < 0.05. Lakes are numbered to correspond with numbers on Figure 1.

	July						August					
Lake	**Camp**	**Big Crooked**	**Lobdell**	**Heron**	**Clear**	**Big Seven**	**Camp**	**Big Crooked**	**Lobdell**	**Heron**	**Clear**	**Big Seven**
1. Camp	-	-	-	-	-	-	-	-	-	-	-	-
2. Big Crooked	**0.043**	-	-	-	-	-	0.512	-	-	-	-	-
3. Lobdell	1.000	1.000	-	-	-	-	1.000	**0.010**	-	-	-	-
4. Heron	1.000	1.000	1.000	-	-	-	1.000	1.000	**0.046**	-	-	-
5. Clear	0.646	1.000	1.000	1.000	-	-	1.000	1.000	0.054	1.000	-	-
6. Big Seven	1.000	1.000	1.000	1.000	1.000	-	1.000	**0.040**	1.000	0.165	0.193	-

FIGURE LEGENDS

Figure 1. Map of Michigan counties and study lakes. 1 = Camp Lake, 2 = Big Crooked Lake, 3 = Lobdell Lake, 4 = Heron Lake, 5 = Clear Lake, 6 = Big Seven Lake.

Figure 2. Weighted frequency of plant species in each lake in the vegetated littoral zone August 1999 (J.D. Madsen *unpublished data*). Lakes are in order from low percent milfoil cover (1) to high percent milfoil cover (6). Full scientific names are: *Cabomba caroliana* Gray, *Ceratophyllum demersum* L., *Elodea canadensis* Michx., *Heteranthera dubia* Jacq., *Myriophyllum spicatum* L., *Najas spp.*, *Potamogeton amplifolius* Tuckerm., *Potamogeton crispus* L., *Potamogeton foliosus* G., *Potamogeton gramineus* L., *Potamogeton illinoensis* Morong., *Potamogeton natans* L., *Potamogeton nodosus* Poir., *Potamogeton pectinatus* L., *Potamogeton praelongus* Wulf., *Potamogeton pusillus* L., *Potamogeton richardsonii* Benn., *Potamogeton robbinsii* Oakes., *Potamogeton strictifolius* Benn., *Potamogeton sp.*, *Potamogeton zosteriformis* Fernald., *Ranunculus sp.*, *Utricularia spp.*, *Valisneria americana* Michx, *Zannichellia sp.* An asterisk (*) indicates plant species that were sampled for epiphytic macroinvertebrates.

Figure 3. The functional feeding groups by macroinvertebrate density (#) and biomass (mg) with the six lakes pooled. Percentages refer to the percentage each functional feeding group makes up of the total macroinvertebrate density or biomass in July and August, respectively.

Figure 4. Average macroinvertebrate density (#) and biomass (mg) per g plant biomass within functional feeding groups in July (A and C) and August (B and D). Data were analyzed by pooling lakes. Bars represent the standard error for each functional feeding group. F. and G. collector stands for filtering and gathering collectors, respectively.

Figure 5. Average macroinvertebrate density (#) (A and B) and biomass (mg) (C and D) per g plant biomass for the three (July) and four (August) plant species that were sampled in 3 - 6 of the lakes. Data were analyzed by pooling lakes. Large circles represent plant species not sampled. Plant species that are italicized are dissected and plant species that are not italicized are undissected. Bars represent the standard error for each plant species.

Figure 6. Average macroinvertebrate density (#) (A and B) and biomass (mg) (C and D) per g plant biomass for the two plant architecture groups. Data were analyzed by pooling lakes. Bars represent the standard error for each architecture type.

Figure 7. Effect size (natural log response ratio) for each study included in the unweighted meta-analysis (A) and the weighted meta-analysis (B). An effect size greater than zero means that dissected plants exhibit higher macroinvertebrate densities than undissected plants. Filled diamonds represent the 18 studies included in the unweighted meta-analysis, empty circles represent the six individual lakes in this study, the filled cross represents the pooled six lakes from this study (not included in the weighted meta-analysis) and the filled square is the mean effect size (calculated as the weighted and unweighted natural log response ratio of the mean macroinvertebrate density on dissected plants/ mean macroinvertebrate density on undissected plants). An asterisk (*) indicates those studies that averaged macroinvertebrate density across multiple lakes. [1] refers to the pooled six lakes in this study, which is shown for comparison only and was not included in the weighted meta-analysis. Memph. is short for Memphremagog.

Figure 8. The proportion of dissected plants present across lakes along the weighted percent milfoil gradient in August (J.D. Madsen *unpublished data*).

Figure 9. Average macroinvertebrate density (#) and biomass (mg) per g plant biomass along the weighted percent milfoil gradient in July (A and C) and August (B and D). Data were analyzed across lakes and each data points represent the average density or biomass for each plant species within each lake.

Figure 10. Average density (#) and biomass (mg) of odonates and chironomids per g plant biomass in Camp Lake in July and August.

Figure 11. Total macroinvertebrate density (#) and biomass (mg) per g plant biomass (A and B) and total macroinvertebrate density (#) and biomass (mg) per m 2 vegetated littoral zone (C and D) across lakes along the weighted percent milfoil gradient in July and August.

Figure 12. Total macroinvertebrate density (#) and biomass associated with milfoil per g plant biomass across lakes along the weighted percent milfoil gradient in July (A and C) and August (B and D).

Figure 13. Cumulative summer (July and August) bluegill densities (#) per m2 across lakes along the weighted percent milfoil gradient (R.D. Valley *unpublished data*). No data was collected from Camp Lake.

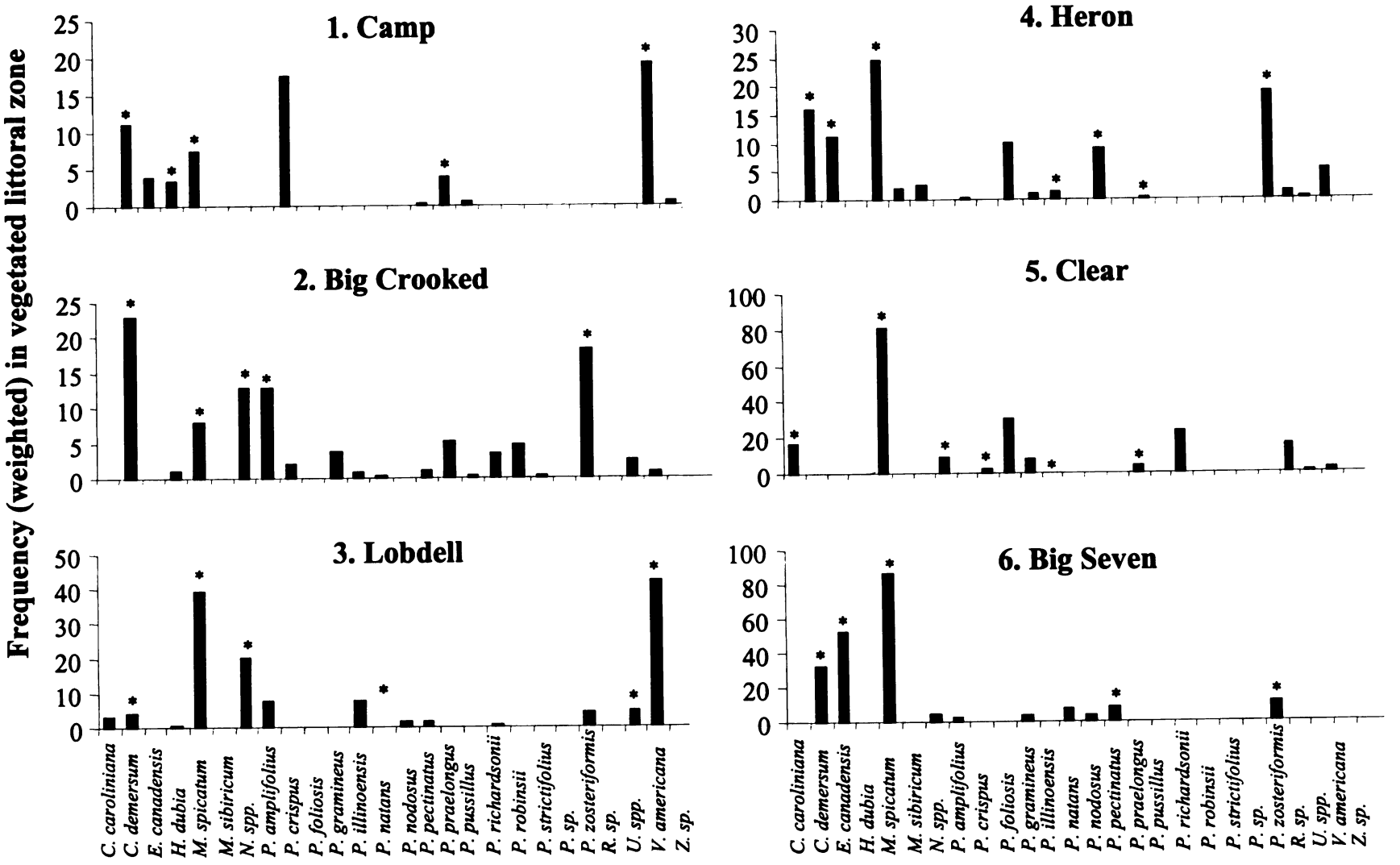
1. Camp
2. Big Crooked
3. Lobdell
4. Heron
5. Clear
6. Big Seven
Frequency (weighted) in vegetated littoral zone
Plant species
C. caroliniana
C. demersum
E. canadensis
H. dubia
M. spicatum
M. sibiricum
N. spp.
P. amplifolius
P. crispus
P. foliosis
P. gramineus
P. illinoensis
P. natans
P. nodosus
P. pectinatus
P. praelongus
P. pussillus
P. richardsonii
P. robinsii
P. strictifolius
P. sp.
P. zosteriformis
R. sp.
U. spp.
V. americana
Z. sp.

Figure 2

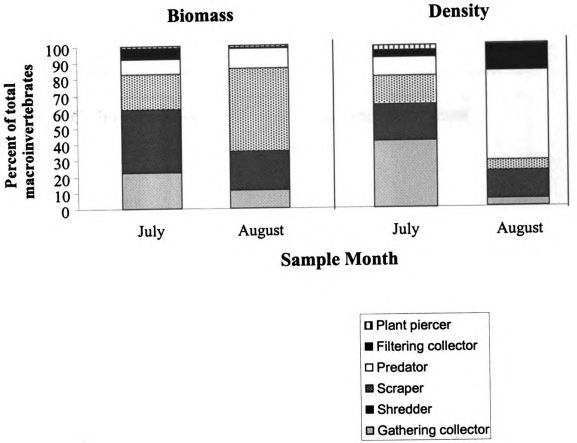
Biomass
Density
Percent of total macroinvertebrates
100
90
80
70
60
50
40
30
20
10
0
July
August
July
August
Sample Month
Plant piercer
Filtering collector
Predator
Scraper
Shredder
Gathering collector

Figure 3

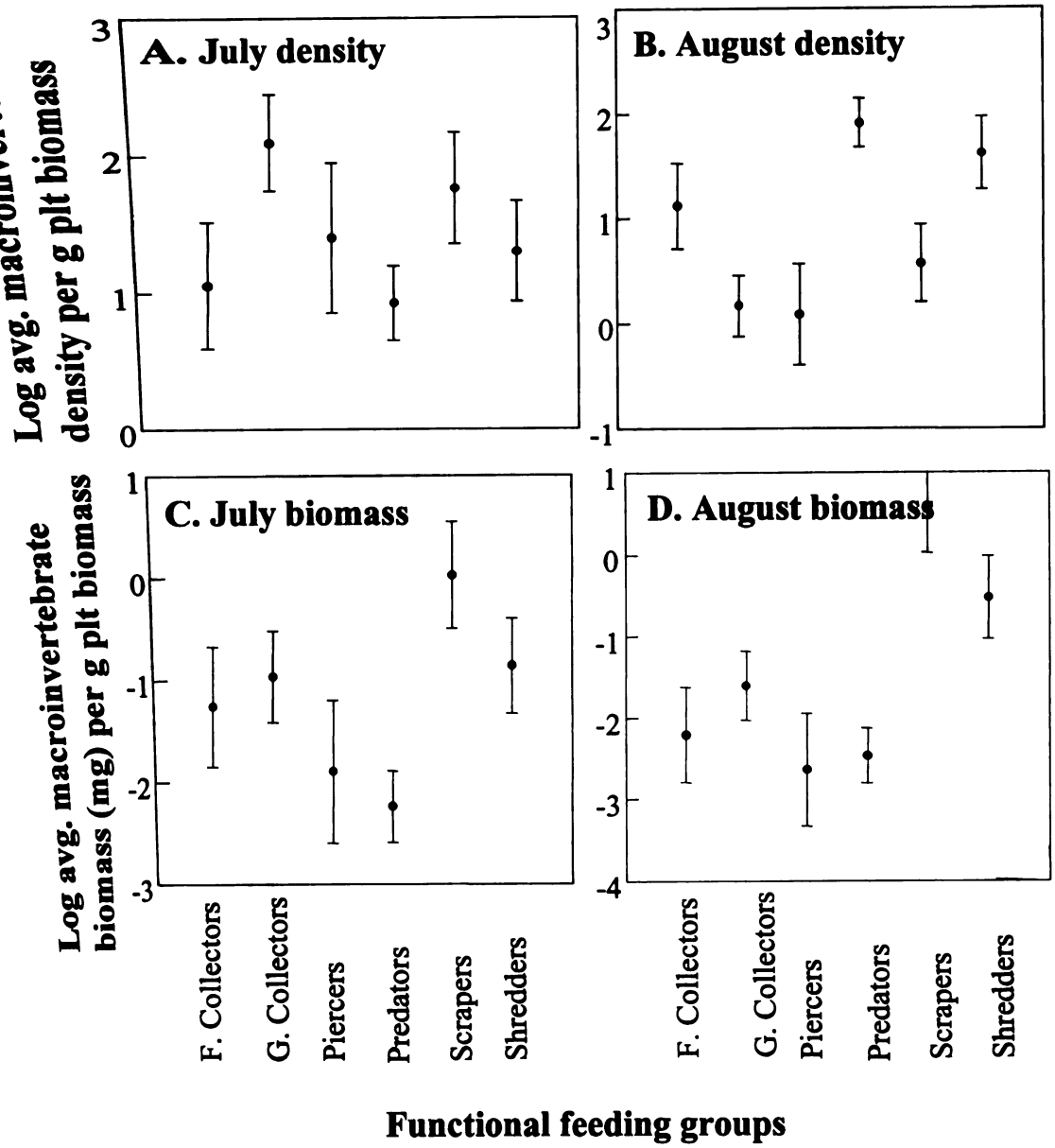
A. July density
B. August density
C. July biomass
D. August biomass
Log avg. macroinvertebrate density per g plt biomass
Log avg. macroinvertebrate biomass (mg) per g plt biomass
F. Collectors
G. Collectors
Piercers
Predators
Scrapers
Shredders
Functional feeding groups

