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THE HABITAT VALUE OF AQUATIC MACROPHYTES
FOR MACROINVERTEBRATES

by

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19. ABSTRACT (Continue on reverse if necessary and identify by block number) In Eau Galle Reservoir, mean densities of bottom-dwelling macroinvertebrates among <i>Ceratophyllum</i> (35,260 organisms/m ²) and <i>Potamogeton</i> (18,387 organisms/m ²) were much greater than in no-plant zones (2,730 organisms/m ²). Immature tubificids (without capilliform chaetae), the most commonly collected oligochaete taxon, were seven times more abundant in sediments associated with <i>Ceratophyllum</i> and nine times more dense in <i>Potamogeton</i> beds than in the no-plant zones. Very little difference in percent organic matter or particulate organic matter was noted among sediments from <i>Ceratophyllum</i> , <i>Potamogeton</i> , and no-plant areas. In the no-plant zones, 90.4 percent of the invertebrates were within the top (0- to 5-cm) depth fraction. Six percent were in the 5- to 10-cm depth fraction, and only 3.6 percent were in the 10- to 15-cm fraction. As in the no-plant zones, over 90 percent of the invertebrates collected below the <i>Ceratophyllum</i> and <i>Potamogeton</i> were in the 0- to (Continued)					
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5-cm depth fraction. Although relatively few animals were found deeper than the 0- to 5-cm depth fraction, the organisms that were present 5 to 15 cm below the water-sediment surface were numerically dominated by nematodes, tubificids, and the gastropod *Amnicola limosa*.

Potamogeton nodosus had means of approximately 155 and 127 organisms per plant in June and August 1987. Seventy-six species of invertebrates were collected on these plants. In June 1987, a single *P. nodosus* plant supported 555 invertebrates (which included 177 chironomid larvae and 143 naiddid worms) representing 36 taxa. Changes in invertebrate species composition occurred from early in the growing season of *P. nodosus* (June) to the peak of plant development (August). The oligochaete *Nais pardalis* existed in large numbers (15.3 individuals/plant) and was numerically dominant in June 1987, whereas it was completely absent from *P. nodosus* in August 1987. Not only did large phenological changes in invertebrate composition occur over the growing season of *P. nodosus*, but these changes were predictable and repeatable year after year.

Studies on zooplankton in Eau Galle Reservoir were conducted during the summer of 1986. In sparse vegetation, rotifers made up 46.9 percent of the zooplankton assemblage, with approximately equal numbers of copepods (26.1 percent) and cladocerans (25.5 percent). However, in dense vegetation, copepods comprised more than 50 percent of the sample, while rotifers (20.2 percent) and cladocerans (21.8 percent) were subdominant. In the sparse vegetation, rotifers were more numerous than copepods.

Macroinvertebrate assemblages were compared on live and imitation (plastic) plants in a Louisiana borrow pit lake to investigate the effects of stem and leaf structure on colonization. These plastic plants were morphologically similar to live plants and were colonized by diatoms, filamentous algae, and macroinvertebrates. Live *Ceratophyllum demersum* contained greater species diversity, species richness, evenness, and from 3 to 10 times as many organisms (per stem length) as the plastic *Ceratophyllum* and plastic *Vallisneria*, respectively. Ephemeropterans were the most common organisms on the live *C. demersum* and plastic *Ceratophyllum*, whereas ephemeropterans and chironomids were approximately codominant on plastic *Vallisneria*. Gastropods comprised 22 percent of the total number of individuals on the live *C. demersum*, which was 3.6 and 6 times their percentage on the plastic *Ceratophyllum* and plastic *Vallisneria*, respectively. Plastic *Vallisneria* and *Ceratophyllum* had a more even distribution of taxa across feeding guilds with a greater percentage of collector/gatherers, piercers/herbivores, and predators than the assemblages on the live plants. Differences between macroinvertebrates associated with live and plastic plants could not be explained by variation in stem and leaf morphology but appeared to be related to the density of the epiphytic algal community (algae growing on plants) that provided additional habitat for macroinvertebrates.

PREFACE

The information presented in this report on the habitat value of aquatic plants for macroinvertebrates was taken from a series of studies undertaken by the US Army Engineer Waterways Experiment Station (WES), Environmental Laboratory (EL), between 1986 and 1988. Funding for this work was provided by the Headquarters, US Army Corps of Engineers (HQUSACE), through the Aquatic Plant Control Research Program (APCRP). The APCRP is managed under the Environmental Resources Research and Assistance Programs, Mr. J. Lewis Decell, Manager. Technical Monitor for the study was Mr. James W. Wolcott, HQUSACE.

This report was prepared by Dr. Andrew C. Miller and Dr. Carl M. Way of the Aquatic Habitat Group (AHG), Environmental Resources Division (ERD), EL; Dr. David C. Beckett of the University of Southern Mississippi (USM), Hattiesburg, MS, employed under the Intergovernmental Personnel Act (IPA); and Dr. Edmond J. Bacon, University of Arkansas at Monticello, also employed under the IPA. Technical assistance was provided by Mr. Thomas Artilla and Mr. Richard Peets, USM; Mr. W. Marc Jordan of the Vicksburg-Warren County School District, employed under the IPA; and Ms. Cindy Burleson, Mr. Ken Conley, and Ms. Christina Miller-Way, EL. The report was edited by Ms. Jessica S. Ruff of the WES Information Technology Laboratory. During the conduct of these studies, Dr. John Harrison was Chief, EL; Dr. C. J. Kirby was Chief, ERD; and Mr. Edwin A. Theriot was Chief, AHG.

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THE HABITAT VALUE OF AQUATIC MACROPHYTES FOR MACROINVERTEBRATES

PART I: INTRODUCTION

Background

1. Submersed macrophytes are commonly found in both lotic and lentic habitats of freshwater and estuarine ecosystems. They tend to predominate in small, shallow basins and in the littoral zone of large lakes. Their complex structures create a diversity of microhabitats for colonizing organisms and provide refuges from predators. As integral components of the aquatic community, submersed macrophytes play a major role in the development and modification of their physical environment. They directly or indirectly affect the chemical composition, nutrient cycles, and biological features of the ecosystem. For decades, submersed macrophytes were viewed as nuisances with little functional role.

2. Management strategy often included complete eradication. Although the complex mechanisms by which macrophytes interact with sediments, water, and biological organisms are still not well known, scientists and resource managers are now beginning to understand some of the interactions involving aquatic macrophytes and to recognize their important role in aquatic ecosystems. Pandit (1984) has stated that freshwater macrophytes have a more dominant influence on their physicochemical environment than do terrestrial plants on the terrestrial environment. Surface area of submersed macrophytes in Lawrence Lake, Michigan, provided almost 10 times more surface area for colonization than the total benthic area of the lake (Losee and Wetzel 1988). The importance and potential impacts of submersed macrophytes on aquatic ecosystems have been summarized in excellent reviews by Seddon (1972), Gregg and Rose (1982, 1985), McDermid and Naiman (1983), Pandit (1984), and Carpenter and Lodge (1986).

Purpose and Scope

3. The purpose of this document is to summarize and discuss recent studies on the value of submersed aquatic macrophytes for macroinvertebrates.

Part II discusses effects of macrophytes on benthic invertebrates; Parts III and IV deal with the colonization of macroinvertebrates on *Potamogeton nodosus* and *Ceratophyllum demersum*, respectively. Part V describes a study on the effects of macrophytes on distribution of zooplankton, and Part VI describes the effects of *C. demersum* structure on macroinvertebrate colonization. Part VII presents a general summary and literature review of the effects of plants on biotic and abiotic factors in aquatic systems. The majority of these studies took place in Eau Galle Reservoir, Wisconsin, except for the final study of *C. demersum* (Part VI), which was conducted in a borrow pit lake in Louisiana. Appendix A presents summary data on macroinvertebrates associated with aquatic macrophytes.

PART II: EFFECTS OF PLANTS ON HORIZONTAL AND VERTICAL DISTRIBUTION
OF BENTHIC MACROINVERTEBRATES IN EAU GALLE RESERVOIR, WISCONSIN

Background

4. One of the important functions of macrophytes in freshwater systems is to serve as substrate for epiphytic invertebrates. Macrophytes provide structure for invertebrates besides that afforded by the lake or stream bottom. McDermid and Naiman (1983) have aptly described macrophytes as the forests of rivers and lakes. Muttkowski (1918), Kreckler (1939), Andrews and Hasler (1943), Rosine (1955), Gerking (1957), Dvorak and Best (1982), and Engel (1985), among others, have shown that these macrophyte "forests" are densely colonized by epiphytic invertebrates.

5. Macrophytes can have profound effects on their aquatic habitats. The plants can reduce water movement and thereby retain silt and particulate organic matter within the macrophyte beds (McDermid and Naiman 1983). Rooted macrophytes also absorb a variety of elements from the substrates (Wetzel 1983a). A few investigators have suggested that macrophytes enhance the standing crop of invertebrates by increasing benthic (bottom-dwelling) invertebrate densities. Watkins, Shireman, and Haller (1983) found that benthic densities of a Florida lake below macrophyte beds were approximately two to three times the benthic densities in the open water. Wisniewski and Dusoge (1983) observed a decrease in benthic invertebrate densities just beyond the littoral zone of Polish lakes, and Engel (1985) observed the same phenomenon in a Wisconsin lake.

6. In those studies, comparisons were made between the benthic invertebrates of the littoral zone and the benthos of the sublittoral or profundal zone. However, physical and chemical conditions in the deeper waters of the sublittoral or profundal zone differ from those of the littoral zone, complicating a comparison based on plant presence or absence.

7. In Eau Galle Reservoir, Wisconsin, sediment samples for benthic (bottom-dwelling) macroinvertebrates were collected from three areas in the littoral zone: beneath *P. nodosus* beds, beneath *C. demersum* beds, and in areas void of vegetation (no-plant zones). Consequently, it was possible to compare benthic invertebrate densities in vegetated areas to those in no-plant zones, both within the littoral zone, to determine if the presence of

macrophytes affected macroinvertebrate density, diversity, and community structure. In addition, a major objective of this work was to determine whether the presence of macrophytes resulted in a vertical distribution of invertebrates different from that observed in nonvegetated sediments.

Study Area

8. Eau Galle Reservoir is a small, eutrophic, dimictic reservoir, constructed by the US Army Corps of Engineers for flood control. Located in west-central Wisconsin, the lake has a surface area of 0.6 km², a maximum depth of 9.5 m, and a mean depth of 3.6 m. The reservoir receives flow from an agricultural drainage area of 166 km². The Eau Galle River contributes 80 to 90 percent of the inflow, with the remainder from three smaller streams. The littoral zone, as defined by the presence of aquatic macrophytes, makes up about 17 percent of the total surface of the lake (Gunkel, Gaugush, and Kennedy 1984). The principal submersed macrophyte in the lake is *C. demersum*; the macrophytes *Potamogeton pectinatus*, *P. nodosus*, *P. foliosus*, and *Najas flexilis* are also present (Filbin and Barko 1985).

Methods

9. On 5 and 6 August 1986, core samples were obtained from three different habitats within the reservoir: from the lake bottom within *C. demersum* beds, from the lake bottom within *P. nodosus* beds, and from small open areas of no vegetation (the no-plant zones) located among the *C. demersum* beds. The no-plant zones were small, approximately circular, with a diameter of 2 m or less, and were located amidst dense beds of *Ceratophyllum*. Five cores were taken from each of the three habitats (*Ceratophyllum* bed, *Potamogeton* bed, and no-plant zone) at each of three different locations: site AA, site BB, and site CC (Figure 1). These three sites were located along the eastern side of the lake.

10. To study the vertical distribution of benthic invertebrates, each core was separated into three depth fractions (0 to 5 cm, 5 to 10 cm, and 10 to 15 cm) as soon as the bottom sample was extruded from the corer. Each of the depth fractions was preserved and processed separately in the laboratory.

11. Samples were collected from a boat using a hand-held benthic corer constructed from polyvinyl chloride (PVC) pipe. This corer, described by Miller and Bingham (1987), has an internal diameter of 5.1 cm and uses a plumber's pipe test plug to exclude water, aquatic plants, and any other materials from entering the corer before the sample is taken. Because the corer is hand-held, it can be positioned exactly at a desired position. The exclusion of water, aquatic plants, and invertebrates from the sampler prior to sample collection was another important feature, since it was necessary to prevent benthic samples from being "contaminated" by epiphytic invertebrates.

12. All cores were taken in shallow water at depths of approximately 1 m. The lake bottom sampled in the no-plant zones and the *Ceratophyllum* beds was clearly visible from the boat (the lake bottom in the *Potamogeton* beds was blocked by floating leaves of this plant). The cores collected within the *Ceratophyllum* beds were taken by moving the sampler at an angle from above a no-plant zone into the *Ceratophyllum* bed, then squaring the corer to the bottom within the macrophyte bed. Using this method it was possible to watch the corer move all the way to the bottom and to avoid collecting portions of *Ceratophyllum*. An added benefit of this sampling procedure was that sediment samples from *Ceratophyllum* beds were usually taken less than a meter away from no-plant zones. When sampling within the macrophyte beds, the corer was lowered slowly and carefully to keep from "knocking" invertebrates off the plants onto the lake bottom. Likewise, the sampler was lowered slowly to minimize sampler "blowout."

13. The core samples were processed using a US Standard No. 35 sieve (openings = 500 μ). The samples were stained with a rose bengal solution (Mason and Yevich 1967) to facilitate the separation of invertebrates from vegetation, detritus, and any remaining sediment. Invertebrates were picked under 6 \times to 12 \times magnification. Larval chironomids and oligochaetes were prepared for identification using the procedure of Beckett and Lewis (1982).

Results

14. Cores from the *Ceratophyllum* beds consistently had higher numbers of organisms than those from the *Potamogeton* beds or from no-plant zones. Among the nine estimations of mean number of invertebrates per square meter of bottom, all three of the highest means (40,556 invertebrates/m²; 39,174

invertebrates/m²; and 26,050 invertebrates/m²) came from the *Ceratophyllum* (Table 1). Mean invertebrate densities estimated for the benthos below the three *Potamogeton* beds were quite similar to each other (16,183 invertebrates/m²; 19,834 invertebrates/m²; and 19,143 invertebrates/m²). In turn, these were all lower than the three means in the *Ceratophyllum* beds, and much higher than the means for the invertebrates in the no-plant zones. Densities in the no-plant zones were very low (grand mean in the no-plant zones equaled 2,730 invertebrates/m²) in comparison to densities below the macrophytes. The mean invertebrate densities in the *Ceratophyllum* beds were approximately 13 times those of the no-plant zones. Similarly, benthic densities in *Potamogeton* beds were approximately seven times the densities in the no-plant zones.

15. The striking difference in densities between vegetated and nonvegetated habitats can be seen clearly among the common invertebrates. Chironomids and oligochaetes comprised 34.2, 53.1, and 65.0 percent of benthic macroinvertebrates at sites in the *Ceratophyllum*, *Potamogeton* and no-plant zones, respectively (Table A1). The densities of the chironomids at the *Ceratophyllum* sites were, on the average, 3.9 times those of the no-plant zone. Chironomids were 2.5 times more dense at the *Potamogeton* sites than in the no-plant zones. Gastropod densities were even more markedly affected by the plants. Snails were 136 and 29 times more dense at sites among the *Ceratophyllum* and *Potamogeton*, respectively, than in the no-plant zones.

16. The overwhelming majority of invertebrates in the no-plant zones were found near the sediment surface. In the no-plant zones, a mean of 90.4 percent of all the collected invertebrates were present within the top (0- to 5-cm) depth fraction (Table 2). Six percent of the invertebrates in the no-plant zones were found in the 5- to 10-cm depth fraction, whereas only 3.6 percent of the invertebrates collected were in the 10- to 15-cm depth fraction.

17. The presence of *C. demersum* or *P. nodosus* did not appear to alter the vertical distribution of littoral-zone invertebrates beyond that exhibited in the no-plant zones. Over 90 percent of the invertebrates collected below the *Ceratophyllum* and *Potamogeton* were in the 0- to 5-cm depth fraction (94.5 percent in the *Ceratophyllum* beds, 93.4 percent in the *Potamogeton* beds) (Table 1). Only 0.6 percent of the invertebrates from the cores in the *Ceratophyllum* beds were in the 10- to 15-cm depth fraction, and only

1.3 percent of the invertebrates in the cores taken below the *Potamogeton* were in the 10- to 15-cm depth fraction.

18. Although relatively few macroinvertebrates were found deeper than the 0- to 5-cm depth fraction in Eau Galle Reservoir, those that were present in depths of 5 to 15 cm below the water-sediment surface were numerically dominated by nematodes, tubificids, and the gastropod *Amnicola limnosa*. In the *Ceratophyllum* beds, 29.4 percent of all the nematodes were found below the 0- to 5-cm depth fraction, with 19.6 percent of the nematodes collected in the *Potamogeton* beds below 5 cm (Table 2). Twenty percent of the nematodes collected in the no-plant zones were between 5 and 15 cm. Although tubificids made up a sizable percentage of the invertebrates that were present below a depth of 5 cm, the majority of tubificids were found near the surface. Only 5.1 percent of the collected tubificids were found below 5 cm in the sediments under the *Ceratophyllum*. Under the *P. nodosus*, only 4.6 percent of the tubificids were found at sediment depths of 5 to 15 cm, whereas in the no-plant zones, 11.1 percent of the tubificids were present at 5 to 15 cm.

Discussion

19. A number of investigators have shown that the macrophytes in littoral zones increase invertebrate production and diversity by serving as additional structure for invertebrate colonization, besides that offered by the lake bottom (Muttkowski 1918; Kreckler 1939; Andrews and Hasler 1943; Rosine 1955; Gerking 1957; Dvorak and Best 1982; Engel 1985; Schramm, Jirka, and Hoyer 1987). This investigation has shown that macrophytes also greatly increase benthic invertebrate densities in vegetated areas. Increased benthic densities and species richness in vegetated zones have been reported elsewhere (Watkins, Shireman, and Haller 1983; Wisniewski and Dusoge 1983; Engel 1985), but in those cases, the comparison was between vegetated areas in the littoral zone versus nonvegetated areas in profundal or sublittoral zones.

20. In this study, the presence of benthic invertebrates in the *Ceratophyllum* beds at a density of 13 times that of nonvegetated areas, and in *Potamogeton* beds at 7 times that of nonvegetated areas, occurred at the same depth within the littoral zone, in sampling areas located, at most, only a few meters apart. The tremendous difference between benthic invertebrate densities in the bottom of the *Ceratophyllum* bed (grand mean =

35,260 invertebrates/m², Table A1) and the no-plant zones (grand mean = 2,730 invertebrates/m²) was especially striking since typically no-plant zone and *Ceratophyllum* bed core samples were separated by less than 1 m. It is notable that the presence of both *Ceratophyllum* and *Potamogeton* resulted in enhanced invertebrate densities, since these macrophyte species are morphologically very dissimilar. *Ceratophyllum demersum* has small leaves positioned in whorls with all of its leaves submersed, and it is rootless, although portions of its stems are often embedded in the bottom. *Potamogeton nodosus*, in contrast, is a rooted plant with a few narrow submersed leaves and a few broad floating leaves.

21. A key feature in this study was the presence of the no-plant zones. The occurrence of small, nonvegetated areas within dense macrophyte beds has been reported by other workers. During an intensive 6-year study of a lake in southwestern Wisconsin, Engel (1985) described "windows" or nonvegetated openings within nearly continuous plant beds. Macan (1977) noticed the same phenomenon in his study of lakes in northwestern England, stating that "a soil which, though illuminated, watered and stable, is devoid of vegetation is a peculiar but often characteristic feature of freshwater situations." Macan (1977) hypothesized that these bare areas may be caused by an overaccumulation of detrital macrophyte remains in the sediments. Although the cause of these no-plant zones in Eau Galle Reservoir is not known, it is apparent that they are ephemeral. In late May 1988, several no-plant zones were marked with a stake. By August, all of the staked no-plant zones had been colonized by *Ceratophyllum*, although other no-plant zones were clearly visible.

22. Engel (1985) suggested that increased benthic invertebrate densities in the littoral zone may be a function of the accumulation of particulate organic matter beneath the plants, since this serves as an important energy source. However, at Eau Galle Reservoir there was very little difference in percent organic matter among the *Ceratophyllum* bed, *Potamogeton* bed, and no-plant zone cores (Table 3). In addition, plant detritus was found in the no-plant zone cores during inspection for invertebrates. These findings indicate that the no-plant zones are ephemeral and that detritus accumulates in them at about the same rate as in the dense plant beds. Low invertebrate densities in no-plant zones are therefore not the result of a lack of a detrital energy base.

23. A partial explanation for increased infaunal densities in the *Ceratophyllum* bed could be the presence of *Ceratophyllum* stems in the bottom sediments. However, care was taken during sampling not to pin any *Ceratophyllum* stems to the bottom. Since it was possible to see the sampler move through the *Ceratophyllum* and see the lake bottom, it was easy to avoid trapping *Ceratophyllum* beneath the corer. However, many of the 0- to 5-cm depth fractions from cores in the *Ceratophyllum* beds had some living *Ceratophyllum* stems and leaves in them. The caddisfly *Leptocerus americanus* is often found in high numbers living epiphytically on *Ceratophyllum* (Wiggins 1977). In Eau Galle Reservoir these caddisflies were also found at fairly high densities in the cores taken beneath the *Ceratophyllum* (grand mean = 3,487 *L. americanus* larvae/m²; Table A1). *Ceratophyllum* anchors itself through the development of stems in the lake bottom (Prescott 1969), and it is probable that *Leptocerus* colonizes these stems as well as the upright stems.

24. Gastropods in the littoral zone are found epiphytically on the macrophytes as well as on the bottom, and it is possible that the presence of the *Ceratophyllum* stems in the bottom may also result in increased numbers of snails in the cores. However, an explanation that benthic macroinvertebrate densities in *Ceratophyllum* beds are high because many epifaunal animals live on embedded stems is not satisfactory.

25. Tubificid densities in sediments below both the *Ceratophyllum* beds and *Potamogeton* beds were eight times the tubificid densities in the no-plant zones (Table A1). Tubificids are infaunal, subsurface deposit feeders (Fisher 1982); extensive studies of the invertebrates living on macrophytes in Eau Galle Reservoir have shown that tubificids do not live as epiphytes. It is clear, then, that one or more factors besides that of epiphytic colonization of embedded plant stems is responsible for enhanced invertebrate numbers in the bottom beneath *Ceratophyllum* plant beds, at least for tubificids. In addition, enhanced invertebrate numbers under the *Potamogeton* beds (seven times those of the no-plant zones) were not due to embedded *Ceratophyllum* stems since a sprig of *Ceratophyllum* was found in only 3 of the 15 cores taken from the *Potamogeton* beds.

26. The factors causing increased tubificid densities (and increased densities of other invertebrate taxa) in plant beds remain unclear. Olsson (1981) found in freezing experiments that all chironomid larvae in a box containing many plants survived, while all those in boxes with few plants died.

If the no-plant zones sampled in August had persisted as nonvegetated areas since the winter, then initial invertebrate numbers in these zones in the spring may have been much lower than invertebrate densities in the sediments below *Ceratophyllum* (*C. demersum* persists throughout the winter in Eau Galle Reservoir). Another possible explanation is that the macrophytes may stabilize the bottom sediments near them. The no-plant zones were in the middle of dense *Ceratophyllum* beds and were not exposed to extensive water movement.

27. The presence of plants did not appear to modify the vertical distribution of benthic invertebrates since over 90 percent of the invertebrates were in the top 5 cm of the sediments in the macrophyte beds as well as in the no-plant zones. Although nematodes and tubificids were found predominantly in the top 5 cm of the sediments, the dominance of these two groups among the few organisms found at depths of 5 to 15 cm is consistent with the results of other studies. Nalepa and Robertson (1981) found immature Tubificidae and nematodes to be among the taxa with some representatives at deeper strata within the bottom of Lake Michigan. In Eau Galle Reservoir, nematodes seemed particularly able to colonize the deeper strata within the sediments. Nematodes can tolerate very low oxygen concentrations (Weiser and Kanwisher 1961) and have been found deep within the sediments in a variety of aquatic habitats (Weiser and Kanwisher 1961, Fenchel and Jansson 1966, Sarkka and Paasivirta 1972, Arlt 1973, Tietjen 1979, Nalepa and Robertson 1981).

PART III: MACROINVERTEBRATES ON *POTAMOGETON NODOSUS* IN
EAU GALLE RESERVOIR, WISCONSIN

Background

28. The genus *Potamogeton* (pondweeds) is distributed worldwide and consists of approximately 120 species (Stodola 1967). *Potamogeton nodosus* is found throughout most of the United States (Muenscher 1944) and also occurs in Canada, Mexico, the West Indies, South America, Eurasia, and Africa (Ogden 1943). In the summers of 1986, 1987, and 1988 the invertebrate community on *P. nodosus* was studied in Eau Galle Reservoir, Wisconsin. This study was designed to accomplish the following objectives:

- a. Berg (1949, 1950a, 1950b, 1950c) conducted a natural history survey on aquatic insect use of *Potamogeton*. The studies at Eau Galle Reservoir were designed to examine aspects of macroinvertebrate-plant relationships not investigated by Berg. Studies of invertebrates inhabiting *P. nodosus* in Eau Galle Reservoir concerned insects and noninsect invertebrates and included quantitative estimates of invertebrate density and species composition.
- b. Schramm, Jirka, and Hoyer (1987) reported significant temporal variation in invertebrate abundance on seven species of macrophytes in Florida. The present study was designed to investigate temporal variation (during the growing season and between years) in invertebrates associated with *P. nodosus*.
- c. The density and community composition of macroinvertebrates on *P. nodosus* were compared with those of the lake bottom in the littoral zone. A complete understanding of the habitat value of macrophytes can be obtained only by determining the relative contribution of plants versus benthic substrates in providing habitat for macroinvertebrates.

Study Area

29. A description of Eau Galle Reservoir is provided in Part II of this document. The principal submersed macrophyte in the lake is *Ceratophyllum demersum* (Filbin and Barko 1985). In Eau Galle Reservoir, *P. nodosus* occurs in beds in shallow water near and along the shoreline. *Potamogeton nodosus* is a rooted macrophyte and has both floating and submersed leaves (Figure 2). The floating leaves are ovate to oblong-ovate in shape; the submersed leaves are semiterete and are much narrower than the floating leaves. At the peak of

its development in Eau Galle Reservoir (August), the floating leaves in the *P. nodosus* beds are so numerous that they form almost a continuous mat at the air-water interface.

30. In the autumn, *P. nodosus* senesces. By late autumn-early winter the portions of the macrophyte in the water are in an advanced state of decay. Stems of new plants first appear above the sediments in late spring. By early June there are substantial numbers of well-developed *P. nodosus* plants, with floating leaves, occurring in beds near shore. The density of individual plants in the beds then increases, generally reaching a peak in August.

Methods

31. Sampling of *P. nodosus* took place in the summers of 1986, 1987, and 1988. Sampling in 1986 was preliminary and took place on 6 August in a *P. nodosus* bed located at site C (Figure 1). On that date, two samples were collected, each consisting of a large number of *P. nodosus* plants.

32. In the summer of 1987, *P. nodosus* was collected on June 22, early in the growing season, and on 5 August (almost exactly 1 year after the 1986 sampling) at the peak of *P. nodosus* development. On each date five individual plants were collected at each of three sites: site A, site B, and site C (Figure 1). Individual plants were collected in 1987 so that invertebrate densities could be reported as number of invertebrates per plant. Each plant stem was snipped at the water-sediment interface, gently raised through the water column, and placed in a container. Consideration was given to placing a net under the plant as it was brought to the surface. However, since *P. nodosus* usually occurs in thick beds, it became evident that placing a net around a single plant was cumbersome and was more likely to dislodge invertebrates than by simply raising the plant slowly and gently through the water column.

33. Both in 1986 and 1987, samples were preserved in 10-percent formalin and stained with rose bengal (Mason and Yevich 1967) to facilitate the separation of invertebrates from the macrophytes and detritus. The preservative was later drained through a US Standard No. 60 sieve (openings = 250 μ) to collect any invertebrates that had been dislodged. The plants were then inspected under 6 \times to 12 \times magnification to remove additional invertebrates that may have remained on the plants. In addition, stems and

leaves of each plant were slit open to look for burrowing invertebrates. A large number of invertebrates, especially chironomid larvae, were found in cases on the plant surfaces and in stems and leaves. Larval chironomids and oligochaetes were prepared for identification using the procedure of Beckett and Lewis (1982).

34. On 22 and 24 June and 15 August 1988, densities of *P. nodosus* at sampling sites A, B, and C were determined using a quadrat constructed from 1.3-cm PVC tubing. The quadrat floated on the water surface and enclosed an area equal to 0.25 m². The quadrat was randomly placed five times in each of the three *Potamogeton* beds; the number of individual *P. nodosus* in each quadrat was then counted.

Results

35. Chironomid larvae and naiddid worms accounted for more than 50 percent of the invertebrates collected from *P. nodosus* (Table A2). During the three sampling periods (August 1986, June 1987, and August 1987), chironomid larvae comprised about one third of all the invertebrates collected from the plants (33.3 percent in August 1986, 48.8 percent in June 1987, and 25.5 percent in August 1987). Seventeen percent of the invertebrates collected on *P. nodosus* during the study were naiddid worms (20.9 percent in August 1986, 15.9 percent in June 1987, and 7.4 percent in August 1987). Other invertebrates besides chironomids and naiddids which were found in high numbers on the plants included (beginning with the highest total number) brown, hard-bodied Hydracarina without long abdominal hairs; brown, hard-bodied Hydracarina with long abdominal hairs (Hydracarina were separated into three morphological groups); ostracods; cladocerans; nematodes; the gastropod *A. limnosa*; and copepods (Table A2).