Figure 4

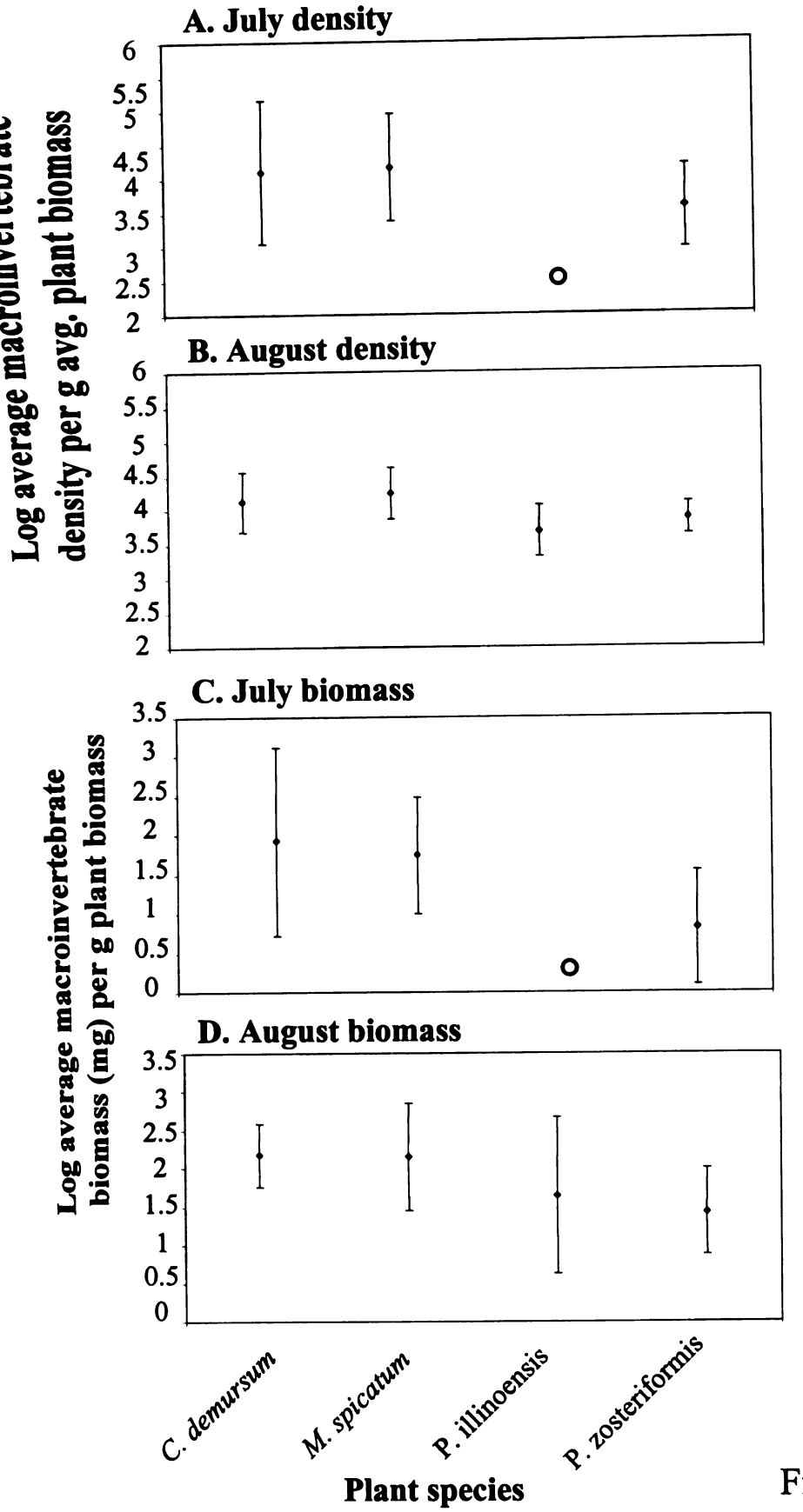
A. July density
B. August density
C. July biomass
D. August biomass
Log average macroinvertebrate density per g avg. plant biomass
Log average macroinvertebrate biomass (mg) per g plant biomass
6
5.5
5
4.5
4
3.5
3
2.5
2
3.5
3
2.5
2
1.5
1
0.5
0
C. demursum
M. spicatum
P. illinoensis
P. zosteriformis
Plant species

Figure 5

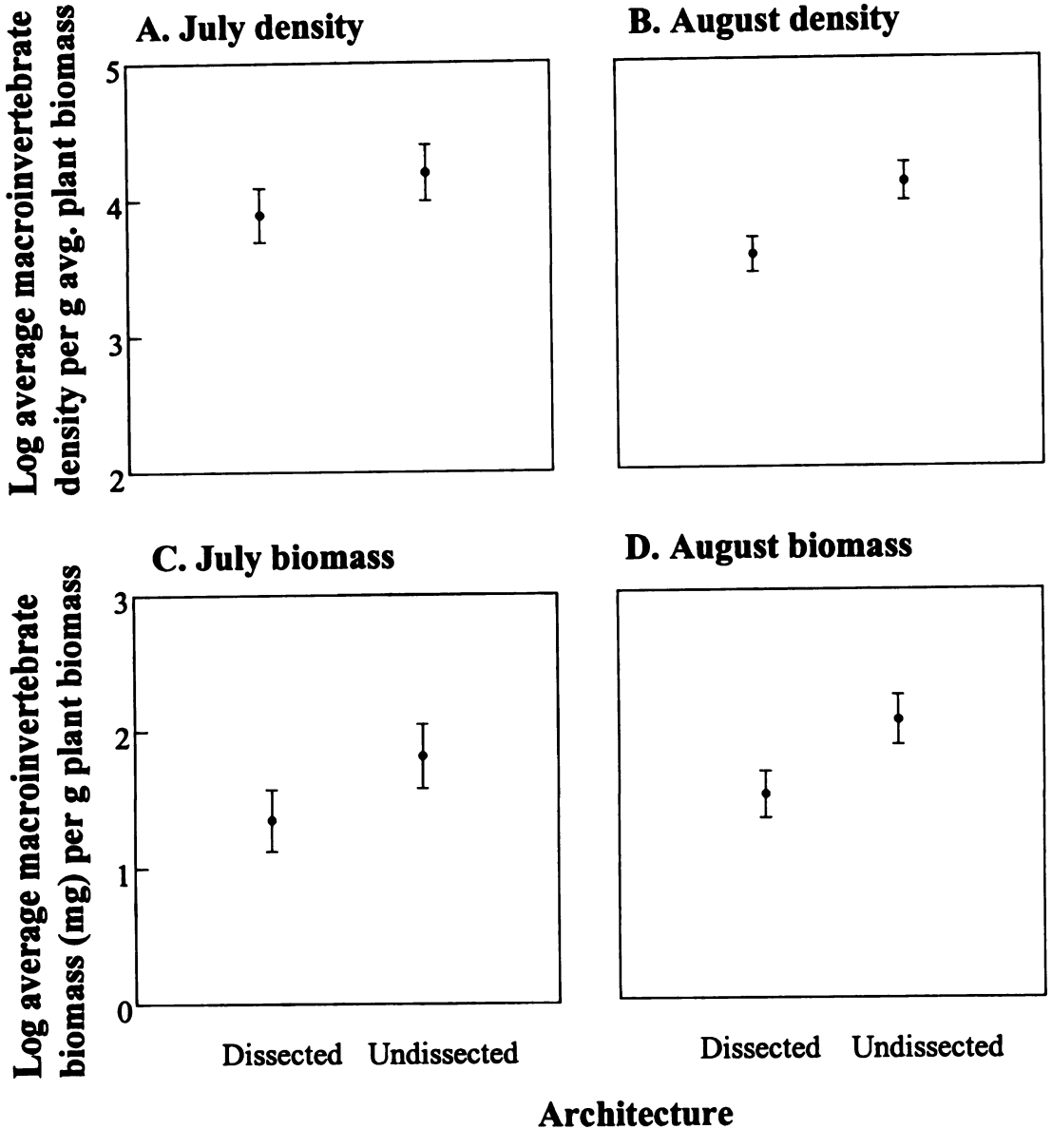
A. July density
B. August density
C. July biomass
D. August biomass
Log average macroinvertebrate density per g avg. plant biomass
Log average macroinvertebrate biomass (mg) per g plant biomass
5
4
3
2
1
0
Dissected
Undissected
Dissected
Undissected
Architecture

Figure 6

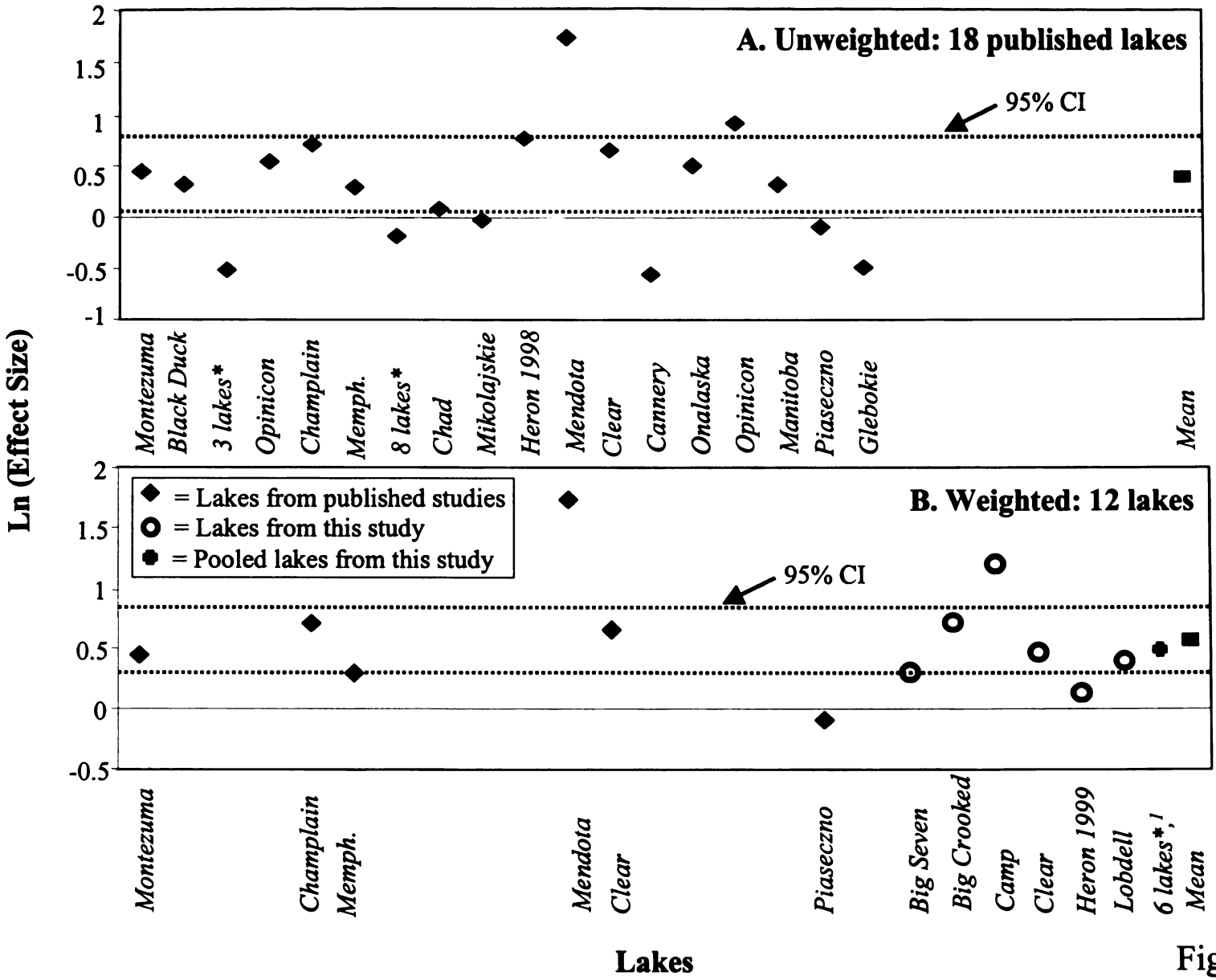
A. Unweighted: 18 published lakes
95% CI
2
1.5
1
0.5
0
-0.5
-1
Montezuma
Black Duck
3 lakes*
Opinicon
Champlain
Memph.
8 lakes*
Chad
Mikolajskie
Heron 1998
Mendota
Clear
Cannery
Onalaska
Opinicon
Manitoba
Piaseczno
Glebokie
Mean
B. Weighted: 12 lakes
= Lakes from published studies
= Lakes from this study
= Pooled lakes from this study
95% CI
2
1.5
1
0.5
0
-0.5
Montezuma
Champlain
Memph.
Mendota
Clear
Piaseczno
Big Seven
Big Crooked
Camp
Clear
Heron 1999
Lobdell
6 lakes*,[1]
Mean
Ln (Effect Size)
Lakes