36. *Potamogeton nodosus* is heavily colonized by invertebrates in Eau Galle Reservoir. The plants sampled in June 1987 had a mean of approximately 155 invertebrates living on (or in) each plant (site A: $\bar{x} = 70$ invertebrates/plant, site B: $\bar{x} = 251$ invertebrates/plant, site C: $\bar{x} = 143$ invertebrates/plant) (Table A2). The mean number of invertebrates per plant in the August sampling was approximately 127 with site B again showing the highest mean number (site A: $\bar{x} = 86.0$ invertebrates/plant, site B: $\bar{x} = 220$ invertebrates/plant, site C: $\bar{x} = 76$ invertebrates/plant).

37. *Potamogeton nodosus* supports a diverse and abundant invertebrate assemblage. Over the course of the study, 76 distinct species were found on the plants. The actual number of species present on plants may be higher since taxa labeled "ostracods" and "nematodes" probably represent a number of species. A diverse chironomid fauna inhabits *P. nodosus*; 24 species of larval chironomids were collected. Ten species of naidd worms were also present.

38. The ability of *P. nodosus* plants to support a diverse and abundant invertebrate assemblage was clearly shown by sampling individual plants. A single *P. nodosus* plant sampled in June held a total of 555 invertebrates representing 36 species (Figure 3). A total of 177 chironomid larvae and 143 naidd worms were found on this plant. Similarly, one of the plants sampled in August supported 321 invertebrates representing 27 species (Figure 4).

39. A clear difference in species composition was exhibited between the invertebrates collected from the plants in June versus those present in August. This was most clearly shown among the chironomids and naidds. In June 1987 the chironomid *Paratanytarsus* sp. was the numerically dominant chironomid larvae on *P. nodosus*. *Paratanytarsus* sp. was the most common chironomid collected at all three sampling sites, contributing 31 percent of the chironomids at site A, 53 percent at site B, and 57 percent at site C. Therefore, it comprised 52.1 percent of the chironomid larvae at all three sites, with a mean of 39.4 *Paratanytarsus* larvae per plant. Of the 15 plants sampled in June, *Paratanytarsus* sp. was the numerically dominant chironomid on 14 of them. In contrast, on 5 August 1987, 44 days after the June sampling, only 15 *Paratanytarsus* sp. were found among all plants sampled, yielding a mean of only 1.0 *Paratanytarsus* larva per plant. *Paratanytarsus* made up only 3.1 percent of the total larval chironomid numbers on the plants at this time.

40. *Polypedilum illinoense*, which averaged 4.3 larvae per plant in June and contributed only 5.73 percent of the chironomid larvae collected at this time, was the numerically dominant chironomid in August. In August, *P. illinoense* was the most common chironomid on the plants at all three sampling sites, averaging 13.1 larvae per plant and comprising 40.5 percent of the chironomids.

41. Other chironomid taxa also showed similar striking phenological changes. The second and third most common chironomid taxa on *P. nodosus* in June were *Thienemanniella* nr. *fusca* and *Corynoneura taris*, respectively. In June, *P. nodosus* supported a mean of 8.3 *T. nr. fusca* larvae and 6.3 *C. taris*

larvae per plant. In August only a single *T. nr. fusca* was collected (0.07 larva/plant), with a mean of only 0.33 *C. taris* larva/plant. In contrast, the chironomid *Endochironomus nigricans*, which was uncommon in June, was the second most common chironomid in August (after *P. illinoense*).

42. The Naididae on *P. nodosus* also showed striking changes in composition from June to August. *Nais pardalis*, the most common naidid on the plants in June, was not even collected in August. *Pristina leidy*, which was present only in low numbers in June (0.7 individual/plant), was the most common naidid on the plants in August, making up 77 percent of all the naidids collected with a mean number of 7.3 worms per plant.

43. The *P. nodosus* invertebrate collection made at site C on 6 August 1986 showed very close agreement with the results from the 5 August 1987 sampling. *Polypedilum illinoense* was the most common chironomid collected in both the August 1986 and the August 1987 samples (Table A2). A comparison of the five most common chironomid taxa collected at site C for the 1986 and 1987 August samplings yielded the same five taxa (*P. illinoense*, *Glyptotendipes dreisbachi*, *E. nigricans*, *Ablabesmyia peleensis*, and *Dicrotendipes* sp.). The chironomid taxa that were common in June 1987, but uncommon in August 1987 (*Paratanytarsus* sp., *T. nr. fusca*, and *C. taris*), were quite uncommon in August 1986 as well. *Pristina leidy* was the most common naidid worm on *P. nodosus* in August 1986, just as it was in August 1987. *Nais pardalis*, which showed such a striking phenological pattern in 1987 (numerically dominant in June and not even present in August), exhibited the same pattern in August 1986 and was completely absent from the plants.

44. Using data from cores taken below plant beds (August 1986), invertebrate numbers per *P. nodosus* plant (August 1987), and quadrat samples to estimate *P. nodosus* densities (August 1988), invertebrate densities below *P. nodosus* were compared with epiphytic invertebrate densities. Although it would have been preferable to have done all the sampling in 1987, these estimates are probably valid; densities of *P. nodosus* in the sampled beds appeared to be about the same in 1987 as in 1988. In addition, benthic invertebrate densities determined in 1986 gave very consistent results for three different areas of the reservoir. Mean density in the no-plant zones at site AA (Figure 1), near the *P. nodosus* bed at site C, was 3,256 invertebrates/m² (Table A1).

45. The presence of plants resulted in greatly enhanced densities below the *P. nodosus* near site C (\bar{x} = 16,183 invertebrates/m² at site AA, Table A1). Mean epiphytic density per square meter of lake bottom at site C equaled 18,275 invertebrates/m² (\bar{x} = 76.4 invertebrates/plant (Table A2) × 239.2 *P. nodosus* plants/m² of lake bottom at that site (Table 4)) giving a mean total of 34,458 (16,183 as benthic + 18,275 as epifauna) invertebrates/m² of lake bottom in the site C *P. nodosus* bed (Figure 5). Similarly, benthic densities in nonvegetated areas at site CC (near the *P. nodosus* bed at site B, Figure 1) equaled 1,677 invertebrates/m² with a mean of 19,143 benthic invertebrates/m² in the plant bed near site B and a mean of 24,618 epiphytic invertebrates (\bar{x} = 219.8 invertebrates/plant × 112.0 plants/m² in the bed) at site B. Mean total invertebrate density in the *P. nodosus* bed at site B therefore equaled 43,761 invertebrates/m² of lake bottom (Figure 5).

Discussion

46. This study demonstrates the importance of chironomid larvae and naiddid worms as colonizers of aquatic plants. These two groups comprised more than half of the invertebrates collected from *P. nodosus* (Table A2). A single plant sampled in June was colonized by 177 chironomid larvae (Figure 3), and the *P. nodosus* sampled in June supported a mean of 76 chironomid larvae/plant (mean number of chironomid larvae/plant = 32.5 in the August plant collections). Other investigators have reported similar findings. Krecker (1939) found chironomid larvae and naiddid worms to be the dominant macroinvertebrates on submersed macrophytes in Lake Erie. A large number of investigators have reported the Chironomidae to be one of the dominant invertebrate groups on submersed macrophytes (Andrews and Hasler 1943; Gerking 1957; Mrachek 1966; Sozka 1975; Martin and Shireman 1976; Dvorak and Best 1982; Engel 1985; Schramm, Jirka, and Hoyer 1987).

47. Fewer studies have reported large numbers of naiddids on submersed plants, perhaps due to the relatively small size of most naiddids or to taxonomic difficulties with this group. It is obvious from this study, and results of Krecker (1939), that naiddids are often present in large numbers on submersed plants. Members of the Hydracarina, which was the most common invertebrate group on *P. nodosus* besides the chironomids and naiddids, were

also abundant on macrophytes in Lake Mendota, Wisconsin (Andrews and Hasler 1943).

48. Berg investigated the relationships between *Potamogeton* and insects in Michigan lakes and streams, studying chironomid larvae (Berg 1950a), insects including chironomid larvae (Berg 1949), aquatic caterpillars (Berg 1950b), and *Hydrellia* (Berg 1950c). He listed nine species of chironomids as occurring on macrophytes in the genus *Potamogeton*, with three chironomid species collected from *P. nodosus* (Berg 1949).

49. The results of the present study indicate that the chironomid community on *Potamogeton* is much more diverse than could be inferred from Berg's studies. In this study, 24 species of larval chironomids were collected from *P. nodosus* in Eau Galle Reservoir. It is possible that Berg concentrated on burrowing chironomid species (see Berg 1950a) and ignored the other, nonburrowing chironomid species.

50. The results of the present study also indicate that a diverse assemblage of naiddid worms occurs on *P. nodosus*. Only a few investigators have examined the species composition of naiddid worms on macrophytes. Krecker (1939) listed three naiddid taxa from macrophytes in Lake Erie, Engel (1985) reported three naiddid taxa from Lake Halverson in Wisconsin, and Dvorak and Best (1982) listed three naiddid species from the macrophytes of Lake Vechten in The Netherlands. In the present study, 10 species of naiddids were collected on *P. nodosus*. If other investigators use finer mesh sieves, it is probable that epiphytic naiddid communities will be found to be more diverse than previously expected.

51. The comparison of epiphytic species composition in June 1987 and that in August 1986 and 1987 demonstrated that large phenological changes in invertebrate species composition occurred from early in the growing season of *P. nodosus* (June) to the peak of plant development (August). These phenological changes were exemplified by the occurrence of *Nais pardalis* in large numbers (15.3 worms/plant) as the numerically dominant naiddid in June 1987, followed by its complete absence from *P. nodosus* in August 1987 (Table A2). Sampling of the plants in August 1986 produced many naiddids, but again *N. pardalis* was not even present. Other naiddid and chironomid species showed similar marked changes in abundance from June to August. These phenological changes took place at all three sampling sites, indicating that variation in epiphytic invertebrate species composition from June to August was not the

result of a chance difference at one site, but was rather a phenomenon occurring throughout the lake. In addition, invertebrate collections from August 1986 and August 1987 were very similar, i.e., the same chironomid and naidid species dominated numerically in August of both years, and the dominant chironomids and naidids of June 1987 were scarce or absent in August 1986 and 1987. This indicates that not only do large phenological changes in invertebrate composition occur over the growing season of *P. nodosus*, but also that these changes are predictable and cyclic.

52. Schramm, Jirka, and Hoyer (1987) observed temporal variations in the abundance of invertebrates on macrophytes but concluded that consistent temporal trends were not evident. Although a number of factors may cause an increase or decrease in numbers of invertebrates per plant, it is obvious from these results that phenological changes are one of the major influences on epiphytic invertebrate species composition and abundance. Moreover, phenological changes in invertebrate composition on *P. nodosus* in Eau Galle Reservoir have appeared to be consistent and predictable. It is likely that the coupling of species-level taxonomy and the investigation of invertebrates on macrophytes through time will show the occurrence of consistent phenological changes in epiphytic invertebrate communities to be a general phenomenon in temperate areas. It is also clear that the succession of epiphytic invertebrate species over the growing season results, overall, in a more diverse epiphytic invertebrate community, since different species use the same plants at different times.

53. All three of the most common chironomid species on *P. nodosus* in June (*Paratanytarsus* sp., *T. nr. fusca*, and *C. taris*) were nonburrowing species. In contrast, in August 1986 and 1987, three of the five most abundant chironomid species on *P. nodosus* (*P. illinoense*, *E. nigricans*, and *G. dreisbachi*) were identified by Berg (1950a) as burrowers in *Potamogeton*. *P. nodosus* senesces and decays in the autumn. Therefore, early in the growing season, this plant had been available for colonization for only a short time. Early colonizers are apparently nonburrowing epiphytic chironomids that either overwinter on plants that persist through the winter (such as *C. demersum*) or are the progeny of chironomids that live on overwintering plants. As the growing season progresses and the *P. nodosus* beds become more dense, burrowing chironomids apparently have increased time and opportunity to establish themselves in the plants. This is also true for lepidopteran larvae that use

Potamogeton plants for food and for case-making. In Eau Galle Reservoir, lepidopteran densities in August averaged 3.13 larvae/plant, values that were over 10 times the lepidopteran densities in June (\bar{x} = 0.27 larva/plant).

54. The value of an aquatic plant is clearly shown by the abundance and diversity of invertebrates present on a single *P. nodosus* plant (Figures 3 and 4). It is obvious that even a few plants can markedly enhance lacustrine invertebrate abundance. Another important consideration regarding the value of aquatic plants concerns how epiphytic invertebrate densities compare with benthic invertebrate densities. In a lake in Indiana, Gerking (1957) found that, per acre of lake bottom, invertebrate density on *C. demersum* was almost three times that of benthic invertebrate density. In a shallow cove in the Hudson River Estuary, Menzie (1980) reported that, per acre of river bottom, invertebrate numbers on the macrophyte *Myriophyllum spicatum* were 7 to 83 percent of benthic densities in the plant bed depending on the sampling date. In the present study, epifaunal and benthic densities (per square meter of reservoir bottom) were fairly equivalent in two *P. nodosus* beds (Figure 5). In this regard, then, macrophytes are important in Eau Galle Reservoir since approximately half of the invertebrates in the littoral zone are epiphytic. As discussed earlier, the presence of macrophytes resulted in enhanced benthic densities as well as the presence of epiphytic invertebrates. Mean total densities (benthic + epifaunal) in the *P. nodosus* bed at site C were 10.6 times the invertebrate densities in nearby nonvegetated areas; total invertebrate densities in the *P. nodosus* bed at site B were 26.1 times the densities of nearby nonvegetated areas (Figure 5). It is apparent that in Eau Galle Reservoir the relatively high density of invertebrates in the littoral zone is dependent on the presence of macrophytes.

55. Another dimension of an epifaunal/benthic comparison concerns the amount of overlap between the species found in the bottom and those on the plants. In a bed of *Myriophyllum* in the Hudson River, Menzie (1980) recognized two assemblages of chironomid species, one living solely in the sediments, the other primarily on the plants. *Dicrotendipes* sp. was found in both habitats. In general, data from the present study agree with those of Menzie (1980). Several common chironomid species on *P. nodosus* (Table A2) were never found in core samples in the littoral zone (Table A1). These species included *C. taris*, *T. nr. fusca*, *E. nigricans*, and *P. illinoense*. Conversely, several chironomid species (*Chironomus* sp., *Cladopelma* sp., *Cladotanytarus* sp.,

Cryptochironomus sp., and *Procladius* sp.) were present solely in the sediments in Eau Galle Reservoir. Menzie (1980) found *Chironomus decorus* and *Procladius subletti* only in the sediments in a *Myriophyllum* bed, with *P. illinoense* present primarily on the *Myriophyllum*.

56. The results of this study indicated, as did Menzie's (1980), that Oligochaeta were represented in the sediments primarily by the Tubificidae. Conversely, the Naididae were found primarily on the plants, although naidids such as *Dero digitata* and *D. nivea* were occasionally common in (or on) the sediments. Several other taxa, including ostracods, water mites, and lepidopteran larvae, were much more common on *P. nodosus* than in the sediments below the plants. Engel (1985) also found naidid worms, water mites, and lepidopteran larvae to be relatively more common on macrophytes than in the sediments.

57. It is apparent from the present study, and those of Menzie (1980) and Engel (1985), that some invertebrate taxa are found only on the plants and not on the bottom. Other taxa are much more abundant on the plants than in the sediments. Removal of macrophytes from the littoral zone of a lake by drawdown, harvesting, or herbicides would therefore not only reduce invertebrate abundance, but also reduce species richness.

PART IV: MACROINVERTEBRATES ON *CERATOPHYLLUM DEMERSUM*
IN EAU GALLE RESERVOIR, WISCONSIN

Background

58. Morphologically, *C. demersum* is very dissimilar to *P. nodosus*. *Ceratophyllum demersum* (Figure 6) has dichotomously forked leaves arranged in whorls; the leaves are numerous and are much smaller than the leaves of *P. nodosus*. The stems of *C. demersum* are also much thinner than the stems of *P. nodosus*, and *C. demersum* lacks roots, although portions of the stems are often found embedded in the sediments. Unlike *P. nodosus* which senesces in the fall, *C. demersum* persists into the winter, and bright green *C. demersum* is present in abundance in the winter beneath the ice.

59. *Ceratophyllum demersum* is found throughout the world with the exception of the colder regions (Cook et al. 1974). In the New World it is present from southern Canada to South America (Gleason and Cronquist 1963). Possibly as a consequence of its worldwide distribution, the invertebrate use of *C. demersum* has been studied fairly extensively. Andrews and Hasler (1943) and Chilton (1986) investigated the invertebrates colonizing *C. demersum* in Wisconsin lakes, while Gerking (1957) and Schramm, Jirka, and Hoyer (1987) studied the invertebrates present on *C. demersum* in a lake in Indiana and in Florida, respectively. Dvorak and Best (1982) studied invertebrates on a number of macrophyte species, including *C. demersum*, in Lake Vechten in The Netherlands.

60. The investigation of invertebrate colonization of *C. demersum* in Eau Galle Reservoir had three principal objectives:

- a. To determine the overall species composition of invertebrates colonizing *C. demersum* in Eau Galle Reservoir, while concentrating on chironomid and naidid assemblages. Dvorak and Best (1982) found high abundances of chironomids and oligochaetes on *C. demersum* in Lake Vechten, and Krecker (1939) and Engel (1985) have reported that these two groups often numerically dominate on macrophytes. Unfortunately, although these two groups are quite abundant on macrophytes (e.g., Gerking 1957 found that larval chironomids made up 58 percent of the invertebrate fauna on *C. demersum* in an Indiana lake), often chironomids are classified only as "Chironomidae" and naidids as "Oligochaeta" in studies of invertebrate macrophyte relationships. This study included a more detailed investigation of epiphytic chironomids and naidids (identified to the species level where possible) in Eau Galle Reservoir.

- b. Although investigators such as Schramm, Jirka, and Hoyer (1987) have observed significant temporal variations in macroinvertebrate abundance on macrophytes, very little study has been made of possible phenological changes occurring in invertebrate communities during the macrophyte growing seasons. In Eau Galle Reservoir the epiphytic invertebrates present on *C. demersum* early in the growing season (June) were compared with the community present late in the growing season (August). By sampling in August of both 1986 and 1987, it was possible to determine if phenological patterns of species composition repeat annually.
- c. Since invertebrates on *C. demersum* and *P. nodosus* were sampled on the same dates and at the same sites, it was possible to determine if these two morphologically dissimilar species supported similar or different faunas.

Study Area

61. Eau Galle Reservoir is described in Part II. The littoral zone, as defined by the presence of aquatic macrophytes during the summer, occupies about 17 percent of the total surface area of the reservoir. The principal macrophyte species in the reservoir, *C. demersum*, extends from the shallow, nearshore areas, where it mixes with *P. nodosus*, to the deepest portions of the littoral zone. A 1981 investigation showed that, in August, the peak period of macrophyte development, *C. demersum* comprised 58 percent of the macrophyte standing crop in Eau Galle Reservoir (Filbin and Barko 1985).

Methods

62. *Ceratophyllum demersum* was sampled in the summers of 1986 and 1987. The work in 1986 was preliminary and occurred on 6 August, when two large samples of *C. demersum* were obtained at site C (Figure 1). The 1986 collection of *C. demersum* took place on the same date and site as the 1986 collection of *P. nodosus*. Specimens of the two species were collected within a few meters of each other.

63. In the summer of 1987 *C. demersum* was obtained on two dates: in June, early in the growing season, and in August (almost exactly 1 year after the 1986 sampling) at the peak of *C. demersum* development. In both June and August 1987, five *C. demersum* samples were taken at each of three sites: sites A, B, and site C (Figure 1). June samples at sites A and B were

obtained on the 19th of the month, whereas sampling at site C took place on the 20th. In August the five samples at the three sites were all obtained on 4 August. Sampling of *C. demersum* in June and August 1987 coincided with *P. nodosus* collections at the same sites.

64. In addition to collecting the five individual *C. demersum* samples, one large supplementary sample of *C. demersum* was obtained at each of the three sampling sites in both June and August. These were obtained in case the invertebrate numbers were too low in the individual samples to adequately assess community composition. These supplementary samples were taken on 23 June and 6 August and were obtained in the same manner as the individual samples; however, they contained much larger amounts of *C. demersum* than the individual samples.

65. Since *C. demersum* has no roots and grows in thick beds with masses of entangled stems, it is extremely difficult to sample a whole, individual plant. Consequently, the sampling unit was a length of *C. demersum* rather than an entire plant. This was accomplished by approaching the *C. demersum* by boat, reaching underwater and snipping off a length of the plant, and gently raising the plant to the surface. Before the plant reached the surface, a fine-mesh net was placed around it. The plant was then placed in a container, and the contents of the net were washed into a bucket. The washings from the net were then sieved through a US Standard No. 60 sieve (openings = 250 μ) to collect any invertebrates that were dislodged while the plant was lifted out of the water. Any invertebrates or objects caught on the sieve were added to the *C. demersum* sample. Any water used in rinsing the net or sieve, as well as any water being added to the container, was first sieved through a US Standard No. 120 sieve (openings = 125 μ) to prevent extraneous invertebrates from being added to the sample.

66. Samples were preserved in 10-percent formalin and stained with a rose bengal solution (Mason and Yevich 1967) to facilitate the separation of invertebrates from the macrophytes. The preservative solution was later drained through a US Standard No. 60 sieve to collect any dislodged invertebrates. The plants were then inspected under 6 \times to 12 \times magnification for invertebrates that might have remained on the plant. A large number of invertebrates, especially chironomid larvae, were found on the plant surfaces at this time. Larval chironomids and oligochaetes were prepared for identification using the procedure of Beckett and Lewis (1982).

67. The amount of *C. demersum* in each sample was determined by measuring the length of each stem. All side stems were snipped off at their junction with the main stem and laid end to end, along with the main stem, to determine total stem length. *Ceratophyllum demersum* stem lengths were determined for all the samples taken in June and August 1987. However, stem lengths were not measured for the two August 1986 samples.

Results

68. *Ceratophyllum demersum* supported a diverse invertebrate assemblage in Eau Galle Reservoir. During the study, 61 distinct species were identified (Table A3). Moreover, the actual number of species present on *C. demersum* in Eau Galle Reservoir is probably higher than 61; groups such as "ostracods" and "nematodes" probably represent a number of taxa. A diverse chironomid community was present on the *C. demersum*. Twenty-one species of larval chironomids were collected (Table A3). Seven species of naidid worms were also present on *C. demersum*.

69. In addition to adding to the diversity of the invertebrate assemblage, naidid worms and chironomid larvae were also very common on *C. demersum*. Naidid and chironomid larvae accounted for a total of 42 percent of the invertebrates collected from *C. demersum* during the three sampling periods (August 1986, June 1987, and August 1987), with naidid worms making up 24 percent of all the invertebrates collected and chironomid larvae accounting for 18 percent. Chironomid larvae and naidids were especially common in the August 1986 samples, contributing 59 percent of all the invertebrates collected (naidids = 40 percent, chironomid larvae = 19 percent). This numerical dominance in August was largely due to the larval chironomid *Paratanytarsus* sp. and the naidid species *Stylaria lacustris* and *Nais pardalis*, all of which occurred abundantly on *C. demersum* at this time (Table A3).

70. A diverse caddisfly fauna inhabited *C. demersum* in Eau Galle Reservoir. Seven species were collected from this macrophyte over the course of the study: *Agraylea* sp., *Leptocerus americanus*, *Oecetis cinarescens*, *Oecetis* sp. (not *O. cinarescens*), *Orthotrichia* sp., *Oxyethira* sp., and *Triaenodes injustus*. In terms of abundance, *L. americanus* was the overwhelming dominant among the caddisflies. Over the three sampling periods, 943 caddisfly larvae were collected and identified to the genus or species level; *L. americanus*

accounted for 92 percent of them (Table A3). In addition, densities of larval *L. americanus* were quite uniform among the three areas of the reservoir. In the August 1987 supplementary sample taken at sampling site A, 8.63 *L. americanus* larvae were present per meter of *C. demersum* stem. Similarly, at site B, the supplementary sample yielded 11.51 *L. americanus* larvae per meter of *C. demersum* stem, and the supplementary sample from site C had 9.76 *L. americanus* larvae per meter of *C. demersum* stem (Table A3). On the basis of these supplementary samples, in Eau Galle Reservoir in early August there was approximately 1.0 *L. americanus* larva per 10 cm of *C. demersum* stem.

71. Although not as abundant as *L. americanus*, damselfly nymphs were quite common on *C. demersum*. Members of the Coenagrionidae were the seventh most abundant taxon collected in June 1987, and were the fifth most common taxon in the August 1987 collections. Almost all the odonates collected from *C. demersum* were damselflies. Only one dragonfly nymph was collected. In addition, all the damselflies collected were members of the family Coenagrionidae, and all the more mature Coenagrionidae collected were members of the *Ischnura*-*Anomalagrion*-*Enallagma* complex.

72. Although insects such as chironomid larvae, the caddisfly *L. americanus*, and damselflies in the family Coenagrionidae were often present in large numbers on *C. demersum*, a number of noninsect invertebrates, in addition to the naiddid worms, were also abundant. For example, in the August 1986 collections, the next four most abundant taxa (after the naiddids *S. lacustris* and *N. pardalis* and the larval chironomid *Paratanytarsus* sp.) were, respectively, copepods, ostracods, soft-bodied Hydracarina, and the gastropod *A. limnosa* (Table A3). In June 1987, ostracods, the gastropod *Gyraulus parvus*, *Hydra* sp., Cladocera, members of the Coenagrionidae, soft-bodied Hydracarina, *A. limnosa*, and first instar *L. americanus* were, in order, the most common non-naiddids and nonchironomids on *C. demersum*. In August 1987 the most common invertebrate (including chironomid larvae and naiddids) was the caddisfly *L. americanus*. Besides *L. americanus*, the most abundant taxa on *C. demersum* (including chironomid larvae and naiddid worms) were, in order of abundance, ostracods, *A. limnosa*, Cladocera, members of the Coenagrionidae, and the amphipod *Hyaella azteca*.

73. Since the length of *C. demersum* stems was measured in 1987 and all invertebrates were counted, it was possible to estimate total invertebrate densities. In June 1987 (considering all three sampling sites), a total of

3,412 invertebrates were collected from 3,150.9 cm of *C. demersum* stems, yielding an overall mean of 1.08 invertebrates/cm of stem (Table A3). The mean density from sampling site C was close to the overall mean (\bar{x} at site C = 1.03 invertebrates/cm of stem length), whereas the mean density from site A was slightly above the overall mean and the mean density at site B was below the overall mean (\bar{x} at site A = 1.55 invertebrates/cm of stem, \bar{x} at site B = 0.61 invertebrate/cm of stem).

74. Since the two August 1986 samples contained a high number of invertebrates and the June samples contained approximately 1 invertebrate per centimeter of stem, the size of each of the August 1987 five plant samples per site was made smaller than in June (the average amount of stem length/sample in June = 210.1 cm; the average amount of stem length/sample in August = 72.6 cm). Using the supplementary samples in August along with the regular samples, it was possible to estimate invertebrate species composition and density. In August a total of 2,465 invertebrates were collected from *C. demersum* having a total stem length of 6,921.2 cm, giving an overall mean of 0.36 invertebrate/cm of stem. Mean densities in August 1987 at the three sampling sites were: \bar{x} at site A = 0.32 invertebrate/cm of stem; \bar{x} at site B = 0.35 invertebrate/cm of stem; \bar{x} at site C = 0.38 invertebrate/cm of stem. The overall mean density in the August 1987 samples was therefore about one third of the mean overall June density.

75. Phenological changes in the population of the caddisfly *L. americanus* were quite apparent in viewing the members of this species collected in August versus June. *Leptocerus americanus* was the most abundant taxon collected from *C. demersum* in August 1987. Almost all the *L. americanus* collected at this time were larvae between, or in, instars II to V (Table A3). In contrast, in the June collections, no instar II to V larval *L. americanus* were collected. Instead, only pupae and first instar larvae of *L. americanus* were present.

76. The clear-cut phenological differences in chironomid and naidid species composition exhibited on *P. nodosus* in June versus August of 1986 and 1987 (discussed in Part III) were not apparent for the chironomids and naidids collected from *C. demersum*. *Paratanytarsus* sp. was the most common larval chironomid collected from *C. demersum* in both August 1986 and June 1987. In addition, four taxa (*Paratanytarsus* sp., *A. peleensis*, *Dicrotendipes* sp., and *Polypedilum bergi*) were among the five most abundant chironomid taxa collected

from *C. demersum* in both August 1986 and June 1987. Likewise, dominance among the naiddid worms on *C. demersum* did not shift from August to June as it did with the naiddid collections from *P. nodosus*. *Stylaria lacustris* was the most abundant naiddid on *C. demersum* in August 1986 as well as in June and August of 1987 (see Table A3 in Appendix A and Table 5 of the main text).

Discussion

77. *Ceratophyllum demersum* in Eau Galle Reservoir supports a diverse and abundant fauna. Sixty-one invertebrate taxa were collected from *C. demersum* in Eau Galle Reservoir. It is also apparent that invertebrates can be abundant on the plants; the June 1987 samples had approximately one invertebrate per centimeter of stem length (which also included leaves). In addition, the caddisfly *L. americanus* was abundant in August 1987, with approximately one larva per 10 cm of *C. demersum* stem, as shown at all three of the sampling sites. In his monograph on the Trichoptera, Wiggins (1977) noted that *L. americanus* larvae were abundant on *C. demersum*. The findings from Eau Galle Reservoir corroborate this but also show that numbers of larval *L. americanus* can become much less common on the macrophyte due to synchronous pupation and emergence of the population.