Figure 7

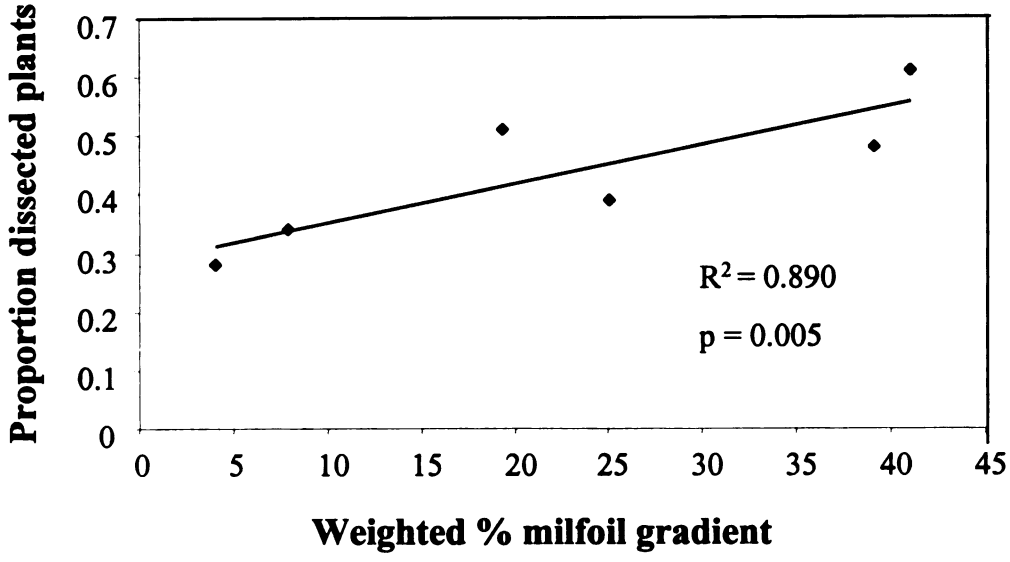
Proportion dissected plants
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
5
10
15
20
25
30
35
40
45
R² = 0.890
p = 0.005
Weighted % milfoil gradient

Figure 8

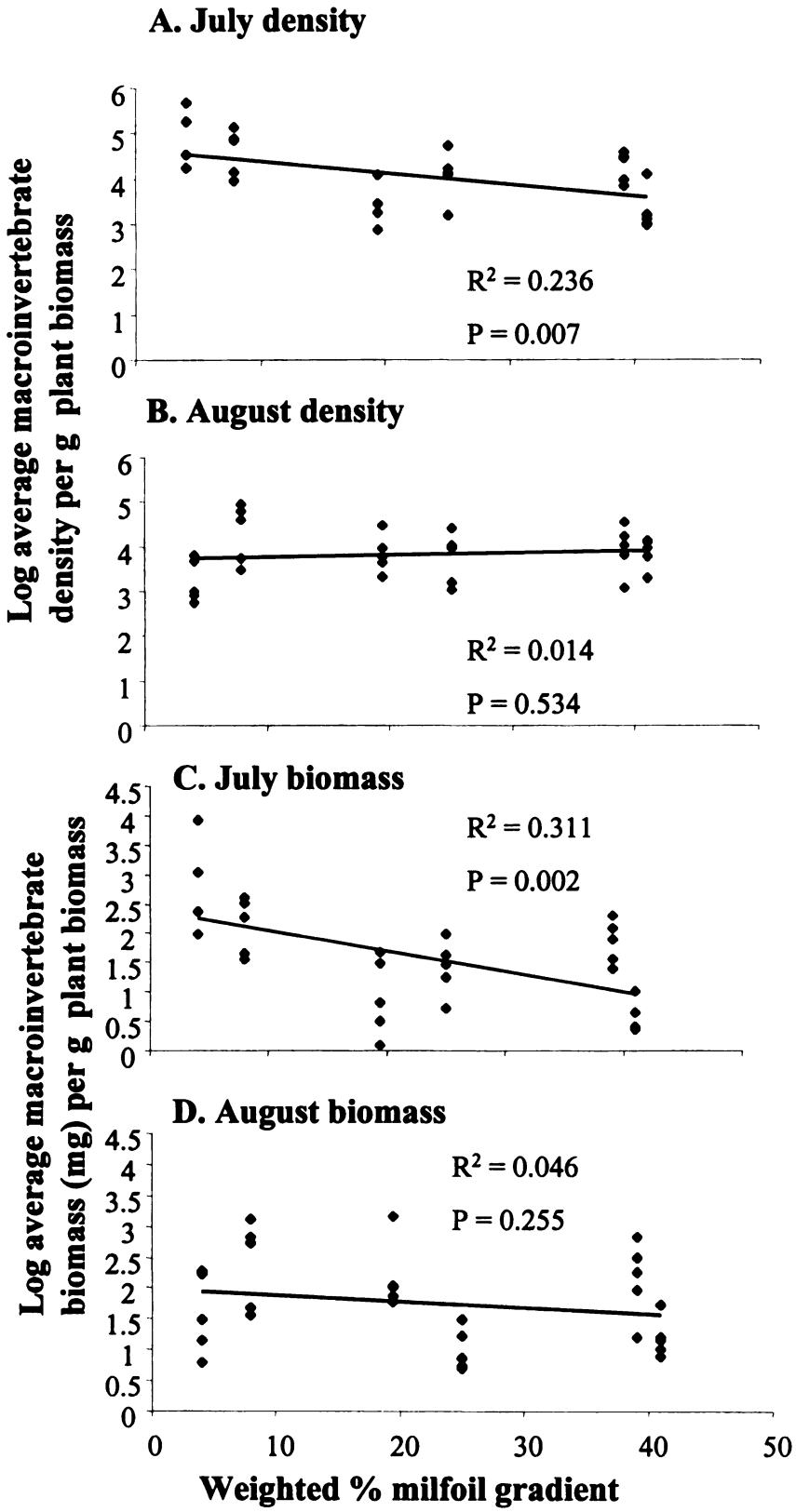
A. July density
Log average macroinvertebrate density per g plant biomass
R² = 0.236
P = 0.007
B. August density
R² = 0.014
P = 0.534
C. July biomass
Log average macroinvertebrate biomass (mg) per g plant biomass
R² = 0.311
P = 0.002
D. August biomass
R² = 0.046
P = 0.255
Weighted % milfoil gradient

Figure 9

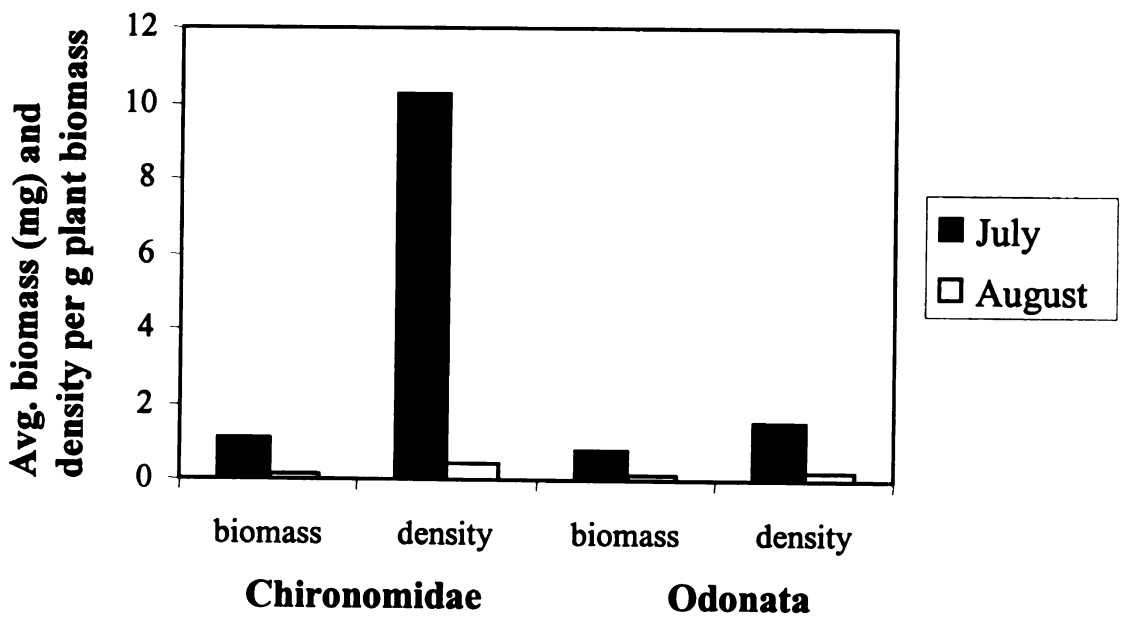
Avg. biomass (mg) and density per g plant biomass
12
10
8
6
4
2
0
biomass
density
biomass
density
Chironomidae
Odonata
July
August

Figure 10

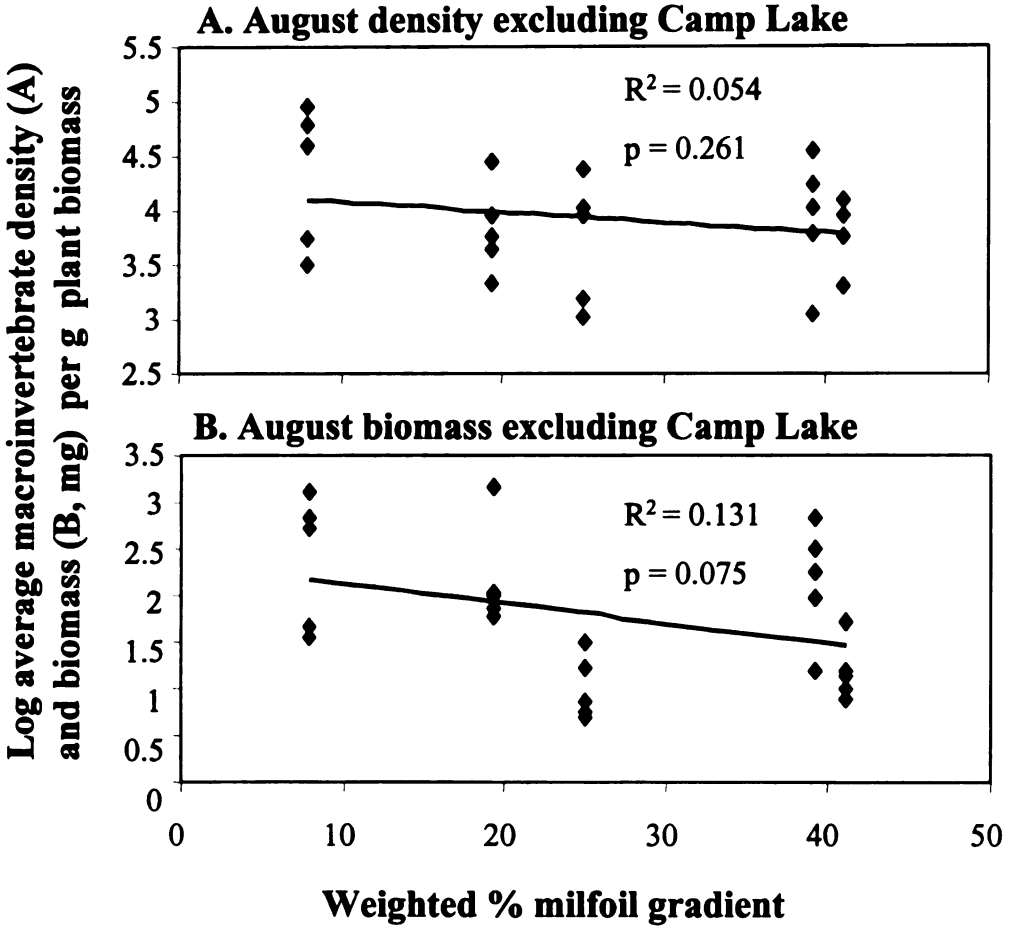
A. August density excluding Camp Lake
$R^2 = 0.054$
p = 0.261
B. August biomass excluding Camp Lake
$R^2 = 0.131$
p = 0.075
Log average macroinvertebrate density (A) and biomass (B, mg) per g plant biomass
Weighted % milfoil gradient
5.5
5
4.5
4
3.5
3
2.5
3.5
3
2.5
2
1.5
1
0.5
0
0
10
20
30
40
50