78. Naidid worms and chironomid larvae were very common on *C. demersum*. The former group comprised almost one fourth of all invertebrates collected. Many investigators, including Krecker (1939), Andrews and Hasler (1943), Gerking (1957), Menzie (1980), Dvorak and Best (1982), Engel (1985), Chilton (1986), and Schramm, Jirka, and Hoyer (1987), have found chironomid larvae to be one of the most abundant invertebrate groups on macrophytes. Some investigators, including Krecker (1939), Menzie (1980), Dvorak and Best (1982), and Engel (1985), have also found oligochaetes to be one of the dominant invertebrate groups on macrophytes. Although the relative abundance of naiddids in comparison to the rest of the invertebrate community certainly varies from place to place, the paucity of naiddids collected in some studies is almost certainly a function of the small size of these invertebrates and the relatively large-mesh sieves used by the investigators. Schramm, Jirka, and Hoyer (1987) reached the same conclusion, when in referring to their own study they stated that "because the samples included only organisms retained by a 1.0 mm mesh screen it is likely that many small oligochaetes and water mites were

excluded from enumeration." Regardless, it is obvious from this research at Eau Galle Reservoir and other studies that naidds often form a very substantial portion of the epiphytic invertebrate community.

79. Although the naidds typically outnumbered the chironomid larvae, the latter group was markedly more diverse than the former. Twenty-one chironomid species were collected versus seven species of naidds. On each of the sampling dates the most abundant larval chironomid on *C. demersum* was a nonburrowing species: *Paratanytarsus* sp. in August 1986 and June 1987 and *T. nr. fusca* in August 1987. Berg (1949, 1950a) identified nine species of chironomids that occur as burrowers in *Potamogeton* spp. Six of these (*Cricotopus elegans*, *Endochironomus nigricans*, *Glyptotendipes dreisbachi*, *Glyptotendipes lobiferus*, *Polypedilum bergi* (called *Polypedilum ophiodes* by Berg; see Maschwitz 1976), and *Polypedilum illinoense*) are present on *P. nodosus* in Eau Galle Reservoir. Four of these species, *E. nigricans*, *G. dreisbachi*, *G. lobiferus*, and *P. bergi*, also occur on *C. demersum* and were occasionally quite common on this plant (Table A3). It is not known whether these species burrow into *C. demersum* or live on its surface. It is obvious, however, that in the littoral zones these four species are not obligate dwellers on *Potamogeton*.

80. Of the 20 chironomid species on *C. demersum*, and the 24 chironomid species found on *P. nodosus*, 17 were common to both plants. Ten chironomid species were found only on *C. demersum* or on *P. nodosus*. Of these 10 species, 9 were very uncommon. Therefore, it is possible that the appearance of these 9 species on a single species of plant may have only been a function of chance. However, the absence of 1 of these 10 species, namely *P. illinoense* from *C. demersum*, was certainly not a chance occurrence. Over all three sampling occasions, a total of 3,395 chironomid larvae were collected from *P. nodosus*, 1,324 of which (39 percent) were *P. illinoense*, making it overall the most abundant chironomid species on *P. nodosus*. Although a total of 2,257 chironomid larvae were collected from *C. demersum* on the same dates as the *Potamogeton* collections, not a single *P. illinoense* larva was found on *C. demersum* throughout the study. This absence of *P. illinoense* from *C. demersum* may be a function of adult female oviposition of *P. illinoense* eggs on *P. nodosus* but not on *C. demersum* and/or avoidance of *C. demersum* by the *P. illinoense* larvae.

81. As reported earlier, *Paratanytarsus* sp. was the most common chironomid collected from *C. demersum* in both August 1986 and June 1987 (Table A3). However, in August 1986 only a few *Paratanytarsus* sp. were found on *P. nodosus* (Table A2). Although these data would appear to indicate that this might be due to a preference by *Paratanytarsus* sp. for *C. demersum*, the June samples revealed that *Paratanytarsus* sp. was abundant on *P. nodosus* at that time. In fact, *Paratanytarsus* sp. made up 52 percent of all the chironomids collected from *P. nodosus* in June with a mean of approximately 39 *Paratanytarsus* sp. per plant. The relative absence of *Paratanytarsus* sp. from *P. nodosus* in August 1986 is difficult to explain. *Thienemanniella* nr. *fusca* exhibited a similar pattern. While *T. nr. fusca* was the most abundant chironomid collected from *C. demersum* in August 1987 (Table A3), only one larva of this species was present on the 15 *P. nodosus* plants collected on this date (Table A2). Again it would appear that *T. nr. fusca* seemed to prefer *C. demersum*. However, in June 1987 *T. nr. fusca* was abundant on *P. nodosus*, and only a few of the larvae were present on *C. demersum*. It is not known if these apparent changes in preference are due to the ability of the invertebrates to colonize the plant or to the proclivity of the plants to be colonized.

82. A comparison of the *C. demersum*-*P. nodosus* naidid communities shows a marked avoidance of *C. demersum* by the worm *Pristina leidy*. Over 1,600 naidids were collected from *P. nodosus* over the course of the study, of which 1,024 (63 percent) were *P. leidy* (Tables A2 and 5). In contrast, only one *P. leidy* was found among the 2,999 naidids present in the *C. demersum* collections (Tables A3 and 5). The contrasting abundance of *S. lacustris* on *C. demersum* and the almost total absence of *P. leidy* from *Ceratophyllum* are especially striking since these two naidid species morphologically are fairly similar, with both bearing long capilliform chaetae and a proboscis.

83. Earlier investigations of differences in invertebrate species composition as a function of macrophyte type have given mixed results. Rooke (1984) found that the invertebrate communities present on four macrophyte species were not greatly different. In Rooke's study the same genera comprised most of the animals in each sample, regardless of plant type, and differences in community composition were due primarily to differences in the proportions of the common species. However, Dvorak and Best (1982) and Chilton (1986) found that, although different macrophyte species had many invertebrate

species in common, some invertebrates demonstrated a preference or were species specific for some plants. Evidence from Eau Galle Reservoir is in agreement with the findings of Dvorak and Best (1982) and Chilton (1986). Although a great deal of overlap existed between *C. demersum* and *P. nodosus* in terms of their species composition, animals such as *L. americanus* were much more common on *C. demersum* than on *P. nodosus*, and some of the numerically dominant animals on *P. nodosus*, such as *P. illinoense* and *P. leidyi*, were either absent or nearly absent from *C. demersum*.

84. On *C. demersum* in Eau Galle Reservoir there were large numbers of noninsect invertebrates such as naiddid worms, snails, water mites, and *H. azteca*. A number of investigators have also found these particular invertebrate groups on various macrophyte species. However, copepods, cladocerans, and ostracods, all of which occurred abundantly on *C. demersum* in Eau Galle Reservoir, have generally not been reported as occurring epiphytically in most plant-invertebrate studies. This may be due to investigators believing that these "zooplankters" really do not occur epiphytically, but rather have been introduced into the samples via the wash water, or to the use of large-mesh sieves that do not effectively collect these animals. Menzie (1980), who used a relatively fine-mesh sieve (openings = 120 μ) in his study of the invertebrate fauna present on *M. spicatum* in an oligohaline estuary, also found that high numbers of copepods, ostracods, and cladocerans occurred epiphytically. Since all sample water was filtered in this study, it is clear that these "zooplankton" groups also occur abundantly on plant surfaces.

85. The cause of the markedly reduced invertebrate densities in August 1987 in comparison with June 1987 densities (mean densities in August were about one third of June densities) is not certain. However, Filbin and Barko (1985) have shown that in Eau Galle Reservoir the period from mid-July to mid-August is the time of maximum increase in standing crop of *C. demersum*. Since our sampling in early August occurred in the midst of this growth, invertebrate densities may have been reduced by a rapid increase in the size of the *C. demersum* habitat, and/or invertebrates may not have had time to colonize all the new growth as densely as they had in June.

PART V: RELATIONSHIP BETWEEN AQUATIC PLANTS AND ZOOPLANKTON
IN EAU GALLE RESERVOIR, WISCONSIN

Background

86. Submersed macrophytes modify water circulation patterns by reducing velocity and altering the direction of flow. Since zooplankton are poor swimmers, they are usually aided by physical structure that reduces flow. In addition, plant stems and leaves provide protection from larval and juvenile fishes and predatory invertebrates. Rabe and Gibson (1984) reported that although phytoplankton species composition was similar in macrophyte and no-plant zones, phytoplankton density was higher in vegetated sites in Findley Lake, Washington. Paller (1987) reported that standing stocks of larval fishes were 160 times higher during the day and 13 times higher at night in macrophyte beds than in open-water areas. (Larval fishes were carried away from macrophytes at night.) Paller also noted that larval fish concentrated in the interior of macrophyte beds rather than in the ecotone.

87. Rabe and Gibson (1984) removed submergent vegetation from sites in Findley Lake and noted that the cladocerans *Chydorus*, *Alonella*, *Graptoleberis*, and *Scapholeberis* were abundant in the vegetated stations whereas *Daphnia schodleri* was collected mostly in open-water areas. The amphipod *H. azteca* seemed to prefer the macrophyte zone, whereas the phantom midge *Chaoborus*, an open-water predator, did not occur in significant numbers at vegetated sites.

88. Studies on zooplankton in Eau Galle Reservoir were conducted during the summer of 1986 as part of studies on the habitat value of aquatic plants. A description of the study area is given in Part II.

Methods

89. Zooplankton were collected using a set of funnel traps mounted on a 0.25-sq m Plexiglas sheet (Figure 7). Each of the 25 funnels and bottles was filled with filtered lake water prior to use. Zooplankton that migrated up in the water column entered the inverted funnel and became trapped in the bottle. Two traps were placed over dense vegetation, and two over sparse vegetation. These traps were left in place for approximately 10 hr during the day; a second set was deployed for 10 hr during the night of 6-7 August 1986.

90. Pump samples for zooplankton were collected using an electric pump powered by a gasoline engine. The end of a 7.5-cm-diam hose was placed 50 cm below the water surface for sampling in both dense and sparse weed beds. The pump was run for about 15 sec until 20 l of water was collected in a carboy; this sample was concentrated by pouring it through a 153- μ zooplankton net. Samples were collected from the dense and sparse sites in *Ceratophyllum* beds once every 4 hr, starting at 12 noon on 6 and 7 August 1986.

91. A pair of zooplankton nets (153 and 63 μ) was used to make vertical hauls at two limnetic sites every other week starting in June 1986. All samples were preserved in 5-percent formalin. In the laboratory, sample aliquots obtained using a Hensen-Stempel pipette were placed in either a zooplankton counting wheel (153- μ net hauls) or a Sedgewick-Rafter chamber (63- μ net hauls) for identification and counting. In the case of the trap and pump samples, the entire sample was enumerated. All species were identified at 400 \times with a compound microscope using the taxonomic keys in Brooks (1957), Voight (1957), and Edmondson (1959).

Results

92. Bimonthly zooplankton hauls with the 153- μ mesh net from the limnetic stations were dominated by crustaceans (copepods and cladocerans) with relatively few numbers of rotifers (Figure 8). *Cyclops bicuspidatus thomasi* comprised about 60 percent of the mature copepods, and *Daphnia retrocurva* made up 70 percent of the cladoceran community. In the hauls taken with the 63- μ mesh net, rotifers numbered about the same as the mature crustaceans, with *Keratella cochlearis* and *Keratella quadrata* dominating this portion of the community.

93. The zooplankton traps captured organisms that crawl about on plants and are not free swimming. *Ceriodaphnia* sp. (cladocerans) and ostracods, which are relatively small crustaceans, comprised the majority of the zooplankton community associated with submersed vegetation. The traps in dense vegetation were dominated by copepods, with relatively few numbers of ostracods, rotifers, and cladocerans. The traps in sparse vegetation obtained about 40 percent fewer individuals (Figure 9).

94. Pump samples collected a slightly different zooplankton community than traps or nets. Ostracods were more abundant in the trap samples than the

pump samples (Figures 9 and 10, respectively). Like the trap samples, the rotifers were more abundant in sparse vegetation than in dense. Densities of copepods and rotifers were dissimilar in the two vegetation types. In the sparse vegetation, rotifers made up 46.9 percent of the community, with equal numbers of copepods (26.1 percent) and cladocerans (25.5 percent). However, in dense vegetation, copepods comprised more than 50 percent of the sample, while rotifers (20.2 percent) and cladocerans (21.8 percent) were subdominant.

Discussion

95. Cladocerans are relatively large and slow moving; hence, they are readily preyed upon by fishes. Rotifers are small, slow moving, and not a preferred food item. Although copepods are small, they move rapidly and are not as likely to be preyed upon by fish. At Eau Galle Reservoir, when densities of rotifers were high, copepods were low, and vice versa. In areas with sparse vegetation, rotifers were more numerous than copepods, suggesting that fishes visually selected and captured the copepods. In the dense vegetation, the faster moving copepods were probably better able to evade predation from small predatory fishes than in sparse vegetation. Also, since the rotifers and cladocerans are distributed more by current than are copepods, advection of these organisms into the weedy areas is reduced. This fact, coupled with the high probability of predation from the larger copepod populations in these areas, could explain the reduced numbers of these plankters in this microhabitat.

PART VI: INVESTIGATION OF *CERATOPHYLLUM DEMERSUM*
IN A BORROW PIT LAKE IN LOUISIANA

Background

96. Macrophytes are known to support a diverse assemblage of epiphytic algae (Brown 1976; Cattaneo and Kalff 1978, 1979; Morin 1986) and invertebrates (Glime and Clemmons 1972; Macan and Kitching 1976; Gerrish and Bristow 1979; Dvorak and Best 1982; Keast 1984; Minshall 1984; Rooke 1984, 1986). Aquatic plants provide a direct food source, indirect food resources through the attached algal community, an egg-laying and nursery area, and refuge from predators as well as an attachment site for associated invertebrates. It is likely that epiphytic algae and many macroinvertebrates become associated with submersed stems and leaves by passive mechanisms. However, Rooke (1986) has recently reported that some macroinvertebrates are capable of discriminating among macrophytes and colonize only those with suitable physical properties.

97. The objective of this study was to investigate macroinvertebrate colonization by comparing assemblages on live *C. demersum* and a plastic imitation that was morphologically very similar. Specifically, the relationship between structure (leaf shape and surface area) and the establishment of macroinvertebrates was studied. Since plastic plants have no food value, they provided an opportunity to investigate the value of structural complexity for macroinvertebrates.