Figure 11

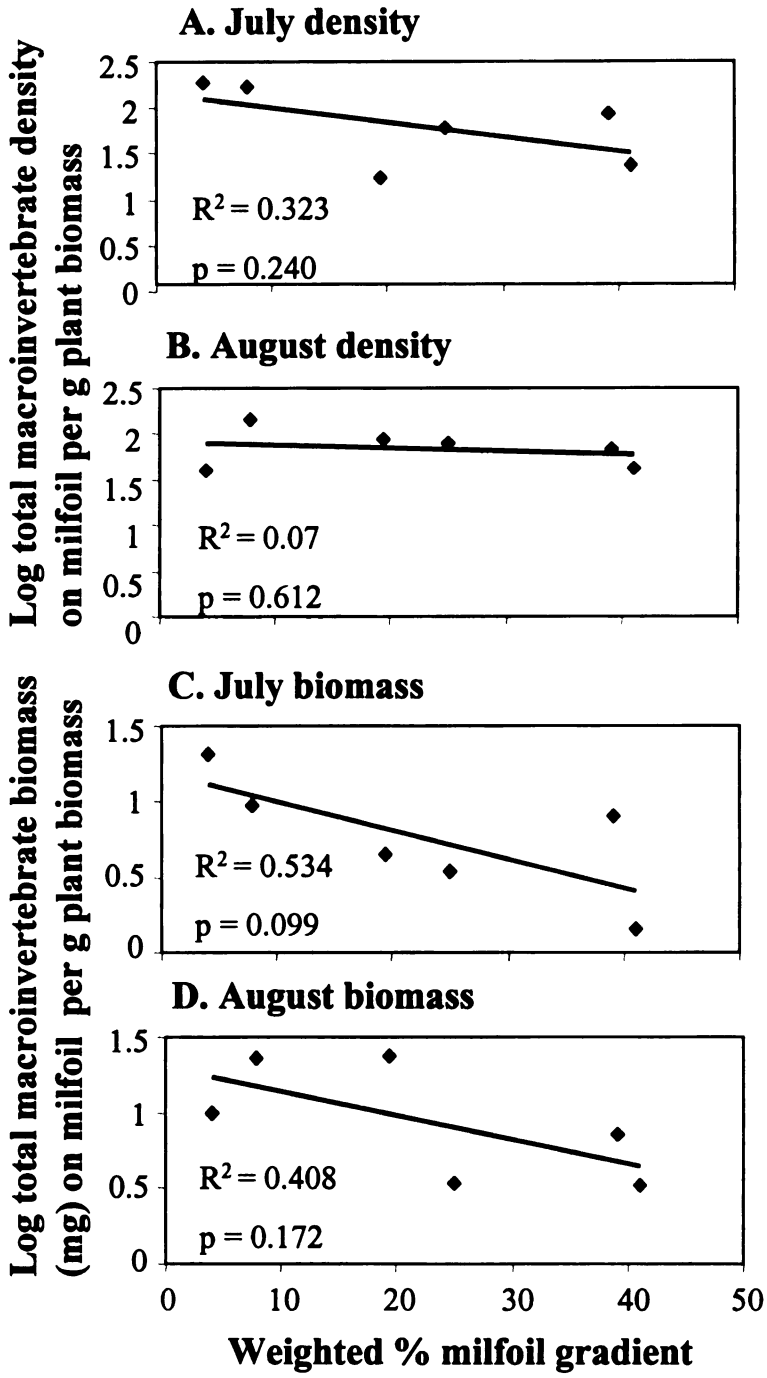
A. July density
B. August density
C. July biomass
D. August biomass
Log total macroinvertebrate density on milfoil per g plant biomass
Log total macroinvertebrate biomass (mg) on milfoil per g plant biomass
R² = 0.323
p = 0.240
R² = 0.07
p = 0.612
R² = 0.534
p = 0.099
R² = 0.408
p = 0.172
0
0.5
1
1.5
2
2.5
0
10
20
30
40
50
Weighted % milfoil gradient

Figure 12

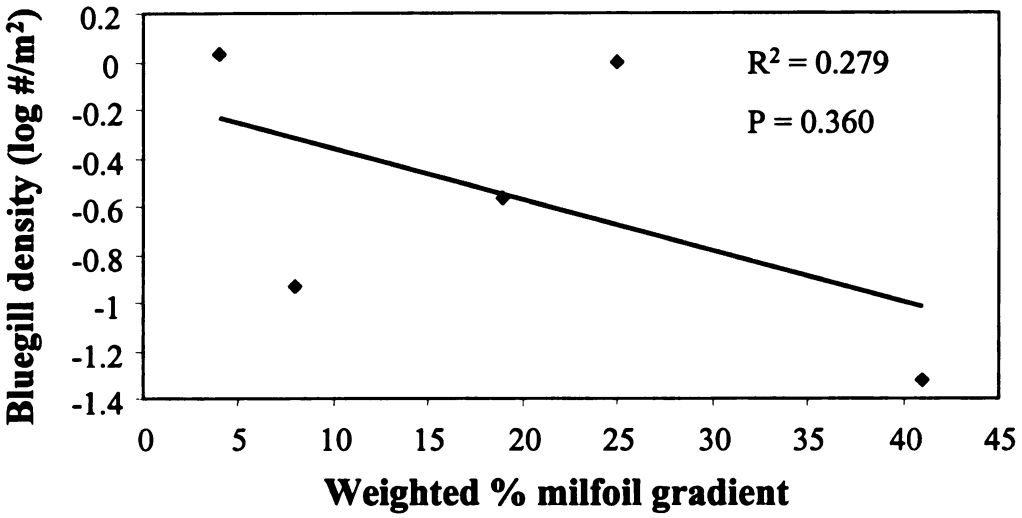
Bluegill density (log #/m²)
0.2
0
-0.2
-0.4
-0.6
-0.8
-1
-1.2
-1.4
0
5
10
15
20
25
30
35
40
45
R² = 0.279
P = 0.360
Weighted % milfoil gradient

Figure 13

APPENDIX 3

Taxa codes, taxa, and functional feeding groups

Appendix 3: Taxa codes, taxa, and functional feeding groups.
F. and G. collectors are short for filtering and gathering collectors, respectively.

Taxa Code	Taxa	Functional Feeding Group
11	Insecta, Diptera, Chironomidae, Orthocladiinae	Shredder
12	Insecta, Diptera, Chironomidae, Tanypodinae	Predator
13	Insecta, Diptera, Chironomidae, Tanytarsini	F. collector
14	Insecta, Diptera, Chironomidae, Chironomini	G. collector
22	Insecta, Ephemeroptera, Tricorythidae	G. collector
23	Insecta, Ephemeroptera, Baetidae	G. collector
24	Insecta, Ephemeroptera, Caenidae	G. collector
27	Insecta, Ephemeroptera, Heptageniidae	G. collector
33	Insecta, Odonata, Coenagrionidae	Predator
35	Insecta, Odonata, Libellulidae	Predator
40	Insecta, Coleoptera, Curculionidae	Shredder
41	Insecta, Coleoptera, Gyrinidae	Predator
44	Annelida, Oligochaeta, Haplotaxida, Naididae	G. collector
45	Annelida, Oligochaeta, Haplotaxida, Tubificidae	G. collector
52	Ostracoda	F. collector
54	Gastropoda, Physidae	Scraper
55	Gastropoda, Hydrobiidae	Scraper
56	Gastropoda, Planorbidae	Scraper
58	Insecta, Lepidoptera, Pyralidae	Shredder
62	Coelenterata, Hydrazoa	Predator
66	Amphipoda, Taltridae, Hyalella	Shredder
75	Insecta, Trichoptera, Hydroptilidae, Orthotrichiini	Piercer
77	Insecta, Trichoptera, Hydroptilidae, Hydroptilinae	Piercer
79	Insecta, Trichoptera, Polycentropodidae, Neureclipsis	F. collector
81	Insecta, Trichoptera, Polycentropodidae, Cernotina	Predator
82	Insecta, Trichoptera, Polycentropodidae, Paranyctiophylax	Predator
83	Insecta, Trichoptera, Leptoceridae, Oecetis	Predator
85	Insecta, Trichoptera, Leptoceridae, Leptocerus	Shredder
86	Insecta, Trichoptera, Leptoceridae, Nectopsyche	Shredder
87	Insecta, Ephemeroptera, Heptageniidae	G. collector
88	Hydracarina	Predator
89	Turbellaria, Tricladida, Planariidae	Predator

APPENDIX 4

Raw data: macroinvertebrate density

Appendix 4: Average macroinvertebrate density (#) per g plant biomass by sample month, lake, plant species, and taxa
See Appendix 3 for taxa codes

Month	Lake	Plant Species	11	12	13	24	33	52	54	55	56	66
July	Big Crooked	C. demersum	3.16	0.79			0.79	3.16	2.37	10.26	1.58	56.82
July	Big Crooked	M. spicatum	2.86	2.14		0.71	1.43	7.86	8.57	61.43	3.57	15.00
July	Big Crooked	N. spp	0.43	1.28	0.43	3.40	2.13	1.70	8.51	50.18	2.13	6.38
July	Big Crooked	P. amplifolius	0.73	0.73		0.36		9.12	0.36	10.95	2.55	3.28
July	Big Crooked	P. zosteriformis	1.22	0.81	0.41		0.41	1.62	1.22	31.60	1.22	3.65
July	Big Seven	C. demersum	1.28	0.71	0.14	0.57	0.14	0.14		0.14	0.57	3.56
July	Big Seven	E. canadensis	1.45	0.80		0.64	0.16			0.16	0.80	1.61
July	Big Seven	M. spicatum	4.35	0.84	0.17	0.67			0.17	0.17	0.17	0.33
July	Big Seven	P. pectinatus	9.26	3.09	1.37	1.37	0.34			0.34		0.34
July	Big Seven	P. zosteriformis	6.01	0.38	0.38		0.19	0.38		0.19	0.94	0.19
July	Camp	C. demersum	4.64	1.03	0.52		2.06	1.03	1.55	1.03		95.81
July	Camp	M. spicatum	4.51		1.13	1.13	1.13	4.51	5.64	12.40	3.38	29.31
July	Camp	P. praelongus	6.91	0.38				2.69	0.38	1.54	0.77	2.30
July	Camp	V. americana	3.94	0.49			1.48	2.46	4.43	7.38	0.98	9.85
July	Clear	C. carolinia	0.52	1.04			0.52	9.84		26.41	3.11	3.62
July	Clear	M. spicatum	1.60				0.53	2.13		4.79	3.19	2.13
July	Clear	P. amplifolius	0.53	1.05				0.79	0.53	11.04	1.31	1.58
July	Clear	P. foliosis	6.29						0.70	0.70		4.89
July	Clear	P. illinoensis	0.80					0.27	0.27	2.66	0.27	2.39
July	Heron	C. demersum	2.45	1.02	1.33	0.41	0.61	0.61	0.61	1.22	0.20	1.02
July	Heron	E. canadensis	4.71	1.05	1.31	1.05	1.75		0.35	3.14		0.35
July	Heron	M. spicatum	3.14	0.77	0.38	0.22	0.11		1.86	2.08	0.22	0.11

Appendix 4 (cont.)