Study Area

98. This study was carried out in a borrow pit lake located 50 m from the Mississippi River, approximately 10 miles (16 km) northwest of Vicksburg, MS. The borrow pits are the result of soil removal for the construction of the main stem levee of the Mississippi River. The borrow pits are found along the Mississippi River from Cairo, IL, to Venice, LA, and range in size from less than 1 acre to more than 100 acres (405,000 m²). The lake is approximately 100 m long and 50 m wide with a maximum depth of 3 m. Many borrow pits are inundated by the floodwaters of the Mississippi River during the late winter and spring months. However, this lake was not flooded during the winter 1986-1987.

99. The following physicochemical characteristics were measured over the 3-month period of the study (June through August): water temperature, 27° to 29° C; dissolved oxygen, 5.3 to 6.8 mg/l; calcium hardness, 45 to 55 mg/l as CaCO₃; and specific conductance, 350 to 410 μmhos/cm. Dense beds of *C. demersum* were located in the littoral zone of the borrow pit to a depth of 1.5 m.

Methods

100. Plastic *Ceratophyllum* and *Vallisneria* plants (Secondnature Company-Plantastics) were selected to serve as artificial substrates for macroinvertebrate colonization. The plastic *Ceratophyllum* was morphologically similar to the natural *C. demersum*; the surface area of a 10-cm stem was 9,428 mm² (SD = 162, n = 10) and 8,240 mm² (SD = 119, n = 10) for the live and plastic *Ceratophyllum*, respectively. Plastic *Vallisneria* was chosen to give a different morphological structure and a smaller surface area for colonization (1,800 mm² for a 10-cm stem; SD = 72, n = 10). Sixteen plastic *Ceratophyllum* or *Vallisneria* were equally spaced in a 4 by 4 rectangular grid on a 0.25-m² piece of 0.64-cm-mesh hardware cloth using plastic wire ties. One quadrat each of plastic *Ceratophyllum* and *Vallisneria* was placed on cleared substrate at the center and one end of a natural *C. demersum* bed on 6 June 1987. Two 0.25-m² quadrats of live *C. demersum* were marked with four stakes at similar locations in the bed.

101. On 5 August 1987, four stems were randomly removed from each quadrat of live and plastic plants. Stems were clipped at their roots and gently lowered into a 250-μ mesh net. The clipped stem and any organisms dislodged in the net were washed into a 500-ml collecting jar and preserved in 7-percent buffered formalin stained with rose bengal. Dislodged organisms and those attached to the plant stem were picked in the laboratory using a dissecting microscope and identified to the lowest possible taxon. Data were expressed as the number of individuals or taxa per 10-cm stem. No significant difference ($P > 0.05$) in either the mean number of individuals or taxa per 10-cm stem was noted between quadrats placed at the center and end of the bed; these data were combined to give a composite number of eight samples for each plant type.

Results

102. The number of invertebrates per 10-cm stem was significantly different on the three plant types (Table 6). Live *C. demersum* contained 3 and 10 times as many organisms as the plastic *Ceratophyllum* and plastic *Vallisneria*, respectively. The live *C. demersum* also contained a significantly greater number of taxa per stem than either the plastic *Ceratophyllum* or plastic *Vallisneria* (Table 6). The total numbers of taxa identified on the plants were 49, 52, and 42 for the live *C. demersum*, plastic *Ceratophyllum*, and plastic *Vallisneria*, respectively. Taxa diversity (H') was significantly greater and evenness (J) was greater on the plastic *Vallisneria* than on the live *C. demersum* and plastic *Ceratophyllum* (Table 6). When the number of individuals per stem was corrected for stem surface area, live *C. demersum* had significantly more individuals than the plastic *Ceratophyllum* and plastic *Vallisneria*, whereas the plastic *Ceratophyllum* had significantly more individuals than the plastic *Vallisneria*.

103. Ephemeropterans, gastropods, and chironomids represented 94, 87, and 77 percent of the total number of organisms on the live *C. demersum*, plastic *Ceratophyllum*, and plastic *Vallisneria*, respectively (Figure 11). Ephemeropterans were the most common organisms on the live *C. demersum* and plastic *Ceratophyllum*, whereas ephemeropterans and chironomids were the co-dominant taxa on plastic *Vallisneria*. Gastropods comprised 22 percent of the total number of individuals on the live *C. demersum*, which was 3.6 and 6 times their percentage abundance on the plastic *Ceratophyllum* and plastic *Vallisneria*, respectively. Chironomids represented 38 percent of the total assemblage on the plastic *Vallisneria*, but only 18 and 24 percent of the total on the live *C. demersum* and plastic *Ceratophyllum*. Naidid and tubificid worms were common on the plastic *Vallisneria*, but were either absent or rare on the live *C. demersum* and plastic *Ceratophyllum* (Figure 11).

104. Six genera made up at least 5 percent of the total number of individuals on at least one of the three plant types (Figure 12). The ephemeropterans, *Callibaetis* sp. and *Caenis* sp., were the dominant taxa, representing 54, 57, and 36 percent of the total assemblage on live *C. demersum*, plastic *Ceratophyllum*, and plastic *Vallisneria*, respectively. The pulmonate gastropods, *Physa* sp. and *Gyraulus* sp., made up 20 percent of the total number of taxa on the live *C. demersum*; these two gastropods made up only 6 percent and

3.5 percent of the assemblage on the plastic *Ceratophyllum* and *Vallisneria*, respectively. Of the 36 chironomid species identified, only *Dicrotendipes* sp. and *Microtendipes* sp. made up 5 percent of the total on any one plant type (Figure 12). These two chironomids represented 11 percent of the total number of taxa on the plastic *Vallisneria*, but only 4 and 7 percent of the total on the live *C. demersum* and plastic *Ceratophyllum*.

105. Differences in the distribution of taxa among feeding guilds were noted on the live *C. demersum*, plastic *Ceratophyllum*, and plastic *Vallisneria* (Figure 13). Scrapers/grazers, organisms that feed upon attached periphyton, were the most abundant feeding guild, representing 76, 63, and 40 percent of the total number of individuals on the live *C. demersum*, plastic *Ceratophyllum*, and plastic *Vallisneria*, respectively (Figure 13). Plastic *Vallisneria* had a more even distribution of taxa across feeding guilds with a greater percentage of collector/gatherers (organisms that feed on deposited or suspended fine particulate organic matter), piercers/herbivores (organisms that consume plant tissues), and predators than the assemblages on the live *C. demersum* and plastic *Ceratophyllum* (Figure 13); the plastic *Ceratophyllum* also had a greater percentage of individuals in these three guilds than the live *C. demersum*.

Discussion

106. The macroinvertebrate assemblage in the borrow pit lake showed significantly higher densities of individuals and a greater number of taxa on the live plant than on the two plastic imitations. These differences remained when the effects of stem and leaf surface area were taken into account. Also, a significantly greater number of individuals colonized the plastic *Ceratophyllum* when compared with the plastic *Vallisneria*; these differences persisted even when stem and leaf surface area were taken into account. The morphology and surface area of the live and plastic *Ceratophyllum* were similar, indicating that some property other than plant form was responsible for the differences seen in the macroinvertebrate assemblage.

107. Glime and Clemmons (1972) and Gerrish and Bristow (1979) reported that plastic plants supported the same taxa as live plants, but the taxa were present in different proportions. However, the plastic plants used were crudely constructed and were not morphologically similar to their live

counterparts. Lethbridge, Borowitzka, and Benjamin (1988) constructed plastic *Ambiholis* (a seagrass) and reported that it quickly colonized with algae and invertebrates that were on live plants. Rooke (1986) found considerable differences in species composition and relative abundance of macroinvertebrates on a variety of live riverine macrophytes and morphologically similar plastic imitations. In his study, the highest number of individuals was found on those live plants with finely dissected leaves (*Myriophyllum* and *Ranunculus*). Additionally, the chironomids *Rheotanytarsus* sp. and *Cricotopus* sp. were dominant on live *Myriophyllum*, while the trichopteran *Oecetis* sp. and the amphipod *Hyalella* were the dominants on plastic *Myriophyllum* (Rooke 1986). Rooke (1986) concluded that factors such as epiphytic coating, surface microstructure, and/or organic exudates may have been important for the differences observed between the live and plastic plants.

108. Scrapers/shredders dominated the macroinvertebrate assemblage on the live *C. demersum* and plastic *Ceratophyllum*. While there were similar percentages of the ephemeropterans *Callibaetis* sp. and *Caenis* sp. on the live and plastic *Ceratophyllum*, the live *C. demersum* assemblage had a greater proportion of gastropods than the plastic *Ceratophyllum* (Figure 12). It was apparent from the laboratory picking of macroinvertebrates from the two plant types that the leaves of the live *C. demersum* contained masses of filamentous green algae in much greater abundance than on the plastic *Ceratophyllum*. Although the surface areas of the two plant types were similar, the leaves of the live *C. demersum* were more finely dissected and more widely separated on the stem than those of the plastic *Ceratophyllum*, providing a more "efficient" trap for the green algae. Field observations indicated that a majority of the ephemeropterans and gastropods were moving among the attached algae. In this study, an attempt was made to assess the periphyton community attached to the stems and leaves of the two types of plant. The live *C. demersum* contained a greater species richness and abundance of diatoms than the plastic *Ceratophyllum*; this could be the result of either a specific property of the live *C. demersum* that facilitated the growth of the diatom community or the longer length of time the live *C. demersum* had for developing a periphyton community.

109. The plastic *Vallisneria* had a greater species diversity and evenness than the live *C. demersum* and plastic *Ceratophyllum* (Table 6). This was due to the lack of dominance by a specific taxon. Only one species (*Callibaetis* sp.) made up greater than 20 percent of the total abundance of

individuals; there was a lack of dominance by *Caenis* sp. and *Physa* sp., organisms that were common on the live *C. demersum* and plastic *Ceratophyllum*. Rooke (1986) reported that the imitation plant with the lowest invertebrate densities in the Eramosa River, Ontario, Canada, was the morphologically simple *Potamogeton gramineus*; this plant also had the most equitable distribution of taxa among feeding guilds. Rooke (1986) suggested that the plastic *P. gramineus* did not provide any special resource for invertebrate colonization except for an attachment site.

110. In the borrow pit lake, the flat, morphologically simple leaves of the plastic *Vallisneria* did not have an attached green algal community. In addition, there were few diatoms attached to the leaves of the plant. These factors may explain the decrease in abundance of scrapers/grazers and an increase in abundance of tube and net-building collector/gatherers (primarily the chironomids *Dicrotendipes* sp., *Microtendipes* sp., and *Nanocladius alternatherae*) that are using the plant primarily as a source of attachment (Figure 13).

111. Rooke (1986) also found that the majority of predaceous invertebrates were found on plastic imitation plants when compared to their live counterparts, with the most common being chironomids in the subfamily Tanypodinae. The plastic *Vallisneria* supported a greater relative abundance of predators than either the live *C. demersum* or the plastic *Ceratophyllum*, with Tanypodinae chironomids comprising 19 percent of the total number of individuals present. In addition, the plastic *Ceratophyllum* assemblage contained a greater percentage of predators than the live *C. demersum*.

112. In this study there were significant differences in the macroinvertebrate assemblage associated with live versus plastic plants. These differences could not be explained by simple differences in stem and leaf morphology. Although the plastic *Ceratophyllum* was morphologically similar to live *C. demersum*, differences in the degree of leaf dissection were readily apparent and resulted in an associated algal community that was reduced in abundance on the plastic plant. This illustrates the difficulty in finding an artificial substrate that is morphologically "identical" to a natural plant. The simple leaves of the plastic *Vallisneria* did not support an associated algal community, and collector/gatherers and predators were relatively more important than the scraper/grazers found on the live and plastic *Ceratophyllum*.

PART VII: A REVIEW OF THE LITERATURE ON THE HABITAT VALUE OF
AQUATIC MACROPHYTES

Habitat Modification

113. As prominent features of the littoral zones of lakes and many river channels, submersed macrophytes have the capacity to alter the physical environment by changing the velocity of waves and currents, modifying sedimentation patterns and substrates, stabilizing habitats, reducing erosion, altering temperature regimes, and influencing available light. Dense populations of macrophytes in rivers have been observed to reduce current velocities and flow patterns and physically alter the environment by reducing water movement and causing a higher retention of silt, sand, and particulate organic matter (Butcher 1933; Westlake 1961, 1975; Minckley 1963; Sculthorpe 1967; Edwards 1969; Fonseca et al. 1982; Gregg and Rose 1982; McDermid and Naiman 1983).

114. Beds of macrophytes in the littoral zones of lakes modify water circulation patterns by reducing the velocity and changing direction of flow. Flow in a *Myriophyllum heterophyllum* bed at a depth of 3 m in Lawrence Lake, Michigan, was less than 1 cm/sec (Losee and Wetzel 1988). Fonseca et al. (1982) observed that seagrass (*Zostera marina*) reduced current velocities inside the plant bed, but current velocities were actually higher over the surface of the plants. Changes in velocities per unit depth were shown to increase with increased plant abundance. These workers proposed that shoot bending accounted for a redirection of current flow and in-canopy reduction of current velocity, and that these mechanisms affected photosynthetic capabilities while providing habitat stability.

115. Gregg and Rose (1982) noted a similar trend in the Portneuf River in southeastern Idaho and observed that macrophytes affected the substrates in streams by increasing the amounts of fine sediments and by providing substantially greater surface areas than unvegetated substrates. Reductions in current velocities also contributed significantly to accumulations of greater amounts of detritus, and submersed macrophytes accounted for the higher densities of diatoms and macroinvertebrates. The complex morphological characteristics and densities of plants enable them to function as mechanical filters of suspended matter and to act as barriers to the entry of pollutants into the

ecosystem (Merezhko 1973; Merezhko, Ryabov, and Tsytsarin 1977). Kokin, Anan'yeva, and Ivanova (1965, cited in Merezhko 1973) noted that the settling of suspended matter on plants was facilitated by a slime layer on macrophytes. Submersed macrophytes may also establish a gradient of physical parameters including light and temperature. Available light at the bottom of plant beds may be reduced to as little as 0.01 percent of surface levels (Westlake 1975). Dale and Gillespie (1977) observed that the daily cycle and distribution of temperatures in Lake Opinicon, Ontario, were greatly influenced by submersed aquatic macrophytes.

116. Colonization and subsequent modifications of the habitat may bring about a succession of other macrophyte species resulting in further changes in the physical environment and associated epiflora and epifauna. Submersed macrophytes also provide substrates for epiphytic algae (Sozka 1975; Cattaneo and Kalff 1978, 1979, 1980; Beer and Wetzel 1982; Carignan and Kalff 1982; Wetzel 1983a; Wetzel, Brammer, and Forsberg 1984; Bronmark 1985; Wetzel et al. 1985; Morin 1986; Carlton and Wetzel 1987; Losee and Wetzel 1988), substrates for the direct colonization by invertebrates (Berg 1949; McGaha 1952; Rosine 1955; Harrod 1964; Krull 1970; Porter 1977; Dvorak 1978; Menzie 1980; Rabe and Gibson 1984; Rooke 1984, 1986; Bronmark 1985; Pardue and Webb 1985; Friday 1987; Schramm, Jirka, and Hoyer 1987), and as oviposition sites for invertebrates and fishes (McGaha 1952; Breder and Rosen 1966; Sozka 1975; Westlake 1975; Lagler et al. 1977; Pandit 1984; Engel 1985, 1988).