Month	Lake	Plant Species	11	12	13	24	33	52	54	55	56	66
July	Heron	P. pusillus	10.19	1.74	13.55		0.35	1.39	2.43	2.08		0.35
July	Heron	P. zosteriformis	2.91	1.42	2.64		0.20		0.20	1.01		0.20
July	Lobdell	C. demersum	2.51	0.84		4.18		0.42		10.04	0.84	6.27
July	Lobdell	M. spicatum	1.57	1.88		1.25	0.31	0.63		4.07	0.63	1.57
July	Lobdell	N. spp	1.53	0.76	0.38	5.72				19.06	2.29	1.53
July	Lobdell	U. spp	5.57	1.59	0.80	2.39		3.19	0.80	10.35		3.98
July	Lobdell	V. americana	0.53	0.89		0.53		0.18		11.54	1.24	0.36
August	Big Crooked	C. demersum	2.27	4.53	0.57		1.70	0.57	0.57	7.93		55.50
August	Big Crooked	M. spicatum	3.15	2.36	1.58		3.94		1.58	13.40	3.15	39.41
August	Big Crooked	N. spp		4.46		1.11	0.56	0.56	1.67	22.28	1.11	13.92
August	Big Crooked	P. amplifolius	1.08	1.29					0.43	6.25	0.86	3.02
August	Big Crooked	P. zosteriformis	0.84	1.41			0.56	0.28		0.56	0.28	2.53
August	Big Seven	C. demersum	1.93	5.01	1.93	0.77						26.98
August	Big Seven	E. canadensis	3.04	3.87	0.55	0.55				3.04		2.76
August	Big Seven	M. spicatum	3.73	7.72	5.06		0.27			0.80		0.53
August	Big Seven	P. pectinatus	4.94	4.94	3.80	0.76	1.14					1.52
August	Big Seven	P. zosteriformis	0.92	1.83	2.29				0.46			
August	Camp	C. demersum	0.74			0.49	0.25	0.25		5.43	0.49	32.83
August	Camp	H. dubia	0.50	0.50						7.79	0.50	4.02
August	Camp	M. spicatum	0.52		0.52	1.81	0.26			28.98	0.26	2.59
August	Camp	P. praelongus	0.11				0.11			3.05	0.45	3.61
August	Camp	V. americana	0.29	0.14		0.14			0.14	8.19	0.29	6.90
August	Clear	C. carolinia	2.01			0.67	5.35			45.46	0.67	0.67

Appendix 4 (cont.)

Month	Lake	Plant Species	11	12	13	24	33	52	54	55	56	66
August	Clear	M. spicatum	6.69	3.35	0.42		0.84	0.84		7.11	1.67	
August	Clear	P. amplifolius	1.42	5.03	0.52	0.13		0.26	0.13	1.03	0.39	0.39
August	Clear	P. illinoensis	2.63	2.92			0.58		0.58	8.17	1.46	
August	Clear	P. pusillus	2.86	2.86	1.63	0.41	0.41			8.17	2.45	0.41
August	Heron	C. demersum	1.66	3.31	2.65		0.33			13.92		23.20
August	Heron	M. spicatum	3.88		1.72	0.43			0.43	69.40		0.43
August	Heron	P. illinoensis	2.20	0.60	1.00				0.60	14.78		0.20
August	Heron	P. pectinatus	2.77	0.27	2.41				0.54	21.94		
August	Heron	P. zosteriformis	7.81	0.88	1.77				1.18	13.55	0.29	2.36
August	Lobdell	M. spicatum	1.54	1.03	0.51	2.57	0.51			2.57		1.54
August	Lobdell	N. spp	1.44	2.15	3.59	1.44				4.31	0.36	2.87
August	Lobdell	P. illinoensis	0.89	0.59	0.59			0.30	0.30	0.30		1.18
August	Lobdell	U. spp	0.44	0.66		0.44		1.09		3.06		1.09
August	Lobdell	V. americana	0.81	0.65	0.16	0.16		0.16	0.16	2.26	0.32	0.97

Appendix 4 (cont.)

Month	Lake	Plant Species	22	35	75	40	62	58	14	44	45	77
July	Big Crooked	C. demersum			5.52				30.78	14.21		0.79
July	Big Crooked	M. spicatum			2.14		0.71		6.43	40.71		
July	Big Crooked	N. spp.		1.28			1.28		8.93	23.39		
July	Big Crooked	P. amplifolius			0.73				4.01	6.57	0.36	
July	Big Crooked	P. zosteriformis		0.41	0.41		0.41		4.05	7.29		
July	Big Seven	C. demersum							1.14	5.98	3.41	0.85
July	Big Seven	E. canadensis							2.09	6.60	1.77	0.97
July	Big Seven	M. spicatum							1.67	10.72	3.01	0.50
July	Big Seven	P. pectinatus						0.34	4.80	23.33	7.89	3.43
July	Big Seven	P. zosteriformis							2.26	4.51	5.07	0.56
July	Camp	C. demersum			2.58				54.60	9.27	2.06	
July	Camp	M. spicatum			2.25				6.76	84.54	2.25	
July	Camp	P. praelongus			3.07		1.92	0.77	16.13	6.53	5.38	1.15
July	Camp	V. americana			1.97				32.49	12.80	5.91	0.49
July	Clear	C. carolinia		0.52	2.07					23.30		1.04
July	Clear	M. spicatum			4.26					50.53	1.60	2.66
July	Clear	P. amplifolius		0.53	1.05					24.72	1.84	
July	Clear	P. foliosis		0.70	4.89					55.89	6.29	6.99
July	Clear	P. illinoensis							0.53	30.30	1.59	1.06
July	Heron	C. demersum										
July	Heron	E. canadensis	0.17	0.17	0.17							
July	Heron	M. spicatum		0.77	0.11	0.11	0.11					

Appendix 4 (cont.)

Month	Lake	Plant Species	22	35	75	40	62	58	14	44	45	77
July	Heron	P. pusillus		1.04	0.35							
July	Heron	P. zosteriformis		1.22	0.81		0.41	0.20				
July	Lobdell	C. demersum	0.42		0.42		0.84		0.84	22.16	4.60	0.84
July	Lobdell	M. spicatum			0.63					46.67		
July	Lobdell	N. spp.							3.81	26.31	1.14	1.14
July	Lobdell	U. spp.			2.39				6.37	69.28	2.39	
July	Lobdell	V. americana			0.36		0.18		1.78	3.91	1.42	
August	Big Crooked	C. demersum							9.63	6.80	0.57	
August	Big Crooked	M. spicatum		1.58	2.36				5.52	44.14	4.73	
August	Big Crooked	N. spp.		0.84	0.56				7.80	17.82	2.78	
August	Big Crooked	P. amplifolius		0.22	0.22				3.02	7.12	1.08	
August	Big Crooked	P. zosteriformis			0.56		0.28	0.28	6.47	17.43	5.90	0.84
August	Big Seven	C. demersum							3.85	0.77	5.78	0.77
August	Big Seven	E. canadensis						0.28	3.87	1.38	3.87	0.28
August	Big Seven	M. spicatum							11.98	3.99	5.86	0.53
August	Big Seven	P. pectinatus							10.64	4.94	20.90	2.28
August	Big Seven	P. zosteriformis							6.87	3.66	39.40	1.37
August	Camp	C. demersum							0.25	0.49	0.49	0.25
August	Camp	H. dubia		0.25			0.75	0.50	0.75	0.50		0.50
August	Camp	M. spicatum			0.78		0.52		0.52	1.29	0.26	0.26
August	Camp	P. praelongus	0.11		0.23		1.58	0.23	0.56	0.45	0.34	
August	Camp	V. americana			0.43				0.14	0.29	0.57	0.29
August	Clear	C. carolinia			8.69				3.34	6.69		7.35

Appendix 4 (cont.)

Month	Lake	Plant Species	22	35	75	40	62	58	14	44	45	77
August	Clear	M. spicatum			5.02				3.35	31.36	2.93	0.84
August	Clear	P. amplifolius		0.65	0.65				1.68	3.61	0.90	
August	Clear	P. illinoensis		0.88	1.46		2.63		3.79	8.46	3.21	0.29
August	Clear	P. pusillus			0.82				7.76	22.88	1.63	1.63
August	Heron	C. demersum			0.83		0.33					
August	Heron	M. spicatum		0.43	0.43		0.43					
August	Heron	P. illinoensis			0.60		0.40					
August	Heron	P. pectinatus			1.87							
August	Heron	P. zosteriformis		0.29	1.33		1.47					
August	Lobdell	M. spicatum		0.51	0.51				2.05	64.15		0.51
August	Lobdell	N. spp.							7.18	28.72	0.72	0.36
August	Lobdell	P. illinoensis							4.15	40.57	2.07	0.59
August	Lobdell	U. spp.	0.87		0.22		0.22		0.66	10.48		
August	Lobdell	V. americana					0.16		1.13	15.65	0.32	0.32

Appendix 4 (cont.)

Month	Lake	Plant Species	86	79	87	41	82	27	89	83	81	88	23	85
July	Big Crooked	C. demersum								0.79		0.79		
July	Big Crooked	M. spicatum		0.71	1.43				8.57			3.57		
July	Big Crooked	N. spp.	6.38		0.43				3.83		0.43	5.10		
July	Big Crooked	P. amplifolius							6.93	0.73		4.74		
July	Big Crooked	P. zosteriformis	0.41						5.27			3.24		
July	Big Seven	C. demersum							0.14			0.85		
July	Big Seven	E. canadensis							0.48			1.77	0.48	
July	Big Seven	M. spicatum										1.17		
July	Big Seven	P. pectinatus								0.34		2.06	0.69	0.34
July	Big Seven	P. zosteriformis	0.19						0.38			0.56		
July	Camp	C. demersum		1.03		0.52			4.64			11.33		
July	Camp	M. spicatum	1.13						12.96			6.76		
July	Camp	P. praelongus		0.38					8.07			1.54		
July	Camp	V. americana							2.95	0.49		1.97		
July	Clear	C. carolinia							5.70			5.70		
July	Clear	M. spicatum	0.53						10.64	0.53		3.19		
July	Clear	P. amplifolius		1.31			1.05		3.16			2.10		
July	Clear	P. foliosis		0.70			0.70					8.38		
July	Clear	P. illinoensis				0.27	0.27		3.99			1.86		
July	Heron	C. demersum							0.61		0.41	1.02		
July	Heron	E. canadensis							0.52			0.17		
July	Heron	M. spicatum							0.44			0.22		

Appendix 4 (cont.)

Month	Lake	Plant Species	86	79	87	41	82	27	89	83	81	88	23	85
July	Heron	P. pusillus							4.86					
July	Heron	P. zosteriformis							10.96			0.61		
July	Lobdell	C. demersum							0.42			5.02		
July	Lobdell	M. spicatum							0.31					
July	Lobdell	N. spp.	0.38						0.38			3.43		
July	Lobdell	U. spp.										2.39		
July	Lobdell	V. americana	0.18						0.18			1.24		
August	Big Crooked	C. demersum	0.57									1.70		28.32
August	Big Crooked	M. spicatum		0.79								7.09		7.09
August	Big Crooked	N. spp.	3.34							0.56		11.14	1.11	6.13
August	Big Crooked	P. amplifolius		0.43		0.65			3.02			3.23		0.65
August	Big Crooked	P. zosteriformis				1.12						1.41		1.69
August	Big Seven	C. demersum										3.08	1.54	
August	Big Seven	E. canadensis							0.55			2.49	0.55	
August	Big Seven	M. spicatum							0.80			1.06	0.53	
August	Big Seven	P. pectinatus							0.38			1.90	1.90	
August	Big Seven	P. zosteriformis							2.75			0.92		
August	Camp	C. demersum	0.25	0.25					1.48			1.23		
August	Camp	H. dubia							1.26			0.50		
August	Camp	M. spicatum							0.52			0.78		
August	Camp	P. praelongus		0.11					3.72		0.34	0.34		
August	Camp	V. americana	0.29						0.72	0.14		1.01		
August	Clear	C. carolinia							1.34			1.34		10.70

Appendix 4 (cont.)

Month	Lake	Plant Species	86	79	87	41	82	27	89	83	81	88	23	85
August	Clear	M. spicatum							2.93	0.42		0.84		
August	Clear	P. amplifolius					3.36		1.03					
August	Clear	P. illinoensis				1.17	3.21		1.75	0.29		0.58		
August	Clear	P. pusillus		0.41			0.41					1.23		
August	Heron	C. demersum		0.33				0.33	0.33			0.33		
August	Heron	M. spicatum							0.43			0.43		
August	Heron	P. illinoensis							0.80			0.60		
August	Heron	P. pectinatus											0.54	
August	Heron	P. zosteriformis							0.88			0.29		
August	Lobdell	M. spicatum							2.05	0.51				
August	Lobdell	N. spp.							1.44			1.44		
August	Lobdell	P. illinoensis							0.59					
August	Lobdell	U. spp.							0.66			0.66		
August	Lobdell	V. americana							0.32			0.48		

APPENDIX 5

Raw data: macroinvertebrate biomass

Appendix 5: Average macroinvertebrate biomass (mg) per g plant biomass by sample month, lake, plant species, taxa
See Appendix 3 for taxa codes

Month	Lake	Plant Species	11	12	13	24	33	52	54	55	56	66	81	88
July	Big Crooked	C. demersum	0.26	0.01			0.20	0.60	0.22	0.36	0.51	9.90		0.06
July	Big Crooked	M. spicatum	0.49	0.13		0.01	0.10	1.59	0.88	2.20	0.82	1.09		0.32
July	Big Crooked	N. spp	0.11	0.02	0.01	0.17	0.25	0.34	3.40	2.00	0.64	1.18	1.70	0.49
July	Big Crooked	P. amplifolius	0.19	0.03		0.01		1.72	0.06	0.36	1.04	0.52		0.52
July	Big Crooked	P. zosteriformis	0.32	0.03	0.03		0.09	0.33	0.50	1.36	0.31	0.35		0.42
July	Big Seven	C. demersum	0.36	0.05	0.01	0.03	0.01	0.02		0.01	0.22	0.54		0.07
July	Big Seven	E. canadensis	0.14	0.14		0.02	0.01			0.00	0.26	0.18		0.16
July	Big Seven	E. canadensis	0.71	0.26	0.07	0.02	0.01			0.02		0.04		0.21
July	Big Seven	M. spicatum	0.32	0.02	0.01	0.02			0.02	0.01	0.06	0.07		0.12
July	Big Seven	P. zosteriformis	0.25	0.02	0.04		0.00	0.07		0.01	0.45	0.01		0.08
July	Camp	C. demersum	2.18	0.19	0.00		0.47	0.21	0.77	0.06		20.03		1.37
July	Camp	M. spicatum	3.81		0.02	0.04	0.02	1.05	5.32	0.77	2.08	3.18		0.82
July	Camp	P. prealongus	2.00	0.01				0.89	0.09	0.07	0.30	0.38		0.13
July	Camp	V. americana	0.23	0.00			1.88	0.53	1.91	0.35	0.34	0.92		0.29
July	Clear	C. cabomba	0.52	0.08			0.05	2.06		1.55	0.77	0.66		0.58
July	Clear	M. spicatum	0.24				0.06	0.48		0.23	1.61	0.34		0.31
July	Clear	P. amplifolius	0.51	0.08				0.16	0.04	0.47	0.68	0.28		0.17
July	Clear	P. foliosis	0.51						0.26	0.07		0.63		0.84
July	Clear	P. illinoensis	0.12					0.05	0.08	0.11	0.15	0.32		0.19
July	Heron	C. demersum	0.23	0.08	0.01	0.01	0.03	0.11	0.90	0.08	0.01	0.17	0.03	0.07
July	Heron	E. canadensis	0.19	0.03	0.06	0.03	0.07		0.13	0.08		0.03		0.02
July	Heron	M. spicatum	0.27	0.07	0.04	0.01	0.00		1.74	0.86	0.04	0.01		0.02

Appendix 5 (cont.)

Month	Lake	Plant Species	11	12	13	24	33	52	54	55	56	66	81	88
July	Heron	P. pusillus	0.77	0.05	0.49		0.01	0.25	1.80	0.34		0.00		
July	Heron	P. zosteriformis	0.19	0.06	0.16		0.01		0.21	0.28		0.01		0.06
July	Lobdell	C. demersum	0.21	0.03		0.28		0.09		1.18	0.49	0.63		0.45
July	Lobdell	M. spicatum	0.14	0.09		0.07	0.01	0.11		0.79	0.11	0.14		
July	Lobdell	N. spp	0.16	0.04	0.01	0.27				1.66	0.45	0.16		0.32
July	Lobdell	U. spp	0.70	0.08	0.02	0.06		0.58	0.09	0.82		0.25		0.22
July	Lobdell	V. americana	0.31	0.04		0.02		0.04		0.86	0.33	0.03		0.13
August	Big Crooked	C. demersum	1.19	0.31	0.01		0.95	0.11	0.06	2.26		8.03		0.16
August	Big Crooked	M. spicatum	3.50	0.08	0.07		2.68		0.17	2.38	1.58	6.28		0.72
August	Big Crooked	N. spp		0.49		0.04	0.03	0.12	0.87	5.76	0.72	1.40		1.36
August	Big Crooked	P. amplifolius	0.20	0.15					0.21	1.42	0.86	0.31		0.40
August	Big Crooked	P. zosteriformis	0.07	0.08			0.10	0.05		0.22	0.39	0.38		0.18
August	Big Seven	C. demersum	0.08	0.24	0.07	0.03						4.19		0.26
August	Big Seven	E. canadensis	0.19	0.32	0.04	0.03				1.06		0.30		0.24
August	Big Seven	E. canadensis	0.34	0.31	0.08	0.03	0.05					0.13		0.16
August	Big Seven	M. spicatum	1.05	0.47	0.18		0.07			0.34		0.10		0.09
August	Big Seven	P. zosteriformis	0.10	0.04	0.07				0.15					0.08
August	Camp	C. demersum	0.90			0.01	0.14	0.06		1.69	0.35	5.74		0.14
August	Camp	H. dubia	0.05	0.03						2.25	0.30	0.38		0.05
August	Camp	M. spicatum	0.25		0.01	0.05	0.01			8.90	0.12	0.32		0.08
August	Camp	P. prealongus	0.17				0.27			0.87	0.19	0.51	0.04	0.03
August	Camp	V. americana	0.14	0.01		0.01			0.27	2.35	0.21	1.19		0.12
August	Clear	C. cabomba	0.76			0.02	2.08			11.61	0.76	0.08		0.15

Appendix 5 (cont.)

Month	Lake	Plant Species	11	12	13	24	33	52	54	55	56	66	81	88
August	Clear	M. spicatum	0.88	0.42	0.00		0.03	0.17		2.56	0.53			0.07
August	Clear	P. amplifolius	0.14	0.52	0.05	0.00		0.04	0.31	0.46	0.37	0.06		
August	Clear	P. illinoensis	0.45	0.23			1.51		2.00	3.29	1.03			0.06
August	Clear	P. pusillus	0.20	0.17	0.08	0.01	0.15			4.57	2.49	0.05		0.13
August	Heron	C. demersum	0.06	0.33	0.10		0.01			3.98		2.95		0.03
August	Heron	E. canadensis	0.11	0.01	0.17				0.34	6.32				
August	Heron	M. spicatum	0.31		0.05	0.01			0.50	22.05		0.04		0.04
August	Heron	P. illinoensis	0.08	0.05	0.04				0.36	4.98		0.06		0.06
August	Heron	P. zosteriformis	0.42	0.06	0.10				0.83	4.12	0.05	0.26		0.03
August	Lobdell	M. spicatum	0.15	0.05	0.04	0.09	0.04			0.72		0.10		
August	Lobdell	N. spp	0.22	0.18	0.29	0.04				1.49	0.30	0.16		0.13
August	Lobdell	P. illinoensis	0.07	0.05	0.02			0.05	0.03	0.09		0.04		
August	Lobdell	U. spp	0.20	0.03		0.03		0.21		1.32		0.08		0.06
August	Lobdell	V. americana	0.11	0.05	0.01	0.00		0.03	0.09	0.89	0.05	0.10		0.05

Appendix 5 (cont.)

Month	Lake	Plant Species	89	22	35	75	40	62	58	14	44	45	77
July	Big Crooked	C. demersum				0.16				0.94	0.38		0.01
July	Big Crooked	M. spicatum	0.04			0.04		0.00		0.34	1.52		
July	Big Crooked	N. spp	0.01		0.12			0.00		0.51	0.93		
July	Big Crooked	P. amplifolius	0.03			0.02				0.32	0.34	0.04	
July	Big Crooked	P. zosteriformis	0.02		0.13	0.01		0.00		0.25	0.35		
July	Big Seven	C. demersum	0.00							0.07	0.35	0.15	0.01
July	Big Seven	E. canadensis	0.00							0.13	0.30	0.09	0.01
July	Big Seven	E. canadensis							0.05	0.25	0.69	0.31	0.05
July	Big Seven	M. spicatum								0.09	0.55	0.14	0.01
July	Big Seven	P. zosteriformis	0.00							0.13	0.19	0.23	0.01
July	Camp	C. demersum	0.04			0.11				2.86	0.30	0.05	
July	Camp	M. spicatum	0.12			0.16				0.33	2.42	0.03	
July	Camp	P. prealongus	0.14			0.14		0.00	0.53	0.85	0.29	0.31	0.04
July	Camp	V. americana	0.03			0.08				1.43	0.43	0.40	0.03
July	Clear	C. cabomba	0.03		0.18	0.09					3.18		0.11
July	Clear	M. spicatum	0.07			0.13					3.87	0.52	0.06
July	Clear	P. amplifolius	0.02		0.17	0.03					1.74	0.11	
July	Clear	P. foliosis			0.01	0.14					3.63	0.37	0.17
July	Clear	P. illinoensis	0.03							0.06	2.22	0.13	0.03
July	Heron	C. demersum	0.00										
July	Heron	E. canadensis	0.00	0.00	0.01	0.00							
July	Heron	M. spicatum	0.00		0.04	0.34	0.07	0.00					

Appendix 5 (cont.)

Month	Lake	Plant Species	89	22	35	75	40	62	58	14	44	45	77
July	Heron	P. pusillus	0.03		0.05	0.00							
July	Heron	P. zosteriformis	0.07		0.05	0.02		0.00	0.01				
July	Lobdell	C. demersum	0.00	0.01		0.02		0.00		0.02	1.00	0.65	0.03
July	Lobdell	M. spicatum	0.00			0.02					2.02		
July	Lobdell	N. spp	0.00							0.47	0.71	0.02	0.02
July	Lobdell	U. spp				0.05				0.18	3.62	0.65	
July	Lobdell	V. americana	0.00			0.01		0.00		0.15	0.10	0.06	
August	Big Crooked	C. demersum								0.65	0.23	0.02	
August	Big Crooked	M. spicatum			2.64	0.05				0.33	1.74	0.04	
August	Big Crooked	N. spp			0.07	0.01				0.37	0.53	0.04	
August	Big Crooked	P. amplifolius	0.02		0.02	0.01				0.18	0.26	0.06	
August	Big Crooked	P. zosteriformis				0.01		0.00	0.00	0.57	0.64	0.14	0.02
August	Big Seven	C. demersum								0.23	0.03	0.25	0.02
August	Big Seven	E. canadensis	0.00						0.00	0.26	0.06	0.15	0.01
August	Big Seven	E. canadensis	0.01							1.13	0.22	0.41	0.04
August	Big Seven	M. spicatum	0.00							0.64	0.11	0.22	0.00
August	Big Seven	P. zosteriformis	0.03							0.62	0.08	1.21	0.06
August	Camp	C. demersum	0.02							0.00	0.01	0.03	0.00
August	Camp	H. dubia	0.01		0.02			0.00	0.02	0.03	0.01		0.01
August	Camp	M. spicatum	0.00			0.02		0.00		0.00	0.04	0.00	0.01
August	Camp	P. prealongus	0.02	0.00		0.00		0.01	0.01	0.04	0.01	0.01	
August	Camp	V. americana	0.00			0.02				0.01	0.01	0.03	0.02
August	Clear	C. cabomba	0.00			0.09				0.30	0.40		0.39

Appendix 5 (cont.)

Month	Lake	Plant Species	89	22	35	75	40	62	58	14	44	45	77
August	Clear	M. spicatum	0.02			0.04				0.21	2.00	0.16	0.01
August	Clear	P. amplifolius	0.00		0.18	0.01				0.16	0.23	0.05	
August	Clear	P. illinoensis	0.01		0.16	0.01		0.00		0.24	0.35	0.23	0.02
August	Clear	P. pusillus				0.01				0.49	0.83	0.11	0.04
August	Heron	C. demersum	0.00			0.02		0.00					
August	Heron	E. canadensis				0.03							
August	Heron	M. spicatum	0.00		0.02	0.00		0.01					
August	Heron	P. illinoensis	0.01			0.01		0.00					
August	Heron	P. zosteriformis	0.00		0.02	0.01		0.01					
August	Lobdell	M. spicatum	0.01		0.02	0.02				0.14	1.99		0.02
August	Lobdell	N. spp	0.01							0.68	0.93	0.03	0.01
August	Lobdell	P. illinoensis	0.00							0.37	1.21	0.07	0.02
August	Lobdell	U. spp	0.00	0.02		0.01		0.00		0.06	0.34		
August	Lobdell	V. americana	0.00					0.00		0.14	0.55	0.01	0.01

Appendix 5 (cont.)

Month	Lake	Plant Species	23	83	85	86	79	87	41	82	27
July	Big Crooked	C. demersum		0.02							
July	Big Crooked	M. spicatum					0.02	0.02			
July	Big Crooked	N. spp				0.30		0.01			
July	Big Crooked	P. amplifolius		0.00							
July	Big Crooked	P. zosteriformis				0.22					
July	Big Seven	C. demersum									
July	Big Seven	E. canadensis	0.05								
July	Big Seven	E. canadensis	0.03	0.00	0.00						
July	Big Seven	M. spicatum									
July	Big Seven	P. zosteriformis				0.01					
July	Camp	C. demersum					1.80		0.25		
July	Camp	M. spicatum				0.69					
July	Camp	P. prealongus					0.50				
July	Camp	V. americana		1.91							
July	Clear	C. cabomba									
July	Clear	M. spicatum		0.00		0.03					
July	Clear	P. amplifolius					0.17			0.09	
July	Clear	P. foliosis					0.02			0.03	
July	Clear	P. illinoensis							0.53	0.01	
July	Heron	C. demersum									
July	Heron	E. canadensis									
July	Heron	M. spicatum									

Appendix 5 (cont.)