117. Submersed macrophytes also serve as an important food source for vertebrates including fishes and waterfowl (Arner, Normwood, and Teels 1975; Werner et al. 1977; Swanson, Krapu, and Serie 1979; Laughlin and Werner 1980; Pandit 1984). Pandit (1984) reported that macrophytes constituted 27 to 36 percent of the principal food in the food chains of fishes, 73.4 to 98.2 percent of the food for wild ducks, and 100 percent for wild geese in five wetland habitats in India.

Water Chemistry

118. Submersed macrophytes undergo complex interactions with abiotic and biotic components and can cause wide diurnal fluctuations in dissolved oxygen (DO), carbon dioxide, and pH. Sediment-water interactions of aquatic macrophytes have been shown to greatly influence the hydrochemistry and

nutrient cycles in aquatic ecosystems (Sculthorpe 1967; Otsuki and Wetzel 1972, 1974; Merezko 1973; Best 1977, 1979; Howard-Williams and Howard-Williams 1978; Mickle and Wetzel 1978a, 1978b, 1979; Howard-Williams and Davies 1979; Landers 1979, 1982; Barko and Smart 1980, 1981; Carignan and Kalff 1980, 1982; Carpenter 1980; McDermid and Naiman 1983; Moore et al. 1984; Filbin and Barko 1985; Smart and Barko 1985; Wylie and Jones 1987; Chen and Barko 1988; Losee and Wetzel 1988). Metabolic activities of the submersed macrophyte-epiphyte community can alter the chemistry of water in the littoral zone (Losee and Wetzel 1988).

119. Wylie and Jones (1987) studied diel changes in DO and pH in a shallow reservoir in Missouri and reported average diel fluctuations of 5.45 mg/l dissolved oxygen and 0.88 pH unit. The widest ranges of diurnal changes (10 to 14 mg/l and 2 to 3 pH units) were observed during summer when macrophyte biomass was the highest. Sculthorpe (1967) observed that DO concentrations were 230 percent higher near submersed macrophyte beds than in no-plant zones.

Nutrient Cycles

120. The effects of submersed macrophytes on the nutrient cycles of aquatic habitats are varied and are related in part to macrophyte morphology and the hydrochemistry of the environment. Nonrooted or weakly rooted macrophytes absorb nutrients primarily from the surrounding medium (Denny 1972, 1980), whereas in rooted species, the primary sources for essential nutrients, including nitrogen and phosphorus, are the sediments (Hill 1979; Patterson and Brown 1979; Barko and Smart 1980, 1981; Carignan and Kalff 1980; Huebert and Gorham 1983; Smart and Barko 1985). Nutrients assimilated by macrophytes during the growing season may be released back to the water during senescence to provide a valuable nutrient resource for phytoplankton (Godshalk and Wetzel 1978a, 1978b, 1978c; Howard-Williams and Howard-Williams 1978; Howard-Williams and Davies 1979; Landers 1979; Wetzel 1979; Carpenter 1980). In transferring nutrients from the sediments back to the water, macrophytes can contribute significantly to nutrient cycles, particularly sedimentary cycles where essential ions are lost to sediments.

121. Otsuki and Wetzel (1972, 1974) found that phosphorus and dissolved organic materials coprecipitated with CaCO_3 , particularly in the vicinity of

submersed macrophyte-epiphyte communities in hard-water lakes (Mickle and Wetzel 1978a, 1978b, 1979). Diurnal changes in photosynthesis rates within the boundary layer of macrophyte beds can cause a depletion of the dissolved inorganic carbon and changes in pH. The hydrochemistry of the macrophyte-epiphyte complex can cause a shift in pH and redox potentials. These changes are typically the greatest in the morning following night respiration and depletion of oxygen and can affect nutrient availability in the complex (Losee and Wetzel 1988). Submersed macrophytes play a major role in maintaining chemical equilibria by undergoing reactions involving the carbon dioxide-bicarbonate buffering system.

Primary Productivity and Energy Budgets

122. Submersed macrophyte-epiphyte communities in the littoral zones of lakes make valuable contributions to the total lake production (Westlake 1969; Wetzel 1969, 1979; Wetzel and Westlake 1969; Rich, Wetzel, and Thuy 1971; Sozka 1975; Cattaneo and Kalff 1978, 1980; Losee and Wetzel 1988). Under comparable conditions, macrophyte communities are more productive per unit area than phytoplankton communities, although macrophyte productivity is usually less in lakes deeper than 10 m (Westlake 1969). It has been well established that the productivity of emergent macrophytes exceeds that of all other freshwater plant communities in the littoral zone (Wetzel 1979).

123. In Lake Memphremagog, Quebec-Vermont, epiphytes synthesized a significant fraction of the productivity in macrophyte beds (Cattaneo and Kalff 1980). Cattaneo and Kalff noted that in most studies the role of epiphytes in macrophyte beds has been underestimated due to the loss of loose epiphyte biomass during sampling. In a marl lake in Michigan, macrophytes contributed more than 60 percent of the annual benthic carbon budget (Rich, Wetzel, and Thuy 1971). Rabe and Gibson (1984) reported that although phytoplankton species composition was similar in both macrophyte zones and no-plant zones in Findley Lake, Washington, phytoplankton density was higher in the vegetated sites. Benthic macrophytes have begun to replace phytoplankton as the predominant primary producers in many soft-water lakes that have become more acidic from anthropogenic sources (Wetzel 1983a; Wetzel et al. 1985).

Macrophytes and Invertebrate Communities

124. The relationships between submersed macrophyte communities and macroinvertebrates include complex interactions relating to macrophyte morphology, invertebrate behavior, life cycles, and predator-prey relationships. Invertebrate abundances on submersed macrophytes tend to be related to plant morphology and physicochemical or environmental factors. The most common invertebrates colonizing submersed macrophytes include crustaceans, midges, oligochaetes, and gastropods. Of the insects that are adapted to live part or all of their lives in aquatic habitats, many species have adapted to the habitats provided by submersed macrophytes. Submersed macrophytes provide valuable substrates to aquatic habitats for direct colonization by invertebrates, and numerous studies have documented the importance of submersed macrophytes to macroinvertebrate communities (Berg 1949; McGaha 1952; Rosine 1955; Harrod 1964; Krull 1970; Glime and Clemmons 1972; Macan and Kitching 1976; Porter 1977; Dvorak 1978; Gerrish and Bristow 1979; Menzie 1980; Keast 1984; Minshall 1984; Pandit 1984; Rabe and Gibson 1984; Rooke 1984, 1986; Bronmark 1985; Engel 1985, 1988; Gregg and Rose 1985; Pardue and Webb 1985; Friday 1987; Schramm, Jirka, and Hoyer 1987).

125. Berg (1949) summarized the limnological relationships of insects to *Potamogeton* and concluded that *Potamogeton* supported a diverse assemblage of 32 species of insects that were intimately related to macrophytes. All major plant organs including roots, stems, and leaves were utilized by various insect species which obtained nutritive, protective, or respiratory benefits. McGaha (1952) expanded Berg's initial study to include limnological relations of insects to 13 more macrophyte species. Macrophyte morphology appears to be an important factor in determining invertebrate diversity and density. Ball and Hayne (1952) reported that macrophyte density and water depth were important parameters in determining invertebrate densities in macrophyte beds.

126. Harrod (1964) studied the invertebrate faunas associated with four different species of aquatic macrophytes in a chalk stream and concluded that morphology, periphyton on the plant surface, chemical nature of the plant, and the habits of the various animals were largely responsible for observed differences in populations on the plants. Rosine (1955) emphasized that plant surface area was an important factor in invertebrate colonization and that quantitative studies of the macroinvertebrates should take surface area into

account. Since macroinvertebrates readily colonize artificial plants, it is apparent that structure is of prime importance. Kreckler (1939) and Rosine (1955) have shown that plants with finely divided leaves supported larger and more diverse invertebrate communities.

127. Studies in both lotic and lentic habitats have usually reported higher species diversities and densities in areas containing submersed macrophytes than in zones without plants. Minckley (1963) reported the highest invertebrate densities from the moss *Fissidens*, intermediate densities among macrophytes, and the lowest densities from bare substrates including sand, gravel, and cobble in Doe Run, a spring-fed stream in Kentucky. Pennak (1971) found that a stream with aquatic macrophytes had an invertebrate biomass 3 to 10 times greater than a similar stream without macrophytes. Martin and Shireman (1976) reported that chironomids (midges) and gastropods were the two most common macroinvertebrates present on *Hydrilla*. A benthic study of an oligohaline section of the Hudson River by Menzie (1980) indicated that 16 to 35 percent of the invertebrate fauna inhabiting a cove were found on the rooted aquatic plant *Myriophyllum spicatum*, and chironomids were the most abundant taxa.

128. Rabe and Gibson (1984) removed submergent vegetation to determine invertebrate reactions to choices between vegetated and nonvegetated areas in Findley Lake, Washington, and observed that the cladocerans *Chydorus*, *Alonella*, *Graptoleberis*, and *Scapholeberis* were found in the vegetated stations whereas *Daphnia schodleri* were collected mostly in open-water areas. Macroinvertebrate predators including the damselfly *Enallagma boreale*, the backswimmer *Notonecta*, and the water boatman *Hesperocorixa leavigata* seemed to prefer sites with submergent plants over no-plant zones. The amphipod *H. azteca* and the mayfly *Callibaetis* were associated with macrophytes whereas the phantom midge *Chaoborus* (an open-water predator) did not occur in significant numbers at vegetated stations (Rabe and Gibson 1984).

129. Infaunal macroinvertebrates in the sediment of a *Hydrilla* bed were found to be four times higher than in the nearby sediments of a no-plant zone (Watkins, Shireman, and Haller 1983). Invertebrate densities were higher on rock and cobble than on any of four species of macrophytes in the Speed River, Ontario (Rooke 1984). However, in a study of the macrofaunas of eight macrophytes, three imitation plants, and exposed rock surfaces in the Eramosa River, Rooke (1986) observed that the highest numbers of invertebrates were

found on two finely dissected plants (*Myriophyllum* and *Ranunculus*) and a plastic imitation of *Elodea*. Pardue and Webb (1985) compared the aquatic macroinvertebrates occurring in association with Eurasian watermilfoil (*M. spicatum*) and those occurring in open-water areas and found greater numbers of taxa and densities in the watermilfoil, although the differences were usually not significant. They found that immature insects, amphipods, naidid worms, and leeches were more abundant in the watermilfoil habitat, whereas the burrowing mayfly *Hexagenia bilineata* was more abundant in the littoral areas and the macrophyte root structures apparently interfered with its burrowing activities.

130. Engel (1985, 1988) conducted a comprehensive study of the role and interactions of submersed macrophytes in Halverson Lake, a 4.2-ha, shallow eutrophic lake in Wisconsin and observed that 75 percent of the macroinvertebrate species were found on or beneath macrophytes during the summer. Schramm, Jirka, and Hoyer (1987) studied the epiphytic macroinvertebrates on seven species of dominant macrophytes in two central Florida lakes and reported large variations in invertebrate densities and biomass colonizing emergent and submersed macrophytes. Quantities of colonizing epiphytic invertebrates were higher on floating and submersed macrophytes than on emergent macrophytes. Significant temporal variations ($P < 0.05$) were observed, although no consistent temporal trends were apparent (Schramm, Jirka, and Hoyer 1987).

131. Some macroinvertebrates have the potential to reduce or eliminate macrophytes through herbivory. Lodge (1987) found that abundances of the crayfish *Orconectes rusticus* greater than 9 g/m^2 reduced total macrophyte biomass 64 percent. Abundances greater than 140 g/m^2 eliminated all macrophytes.

Predator-Prey Relationships

132. Predator-prey relationships of macroinvertebrates are complex and poorly understood. Additional studies of predator-prey interactions are needed, although studies of this type are difficult to conduct. Peckarsky (1984) provided a comprehensive review of the literature concerning predator-prey interactions among aquatic insects and presented results of empirical studies.

133. The majority of macroinvertebrates associated with submersed macrophytes are herbivores including scrapers, shredders, collectors, and filterers. The dominant forms colonizing submersed macrophytes are snails, crustaceans, and chironomids (midges). These organisms use the macrophytes as substrate, food, and shelter. In addition, macrophyte decomposition contributes significantly to the detritus-based food chains. Although many consumers in the littoral zone feed on the organic film covering macrophytes, little is known about the relationships among periphyton, macrophytes, and grazers (Lodge 1986). Wetzel (1983b) stated that less than 10 percent of the organic matter produced by attached microflora is consumed and that most of it is released as dissolved organic compounds. Food choice was considered to be the most important proximate factor in the distribution of two species of gastropods in a eutrophic pond in southern England (Lodge 1986).

134. Many species of macroinvertebrates undergo dietary shifts from herbivory and become predators in the later stages of their life cycle. Some stoneflies become highly predaceous on chironomids that usually dominate macrophyte fauna. Many predators are opportunistic and feed on abundant organisms provided that they are palatable. Notable predators occur among the orders Coleoptera (beetles), Odonata (damselflies and dragonflies), and Hemiptera (giant water bugs, backswimmers, water scorpions, and water boatmen).

135. Nymphs of odonates are usually found in macrophyte beds and can easily conceal themselves among the stems and leaves. Most zygopterans (damselflies) and aeshnid dragonflies are classified as climbers, lurking in the vegetation or resting on aquatic plant stems (Westfall 1984). The nymphs stalk their prey and in some cases have developed protective colorations that match the immediate surroundings. Nymphs of *Aeshna grandis* have been reported to undergo seasonal changes in coloration from green in summer to brown in winter as a probable strategy for predation. These nymphs have been observed climbing plant stems to prey on macroinvertebrates (Westfall 1984).

136. Damselflies are also climbers and invertebrate predators. Submersed macrophytes provide them access to the entire water column. In addition, they may be preyed upon by other macroinvertebrates, fishes, and birds. Crowder and Cooper (1982) reported that, in high densities of macrophytes, odonate nymphs were able to seek refuge from bluegills. Heads (1985) observed that the damselfly *Ischnura elegans* was able to alter its foraging behavior in

the presence of the backswimmer *Nototecta glauca* or fish. In a study of the effects of weed density on damselfly larval mortality due to predation by the backswimmer *Notonecta*, Thompson (1987) found that at very high plant densities there was a wide range of larval densities over which density-dependent mortality occurred.