Month	Lake	Plant Species	23	83	85	86	79	87	41	82	27
July	Heron	P. pusillus									
July	Heron	P. zosteriformis									
July	Lobdell	C. demersum									
July	Lobdell	M. spicatum									
July	Lobdell	N. spp				0.01					
July	Lobdell	U. spp									
July	Lobdell	V. americana				0.00					
August	Big Crooked	C. demersum			0.58	0.80					
August	Big Crooked	M. spicatum			0.12		0.18				
August	Big Crooked	N. spp	0.04	0.00	0.12	4.79					
August	Big Crooked	P. amplifolius			0.01		0.06		1.10		
August	Big Crooked	P. zosteriformis			0.02				1.85		
August	Big Seven	C. demersum	0.24								
August	Big Seven	E. canadensis	0.08								
August	Big Seven	E. canadensis	0.26								
August	Big Seven	M. spicatum	0.02								
August	Big Seven	P. zosteriformis									
August	Camp	C. demersum				0.01	0.07				
August	Camp	H. dubia									
August	Camp	M. spicatum									
August	Camp	P. prealongus					0.03				
August	Camp	V. americana		0.00		0.00					
August	Clear	C. cabomba			0.26						

Appendix 5 (cont.)

Month	Lake	Plant Species	23	83	85	86	79	87	41	82	27
August	Clear	M. spicatum		0.00							
August	Clear	P. amplifolius								0.68	
August	Clear	P. illinoensis		0.00					1.72	0.75	
August	Clear	P. pusillus					0.01			0.12	
August	Heron	C. demersum					0.02				0.01
August	Heron	E. canadensis	0.11								
August	Heron	M. spicatum									
August	Heron	P. illinoensis									
August	Heron	P. zosteriformis									
August	Lobdell	M. spicatum		0.00							
August	Lobdell	N. spp									
August	Lobdell	P. illinoensis									
August	Lobdell	U. spp									
August	Lobdell	V. americana									

APPENDIX 6

Raw data: macroinvertebrate length

Appendix 6: Average macroinvertebrate length (mm) per g plant biomass by sample month, lake, plant species, and taxa
See Appendix 3 for taxa codes

Month	Lake	Plant Species	11	12	13	24	33	52	54	55	56	66	81
July	Big Crooked	C. demersum	3.33	2.73			3.57	0.58	1.16	1.05	1.82	3.10	
July	Big Crooked	M. spicatum	4.55	4.53		1.49	2.21	0.62	1.21	1.07	1.61	2.27	
July	Big Crooked	N. spp	5.42	2.97	2.79	2.14	2.67	0.61	1.96	1.11	1.77	3.16	10.35
July	Big Crooked	P. amplifolius	5.50	4.20		1.40		0.58	1.40	1.03	1.96	2.99	
July	Big Crooked	P. zosteriformis	5.49	4.02	4.16		3.44	0.62	1.98	1.15	1.67	2.51	
July	Big Seven	C. demersum	5.63	4.66	4.30	2.06	1.83	0.53		1.08	1.94	2.95	
July	Big Seven	E. canadensis	3.56	6.44		1.67	1.68			0.79	1.80	2.62	
July	Big Seven	E. canadensis	3.21	5.05	3.74	1.43	1.53			1.33		2.77	
July	Big Seven	M. spicatum	3.17	3.37	3.19	1.84			1.19	1.07	1.91	3.31	
July	Big Seven	P. zosteriformis	2.48	4.22	4.86		1.40	0.58		1.08	2.08	2.22	
July	Camp	C. demersum	7.03	6.44	1.33		3.42	0.61	2.11	1.29		3.29	
July	Camp	M. spicatum	9.05		2.27	1.90	1.26	0.70	2.65	1.32	2.28	2.62	
July	Camp	P. prealongus	5.70	3.70				0.97	1.62	1.20	1.93	3.04	
July	Camp	V. americana	2.88	2.48			6.50	0.65	2.01	1.19	1.86	2.48	
July	Clear	C. carolinia	9.79	5.01			2.53	0.63		1.29	1.65	3.15	
July	Clear	M. spicatum	4.29				2.61	0.68		1.19	2.12	3.01	
July	Clear	P. amplifolius	9.62	4.91				0.60	1.08	1.14	2.14	3.12	
July	Clear	P. foliosis	3.30						1.90	1.56		2.78	
July	Clear	P. illinoensis	4.26					0.61	1.79	1.11	2.20	2.83	
July	Heron	C. demersum	3.52	4.92	3.07	1.54	1.82	0.56	3.10	1.33	0.84	3.03	2.66
July	Heron	E. canadensis	2.70	3.54	2.98	1.73	1.81		1.91	0.96		2.54	
July	Heron	M. spicatum	3.34	5.27	4.86	2.01	1.84		2.64	2.73	1.52	2.59	

Appendix 6 (cont.)

Month	Lake	Plant Species	11	12	13	24	33	52	54	55	56	66	81
July	Heron	P. pusillus	3.34	3.54	3.30		1.35	0.55	2.43	1.92		1.22	
July	Heron	P. zosteriformis	3.01	4.14	3.42		1.61		2.75	2.34		1.69	
July	Lobdell	C. demersum	3.36	4.00		2.39		0.67		1.69	2.23	2.55	
July	Lobdell	M. spicatum	3.38	4.22		2.24	1.55	0.53		2.04	1.46	2.45	
July	Lobdell	N. spp	3.68	4.41	3.12	2.09				1.50	1.52	2.60	
July	Lobdell	U. spp	3.98	4.28	2.93	1.67		0.56	1.26	1.45		2.17	
July	Lobdell	V. americana	7.74	4.14		1.84		0.64		1.41	1.68	2.47	
August	Big Crooked	C. demersum	7.37	4.77	1.88		4.77	0.58	1.20	2.36		2.90	
August	Big Crooked	M. spicatum	10.18	3.77	3.64		5.14		1.22	1.97	2.12	3.00	
August	Big Crooked	N. spp		5.52		1.87	2.07	0.66	2.15	2.28	2.32	2.55	
August	Big Crooked	P. amplifolius	4.71	5.55					2.10	2.17	2.70	2.56	
August	Big Crooked	P. zosteriformis	3.25	4.49			3.11	0.58		2.67	3.04	2.95	
August	Big Seven	C. demersum	2.46	4.28	3.33	1.90						2.97	
August	Big Seven	E. canadensis	2.94	5.05	4.26	2.26				2.56		2.64	
August	Big Seven	E. canadensis	3.05	4.61	2.64	1.96	1.88					2.43	
August	Big Seven	M. spicatum	5.65	4.59	3.29		3.52			2.77		3.18	
August	Big Seven	P. zosteriformis	3.75	3.25	3.12				1.81				
August	Camp	C. demersum	10.58			1.47	4.85	0.72		2.44	2.40	3.10	
August	Camp	H. dubia	3.46	4.54						2.38	2.24	2.50	
August	Camp	M. spicatum	7.11		2.12	1.71	2.04			2.43	2.07	2.75	
August	Camp	P. prealongus	11.62				8.20			2.37	1.98	2.88	3.22
August	Camp	V. americana	7.08	3.99		2.38			3.38	2.37	2.42	3.09	
August	Clear	C. carolinia	6.40			1.70	4.17			2.27	2.84	2.77	

Appendix 6 (cont.)

Month	Lake	Plant Species	11	12	13	24	33	52	54	55	56	66	81
August	Clear	M. spicatum	4.05	5.77	1.55		1.73	0.62		2.59	1.81		
August	Clear	P. amplifolius	3.61	5.43	4.91	1.35		0.52	3.70	2.81	2.67	2.94	
August	Clear	P. illinoensis	4.57	5.00			8.48		4.18	2.70	2.39		
August	Clear	P. pusillus	3.11	4.54	3.63	1.50	4.12			3.06	2.72	2.70	
August	Heron	C. demersum	2.54	5.37	3.35		1.38			2.37		2.77	
August	Heron	E. canadensis	2.39	3.76	3.92				2.29	2.37			
August	Heron	M. spicatum	3.53		3.10	1.39			2.85	2.47		2.43	
August	Heron	P. illinoensis	2.14	5.04	2.55				2.25	2.52		3.78	
August	Heron	P. zosteriformis	3.15	4.86	3.29				2.39	2.42	1.42	2.64	
August	Lobdell	M. spicatum	3.57	4.21	4.44	1.83	2.36			2.35		2.17	
August	Lobdell	N. spp	4.37	5.11	4.52	1.65				2.55	2.55	2.08	
August	Lobdell	P. illinoensis	3.27	4.92	3.18			0.47	1.23	2.45		1.73	
August	Lobdell	U. spp	6.89	4.23		2.42		0.60		2.77		2.31	
August	Lobdell	V. americana	4.20	5.04	3.69	1.20		0.56	2.24	2.68	1.35	2.58	

Appendix 6 (cont.)

Month	Lake	Plant Species	88	89	22	35	75	40	62	58	14	44	45
July	Big Crooked	C. demersum	0.59				2.39				3.08	2.03	
July	Big Crooked	M. spicatum	0.70	1.65			2.06		0.60		3.85	2.36	
July	Big Crooked	N. spp	0.76	1.32		2.01			1.03		3.96	2.42	
July	Big Crooked	P. amplifolius	0.88	1.69			2.39				4.54	2.72	3.92
July	Big Crooked	P. zosteriformis	1.08	1.66		3.07	2.54		0.70		4.09	2.63	
July	Big Seven	C. demersum	0.63	0.87							4.14	2.87	2.51
July	Big Seven	E. canadensis	0.72	1.48							4.03	2.56	2.68
July	Big Seven	E. canadensis	0.80							3.03	3.78	2.14	2.40
July	Big Seven	M. spicatum	0.78								3.82	2.70	2.62
July	Big Seven	P. zosteriformis	1.16	1.61							3.96	2.48	2.56
July	Camp	C. demersum	1.00	2.01			2.75				3.82	2.21	1.90
July	Camp	M. spicatum	1.01	2.25			3.21				3.69	2.10	1.45
July	Camp	P. prealongus	0.65	4.27			2.78		1.22	5.90	3.82	2.53	2.86
July	Camp	V. americana	1.26	2.59			2.68				3.56	2.25	3.05
July	Clear	C. carolinia	0.81	1.65		3.16	2.68					4.12	
July	Clear	M. spicatum	0.77	1.81			2.41					3.22	6.01
July	Clear	P. amplifolius	0.64	1.91		3.11	2.30					3.10	2.83
July	Clear	P. foliosis	0.80			0.96	2.37					3.00	2.88
July	Clear	P. illinoensis	0.83	2.03							5.06	3.15	3.35
July	Heron	C. demersum	0.54	1.97									
July	Heron	E. canadensis	0.95	0.96	1.52	1.34	1.90						
July	Heron	M. spicatum	0.75	1.88		1.58	7.65	2.62	1.41				

Appendix 6 (cont.)

Month	Lake	Plant Species	88	89	22	35	75	40	62	58	14	44	45
July	Heron	P. pusillus		1.72		1.54	1.81						
July	Heron	P. zosteriformis	0.76	1.83		1.44	2.37		1.91	1.77			
July	Lobdell	C. demersum	0.70	1.28	1.54		2.88		1.55		2.94	2.56	4.19
July	Lobdell	M. spicatum		1.67			2.53					2.52	
July	Lobdell	N. spp	0.72	1.44							5.37	2.05	1.81
July	Lobdell	U. spp	0.71				2.21				2.99	2.73	5.55
July	Lobdell	V. americana	0.86	1.07			2.28		1.30		4.64	2.00	2.42
August	Big Crooked	C. demersum	0.72								4.22	2.27	2.19
August	Big Crooked	M. spicatum	0.80			5.59	2.12				4.05	2.41	1.31
August	Big Crooked	N. spp	1.01			1.93	1.72				3.66	2.14	1.63
August	Big Crooked	P. amplifolius	1.03	1.82		1.99	2.94				4.06	2.35	2.88
August	Big Crooked	P. zosteriformis	1.07				1.67		1.52	0.99	4.71	2.34	1.94
August	Big Seven	C. demersum	0.64								4.05	2.34	2.51
August	Big Seven	E. canadensis	0.78	1.53						1.43	4.19	2.53	2.38
August	Big Seven	E. canadensis	0.62	2.46							5.07	2.52	1.79
August	Big Seven	M. spicatum	0.63	1.47							3.84	2.05	2.35
August	Big Seven	P. zosteriformis	0.66	2.12							4.75	1.84	2.17
August	Camp	C. demersum	0.93	2.35							2.05	1.70	3.10
August	Camp	H. dubia	0.85	1.63		1.87			1.14	1.97	3.19	1.94	
August	Camp	M. spicatum	0.81	1.44			2.12		1.38		1.91	2.11	1.39
August	Camp	P. prealongus	0.67	1.82	1.98		2.10		1.46	2.30	4.46	2.07	1.66
August	Camp	V. americana	1.03	1.48			2.94				4.17	2.11	2.75
August	Clear	C. carolinia	0.92	1.15			1.74				4.73	2.89	

Appendix 6 (cont.)

Month	Lake	Plant Species	88	89	22	35	75	40	62	58	14	44	45
August	Clear	M. spicatum	0.68	2.01			1.56				4.09	2.97	2.80
August	Clear	P. amplifolius		1.46		2.91	2.17				4.91	2.97	2.82
August	Clear	P. illinoensis	0.81	1.79		2.54	1.61		1.13		4.12	2.47	3.15
August	Clear	P. pusillus	0.82				1.78				4.10	2.33	3.00
August	Heron	C. demersum	0.67	1.41			1.58		1.31				
August	Heron	E. canadensis					2.01						
August	Heron	M. spicatum	0.80	1.59		1.54	1.36		2.48				
August	Heron	P. illinoensis	0.84	2.21			1.72		1.77				
August	Heron	P. zosteriformis	0.89	1.71		1.79	1.53		1.54				
August	Lobdell	M. spicatum		1.67		1.41	2.81				4.25	2.18	
August	Lobdell	N. spp	0.69	1.57							4.84	2.22	2.31
August	Lobdell	P. illinoensis		1.90							4.75	2.14	2.29
August	Lobdell	U. spp	0.77	1.69	1.52		3.03		1.66		4.79	2.22	
August	Lobdell	V. americana	0.89	1.83					2.20		5.39	2.30	2.17

Appendix 6 (cont.)

Month	Lake	Plant Species	23	83	85	86	79	87	41	82	27	77
July	Big Crooked	C. demersum		2.30								2.01
July	Big Crooked	M. spicatum					1.96	1.74				
July	Big Crooked	N. spp				2.81		2.35				
July	Big Crooked	P. amplifolius		0.87								
July	Big Crooked	P. zosteriformis				6.09						
July	Big Seven	C. demersum										1.99
July	Big Seven	E. canadensis	3.35									1.86
July	Big Seven	E. canadensis	2.60	0.99	1.91							1.94
July	Big Seven	M. spicatum										2.03
July	Big Seven	P. zosteriformis				2.46						2.06
July	Camp	C. demersum					7.85		1.78			
July	Camp	M. spicatum				6.37						
July	Camp	P. prealongus					7.14					2.63
July	Camp	V. americana		11.50								2.91
July	Clear	C. carolinia										3.66
July	Clear	M. spicatum		1.43		3.08						2.19
July	Clear	P. amplifolius					3.29			2.90		
July	Clear	P. foliosis					1.95			2.26		2.28
July	Clear	P. illinoensis							8.61	2.43		2.49
July	Heron	C. demersum										
July	Heron	E. canadensis										
July	Heron	M. spicatum										

Appendix 6 (cont.)

Month	Lake	Plant Species	23	83	85	86	79	87	41	82	27	77
July	Heron	P. pusillus										
July	Heron	P. zosteriformis										
July	Lobdell	C. demersum										2.64
July	Lobdell	M. spicatum										
July	Lobdell	N. spp				1.92						1.91
July	Lobdell	U. spp										
July	Lobdell	V. americana				2.09						
August	Big Crooked	C. demersum			2.15	8.33						
August	Big Crooked	M. spicatum			2.02		3.97					
August	Big Crooked	N. spp	2.28	0.98	2.10	8.36						
August	Big Crooked	P. amplifolius			2.07		3.44		7.18			
August	Big Crooked	P. zosteriformis			1.85				6.95			2.09
August	Big Seven	C. demersum	3.99									2.24
August	Big Seven	E. canadensis	3.87									2.55
August	Big Seven	E. canadensis	3.82									2.10
August	Big Seven	M. spicatum	2.41									1.66
August	Big Seven	P. zosteriformis										2.75
August	Camp	C. demersum				2.43	4.32					1.65
August	Camp	H. dubia										1.94
August	Camp	M. spicatum										2.60
August	Camp	P. prealongus					4.18					
August	Camp	V. americana		1.39		2.01						3.00
August	Clear	C. carolinia			2.28							2.90

Appendix 6 (cont.)

Month	Lake	Plant Species	23	83	85	86	79	87	41	82	27	77
August	Clear	M. spicatum		1.24								1.95
August	Clear	P. amplifolius								3.83		
August	Clear	P. illinoensis		2.01					6.13	4.01		3.36
August	Clear	P. pusillus					1.98			4.34		2.33
August	Heron	C. demersum					2.48				1.35	
August	Heron	E. canadensis	4.43									
August	Heron	M. spicatum										
August	Heron	P. illinoensis										
August	Heron	P. zosteriformis										
August	Lobdell	M. spicatum		1.12								2.49
August	Lobdell	N. spp										2.25
August	Lobdell	P. illinoensis										2.44
August	Lobdell	U. spp										
August	Lobdell	V. americana										2.24

APPENDIX 7

Raw data: macrophytes

Appendix 7: Macrophyte data. The number of samples taken (N), mean macrophyte biomass (g), standard deviation (S.D.), coefficient of variation (C.V.), and total macrophyte biomass by month, lake, and plant species.

Month	Lake	Plant species	N	Mean biomass	S.D	C.V.	Total biomass
July	Big Seven	*C. demersum*	14	0.59	0.28	47.13	8.20
July	Big Seven	*E. canadensis*	13	0.56	0.21	36.82	7.25
July	Big Seven	*M. spicatum*	12	0.87	0.57	64.96	10.45
July	Big Seven	*P. pectinatus*	14	0.49	0.19	38.63	6.80
July	Big Seven	*P. zosteriformis*	13	0.57	0.32	55.33	7.45
July	Big Crooked	*C. demersum*	13	0.68	0.38	55.26	8.87
July	Big Crooked	*M. spicatum*	13	0.38	0.22	58.80	4.90
July	Big Crooked	*N. spp.*	13	0.63	0.41	64.08	8.23
July	Big Crooked	*P. amplifolius*	13	0.74	0.37	49.54	9.59
July	Big Crooked	*P. zosteriformis*	13	0.44	0.23	51.99	5.76
July	Camp	*C. demersum*	13	1.05	0.50	47.54	13.59
July	Camp	*M. spicatum*	12	0.52	0.26	50.63	6.21
July	Camp	*P. praelongus*	13	0.70	0.30	42.71	9.11
July	Camp	*V. americana*	13	0.36	0.36	99.85	4.74
July	Clear	*C. carolinia*	13	0.52	0.16	30.45	6.76
July	Clear	*M. spicatum*	14	0.47	0.17	35.93	6.58
July	Clear	*P. amplifolius*	13	1.02	0.24	23.12	13.31
July	Clear	*P. foliosis*	12	0.28	0.18	66.40	3.34
July	Clear	*P. illinoensis*	13	0.68	0.33	48.20	8.78
July	Heron	*C. demersum*	13	0.38	0.22	58.52	4.90
July	Heron	*E. canadensis*	14	0.41	0.23	56.73	5.73
July	Heron	*M. spicatum*	13	1.23	0.72	58.89	15.98

Appendix 7 (cont.)

Month	Lake	Plant species	N	Mean biomass	S.D	C.V.	Total biomass
July	Heron	*P. pusillus*	13	0.31	0.18	58.87	4.03
July	Heron	*P. zosteriformis*	12	0.48	0.20	41.90	5.75
July	Lobdell	*C. demersum*	13	0.21	0.07	32.65	2.79
July	Lobdell	*M. spicatum*	12	0.62	0.24	38.99	7.45
July	Lobdell	*N. spp.*	13	0.47	0.36	75.67	6.12
July	Lobdell	*U. spp.*	13	0.23	0.11	47.19	2.93
July	Lobdell	*V. americana*	13	0.51	0.30	59.58	6.57
Aug	Big Seven	*C. demersum*	13	0.70	0.32	45.89	9.08
Aug	Big Seven	*E. canadensis*	13	0.28	0.14	48.64	3.62
Aug	Big Seven	*M. spicatum*	13	0.40	0.14	34.73	5.26
Aug	Big Seven	*P. pectinatus*	13	0.47	0.18	38.68	6.14
Aug	Big Seven	*P. zosteriformis*	12	0.32	0.24	76.29	3.82
Aug	Big Crooked	*C. demersum*	13	0.95	0.39	41.36	12.36
Aug	Big Crooked	*M. spicatum*	13	0.34	0.48	141.75	4.44
Aug	Big Crooked	*N. spp.*	13	0.32	0.18	55.59	4.19
Aug	Big Crooked	*P. amplifolius*	12	0.90	0.40	44.92	10.82
Aug	Big Crooked	*P. zosteriformis*	13	0.32	0.12	38.48	4.15
Aug	Camp	*C. demersum*	13	1.09	0.42	38.42	14.18
Aug	Camp	*H. dubia*	13	0.31	0.16	52.47	3.98
Aug	Camp	*M. spicatum*	13	0.42	0.18	43.10	5.41
Aug	Camp	*P. praelongus*	13	0.68	0.30	43.31	8.86
Aug	Camp	*V. americana*	13	0.62	0.41	65.47	8.12
Aug	Clear	*C. carolinia*	13	0.27	0.11	40.11	3.49

Appendix 7 (cont.)

Month	Lake	Plant species	N	Mean biomass	S.D	C.V.	Total biomass
Aug	Clear	*M. spicatum*	13	0.43	0.18	42.32	5.58
Aug	Clear	*P. amplifolius*	13	1.04	0.35	33.73	13.56
Aug	Clear	*P. illinoensis*	13	0.37	0.17	45.22	4.80
Aug	Clear	*P. pusillus*	13	0.44	0.31	71.10	5.71
Aug	Heron	*C. demersum*	13	0.81	0.49	60.51	10.56
Aug	Heron	*M. spicatum*	12	0.68	0.27	40.16	8.12
Aug	Heron	*P. illinoensis*	13	0.45	0.20	44.65	5.84
Aug	Heron	*P. pectinatus*	12	0.36	0.19	50.94	4.36
Aug	Heron	*P. zosteriformis*	13	0.30	0.13	42.84	3.96
Aug	Lobdell	*M. spicatum*	13	0.52	0.24	46.70	6.82
Aug	Lobdell	*N. spp.*	13	0.50	0.23	45.81	6.50
Aug	Lobdell	*P. illinoensis*	13	0.45	0.14	31.81	5.91
Aug	Lobdell	*U. spp.*	13	0.35	0.15	43.64	4.58
Aug	Lobdell	*V. americana*	13	0.48	0.52	109.61	6.20

APPENDIX 8

Aggregated raw data: macroinvertebrates per plant stem

Appendix 8: The average macroinvertebrate density (#) and biomass (mg) you might expect to find on a single plant for each species sampled, the percent of those macroinvertebrates that are insects, gastropods, and oligochaetes, and the percent that make up each of the five functional feeding groups on each plant species. Averages and percentages were calculated after pooling the six lakes and two dates.

Plant species	Plant arch	Macroinvert. biomass	Macroinvert. density	% Insecta	% Gastropoda	% Oligochaeta	% Other
C. carolinia	Dis	4.83	34.33	50	15	7	28
C. demersum	Dis	11.13	74.19	51	8	6	35
E. canadensis	Undis	0.69	9.96	56	12	10	22
H. dubia	Undis	0.96	5.62	54	15	8	23
M. spicatum	Dis	4.92	40.23	53	16	10	21
N. spp	Undis	4.35	43.12	53	16	11	20
P. amplifolius	Undis	4.13	35.43	45	19	13	23
P. foliosis	Undis	1.71	24.95	50	17	17	16
P. illinoensis	Undis	2.69	20.96	48	19	11	22
P. pectinatus	Dis	1.81	24.08	67	8	11	14
P. praelongus	Undis	3.33	29.33	52	15	12	21
P. pusillus	Undis	2.90	21.39	59	15	7	19
P. zosteriformis	Undis	1.31	16.52	54	15	8	23
U. spp	Dis	1.24	16.18	50	12	12	26
V. americana	Undis	2.18	17.56	46	17	13	24

Appendix 8 (cont)

		Functional feeding group percentages					
Plant species	**Plant arch**	**scraper**	**shredder**	**piercer**	**g. collector***	**f. collector***	**predator**
C. carolinia	Dis	16	16	16	16	4	32
C. demersum	Dis	13	17	7	22	13	28
E. canadensis	Undis	12	17	7	29	5	29
H. dubia	Undis	15	23	8	15	0	38
M. spicatum	Dis	16	16	9	21	9	29
N. spp	Undis	16	17	5	27	8	28
P. amplifolius	Undis	19	15	6	21	10	29
P. foliosis	Undis	17	17	17	17	8	25
P. illinoensis	Undis	19	13	9	17	7	35
P. pectinatus	Dis	8	19	8	31	8	25
P. praelongus	Undis	15	18	9	21	9	27
P. pusillus	Undis	15	15	11	15	15	30
P. zosteriformis	Undis	15	19	8	13	10	35
U. spp	Dis	12	15	8	31	12	23
V. americana	Undis	17	16	10	24	6	27

* G. and F. collector are short for gathering and filtering collector, respectively

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