137. Macroinvertebrates appear to be more vulnerable to predators at higher population densities because of increased intraspecific competition (Harvey and Corbet 1985). The aquatic hemipterans (true bugs) are equipped with a piercing beak and are highly adapted for predation. Common representatives in littoral habitats include the giant water bugs (*Belostoma*, *Lethocerus*), the water scorpions (*Ranatra*), backswimmers (*Notonecta*), and several genera of corixiids (water boatmen) that use macrophytes (Polhemus 1984). The giant water bugs and water scorpions even prey on larval and adult fishes. The order Coleoptera (beetles) contains approximately 5,000 species that are aquatic or semiaquatic. Larvae and adults of the families Dytiscidae (predaceous diving beetles) and Hydrophilidae (water scavenger beetles) are some of the most voracious predators associated with macrophyte beds. Some of the large dytiscids can attack small fish and tadpoles (White, Brigham, and Doyen 1984).

Fishes

138. Aquatic macrophytes and fishes are intimately related in that the pattern and density of submersed macrophyte beds greatly influence fish behavior and life history. Macrophytes provide shelter, food, foraging areas, and spawning sites for fishes. Species diversity, community organization, and population densities of fishes inhabiting macrophyte beds are usually different from open-water areas. Larval fishes are typically more abundant in submersed macrophyte beds, whereas larger adults frequently use deep-water areas outside the littoral zone. In a study of food partitioning between rock bass and smallmouth bass, George and Hadley (1979) found that smallmouth bass young-of-the-year seemed to prefer a rocky substrate, and rock bass were found in a heavily vegetated site. Killgore (1979) reported that largemouth bass and other game species were more abundant in beds of *Hydrilla* in shallow water. Numbers of smaller bluegill and longear sunfish were positively

correlated with the height of vegetation, and few adults of either species were in no-plant zones.

139. A study of food partitioning among fishes associated with aquatic macrophytes revealed that macrophyte beds supported higher densities of fishes than areas between beds (Savitz 1981). Savitz, Fish, and Weszely (1983) noted significant differences in behavior and movement of bluegills and largemouth bass in a lake with vegetation as compared to a lake without vegetation. Average catches of northern pike from areas with submersed macrophytes were 10 times higher than from areas without macrophytes (Holland and Lester 1984). Hall and Werner (1977) and Mittelbach (1981) have shown that small bluegills are subjected to higher predation rates by larger fish in open-water areas devoid of macrophytes and that small fish tend to avoid these areas. Holt, Kitting, and Arnold (1983) reported that juvenile red drum concentrated in regions between sea grass beds and open-water areas.

140. In a study of fishes in Lake Michigan, larval fish were found to concentrate in shallow areas in a coastal wetland (Chubb and Liston 1986). Floyd, Hoyt, and Timbrook (1984) and Paller (1987) reported higher densities of larval fishes in macrophyte beds than in open channels of Steel Creek, South Carolina. Standing stocks of larval fishes in the macrophyte beds were 160 times higher during the day and 13 times higher at night than in open-water areas (Paller 1987). The decreased densities of larval fishes in the macrophyte beds at night were attributed to larval drift. Paller (1987) also noted that larval fish concentrated in the interior of macrophyte beds rather than in the ecotone.

141. Poe et al. (1986) found that fish species composition and richness differed in altered and unaltered littoral habitats in Lake St. Clair, Michigan. A percid-cyprinid-cyprinodontid assemblage dominated in the unaltered areas whereas a centrarchid fauna dominated in the altered zones. The centrarchid fauna was significantly correlated with four species of macrophytes, and the percid-cyprinid-cyprinodontid assemblage was correlated with six species of macrophytes. Poe et al. (1986) concluded that the abundance of aquatic macrophytes had the most influence on the community structure of fishes in altered and unaltered areas. Engel (1985, 1987, 1988) studied the impacts of submersed macrophytes on macroinvertebrates and fishes in a shallow eutrophic impoundment in southern Wisconsin. He observed that fishes under 120-mm total length were sheltered by plant beds denser than 200 g dry

weight/m², and that small bass and bluegills avoided no-plant zones along-shore. Larger bluegills and largemouth bass use lower densities of macrophytes or remained offshore. Fish movements were selectively restricted by submersed macrophytes.

142. The presence of submersed macrophyte beds typically alters fish behavior and impacts on predator-prey interactions and feeding strategies. Healey (1984) summarized relationships between fish predation on aquatic insects and interactions in freshwater habitats. Larval fishes use the shelter provided by macrophytes as a refuge from predators and feed on zooplankton associated with macrophytes.

PART VIII: RECOMMENDATIONS

Optimal Densities of Macroinvertebrates

143. The numerous beneficial influences of submersed macrophytes on aquatic ecosystems have been discussed. Although submersed macrophytes affect physical, chemical, and biological components of aquatic systems, they may become overabundant to the extent that significant negative impacts to the ecosystem occur. An excess of submersed macrophytes may be harmful by causing wide fluctuations in dissolved oxygen and pH and accumulations of hydrogen sulfide and ammonia. In addition, luxuriant growths of macrophytes may interfere or prohibit recreational activities and sport fishing. High densities of submersed macrophytes may cause an imbalance in fish populations because larvae and juveniles seek refuge among the plant beds and avoid predation by large fish. This can result in overpopulation, stunted growth, and poor condition factors of fishes.

144. Heck and Thoman (1981) reported that high densities of simulated aquatic vegetation (674 shoots/m^2) had a negative impact on feeding efficiencies of killifish (*Fundulus heteroclitys*). In a similar study, only 250 shoots/m^2 were required to diminish the ability of largemouth bass, *Micropterus salmoides*, to capture prey (Savino and Stein 1982). The condition of harvestable-sized largemouth bass was affected when *Hydrilla* density exceeded 30 percent (Colle and Shireman 1980). These workers reported that the condition factors of juvenile bass were not affected until plant densities exceeded 50 percent.

145. In a study of fishes in Orange Lake, Florida, Colle et al. (1987) found that an infestation of *Hydrilla* caused an 85-percent reduction in angler effort although the number of fish caught per hour during the same time period was equivalent to or greater than years prior to the infestation. These workers also observed that the numbers of harvestable bluegill and redear sunfish were negatively correlated with *Hydrilla* coverage, but the populations of largemouth bass and black crappie were not lowered by the overabundance of *Hydrilla*. Reduced angler use of Orange Lake resulted in a 90-percent loss in revenue for the area (Colle et al. 1987). Wiley et al. (1984) recommended that the optimal standing crop of submersed macrophytes in ponds in central Illinois should not exceed 52 g m^2 (dry weight). Because of the potential

detrimental effects of submersed macrophytes on water quality, macroinvertebrates, and fishes, it is highly desirable to have no more than 20 to 30 percent of the water surface covered with plants.

Spatial Distribution of Macroinvertebrates

146. Since submersed macrophytes have the ability to disrupt food chains, modify physicochemical cycles, and interfere with recreational activities, a management plan for a given body of water should include not only the desired amounts of aquatic macrophytes but also the precise locations of plants for maximum benefit. Engel (1984, 1985, 1987) has proposed that lake managers consider themselves as landscape architects and develop more creative approaches to managing aquatic vegetation.

147. Engel further proposed that the management strategy include the preparation of a morphometric map to delineate plant beds in relation to areas designated for swimming, boating, and fishing. A lake should be divided into zones where the management strategy would include a plan for each area based on the designated use. Bottom screening, selective harvesting, and other techniques can be used to improve rather than destroy littoral zones (Engel 1984). Since available light is one of the most important limiting factors in the abundance and distribution of vegetation in a lake or stream, submersed macrophytes are usually restricted to shallow-water areas, except in deep oligotrophic lakes.

148. It is recognized that resource managers frequently must remove vegetation from water bodies that are used for recreation, navigation, and water supply. However, areas with submersed macrophytes are useful for fish and should include a variety of species. Predominantly larger beds should be located in shallow-water areas. Macrophyte beds should allow open-water lanes so that larger fishes would have access to macroinvertebrates and smaller fishes.

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Table 1
Mean Number of Invertebrates (Individuals/m²) in Three Sediment-Depth Fractions from *Ceratophyllum* and *Potamogeton* Beds and No-Plant Zones, Eau Galle Reservoir

Depth, cm	Site			Grand Mean
	AA	BB	CC	
<u><i>Ceratophyllum</i></u>				
0-5	38,681 (95.4)**	38,582 (98.5)	22,695 (87.1)	33,320* (94.5)
5-10	1,480 (3.6)	493 (1.3)	3,256 (12.5)	1,743 (4.9)
10-15	395 (1.0)	99 (0.3)	99 (0.4)	197 (0.6)
Total	40,556	39,174	26,050	35,260
<u><i>Potamogeton</i></u>				
0-5	15,788 (97.6)	18,748 (94.5)	16,972 (88.7)	17,170 (93.4)
5-10	395 (2.4)	592 (3.0)	1,974 (10.3)	987 (5.4)
10-15	0 (0.0)	493 (2.5)	197 (1.0)	230 (1.3)
Total	16,183	19,833†	19,143	18,387
<u>No-Plant Zones</u>				
0-5	2,862 (87.9)	2,862 (87.9)	1,677 (100.0)	2,467 (90.4)
5-10	296 (9.1)	197 (6.1)	0 (0.0)	164 (6.0)
10-15	99 (3.0)	197 (6.1)	0 (0.0)	99 (3.6)
Total	3,257	3,256	1,677	2,730

Note: Five cores were taken from each of three sites (AA, BB, and CC).

* Some grand means may differ slightly from the means of the values given for the three sites due to arithmetical rounding.

** Number within parentheses indicates percentage of invertebrates in that depth fraction as compared with the total number of invertebrates collected from all three depth fractions (0 to 15 cm).

† Some totals may differ slightly from total macroinvertebrate densities listed in Table A1 due to arithmetical rounding.

Table 2

Total Number of Invertebrates, for Several Taxa, Present in Three Sediment-
Depth Fractions from *Ceratophyllum* and *Potamogeton* Beds and No-Plant
Zones, Eau Galle Reservoir

<u>Depth, cm</u>	<u>Nematodes</u>	<u>Tubificid Oligochaetes</u>	<u><i>A. limosa</i></u>	<u>All Other Invertebrates</u>	<u>Total</u>
<u><i>Ceratophyllum</i></u>					
0-5	12 (70.6)*	204 (94.9)	305 (93.6)	492 (95.7)	1,013 (94.5)
5-10	5 (29.4)	9 (4.2)	19 (5.8)	20 (3.9)	53 (4.9)
10-15	0 (0.0)	2 (0.9)	2 (0.6)	2 (0.4)	6 (10.6)
<u><i>Potamogeton</i></u>					
0-5	82 (80.4)	209 (95.4)	78 (98.7)	153 (96.2)	522 (93.4)
5-10	18 (17.6)	10 (4.6)	0 (0.0)	2 (1.3)	30 (5.4)
10-15	2 (2.0)	0 (0.0)	1 (1.3)	4 (2.5)	7 (1.3)
<u>No-Plant Zones</u>					
0-5	12 (80.0)	24 (88.9)	2 (100.0)	37 (94.9)	75 (90.4)
5-10	2 (13.3)	1 (3.7)	0 (0.0)	2 (5.1)	5 (6.0)
10-15	1 (6.7)	2 (7.4)	0 (0.0)	0 (0.0)	3 (3.6)

Note: Numbers are the actual totals of individuals present in cores collected from all three sampling sites (AA, BB, CC).

* Number within parentheses indicates percentage of invertebrates of that taxon in that depth fraction as compared with the total number of invertebrates of that taxon collected from all three depth fractions (0 to 15 cm).

Table 3
Percentage Organic Matter and Percent Moisture in Sediments Collected
from *Ceratophyllum* and *Potamogeton* Beds and a No-Plant Zone in
Eau Galle Reservoir, August 1986

Depth of Sample cm	<i>C. demersum</i> Bed		<i>P. nodosus</i> Bed		No-Plant Zone	
	Mean Percent Organic Matter	Mean Percent Moisture Content	Mean Percent Organic Matter	Mean Percent Moisture Content	Mean Percent Organic Matter	Mean Percent Moisture Content
0-5	4.5 (0.1)*	28.9 (0.8)	5.6 (1.6)	33.1 (2.8)	4.3 (1.1)	27.2 (1.1)
5-10	2.9 (0.4)	21.8 (0.7)	6.5 (1.6)	29.2 (0.6)	5.7 (2.3)	29.4 (2.0)
10-15	3.3 (0.4)	20.6 (0.8)	4.4 (0.7)	23.6 (0.3)	3.2 (1.5)	26.6 (1.7)

* Number within parentheses indicates standard deviation (SD).

Table 4
Mean Number of *Potamogeton nodosus* per Square Meter in Eau Galle
Reservoir, June and August 1988

Site	June*		August**	
	Mean	SD	Mean	SD
A	100.0	31.4	239.2	48.1
B	108.8	26.1	112.0	25.3
C	111.2	28.6	239.2	86.4

* Samples collected on 22 June for site B and 24 June for sites A and C.

** Samples collected on 15 August for all three sites.

Table 5

Abundance of the Numerically Dominant Naidid Taxa on *C. demersum* and
P. nodosus in Eau Galle Reservoir

Date	Naidid Species	<i>C. demersum</i>		<i>P. nodosus</i>	
		RA,* percent	Number**	RA, percent	Number
August 1986	<i>S. lacustris</i>	52	(1,372)	15	(169)
	<i>N. pardalis</i>	42	(1,104)	0	(0)
	<i>P. leidy</i>	0	(0)	81	(904)
June 1987	<i>S. lacustris</i>	63	(196)	13	(48)
	<i>N. pardalis</i>	17	(52)	62	(229)
	<i>P. leidy</i>	<1%	(1)	3	(11)
August 1987	<i>S. lacustris</i>	96	(54)	2	(3)
	<i>N. pardalis</i>	0	(0)	0	(0)
	<i>P. leidy</i>	0	(0)	77	(109)

* Indicates the relative abundance of the listed species of Naididae in comparison to all the naidids collected from that macrophyte on that sampling date.

** Indicates the actual number of naidids of the listed species that were collected from that macrophyte species on that sampling date.

Table 6

Macroinvertebrate Assemblage on Live *C. demersum*, Plastic *Ceratophyllum*,
and Plastic *Vallisneria* from a Borrow Pit Lake, Louisiana, 1987

Plant Type	Ave. No.	Ave. No.	Taxa	Evenness	Ave. No.
	Individuals/ 10-cm Stem (SD)	Taxa/ 10-cm Stem (SD)	Diversity (H')	(J)	Individuals Corrected for Surface Area (SD)
Live <i>C. demersum</i>	274.7 ^a (66.1)	21.9 ^a (3.2)	2.239 ^a	0.578	52.4 ^a 12.6
Plastic <i>Ceratophyllum</i>	79.1 ^b (23.9)	17.9 ^b (3.0)	2.374 ^a	0.601	17.2 ^b 5.2
Plastic <i>Vallisneria</i>	27.6 ^c (6.5)	17.6 ^b (3.1)	2.983 ^b	0.798	27.6 ^c 6.5

Note: Numbers in the same column with different letters (a,b,c) are not significantly different ($P > 0.05$); $n = 8$ for all means.

Figure 1. Map of Eau Galle Reservoir, Wisconsin (letters refer to macroinvertebrate sampling sites; see para 9)

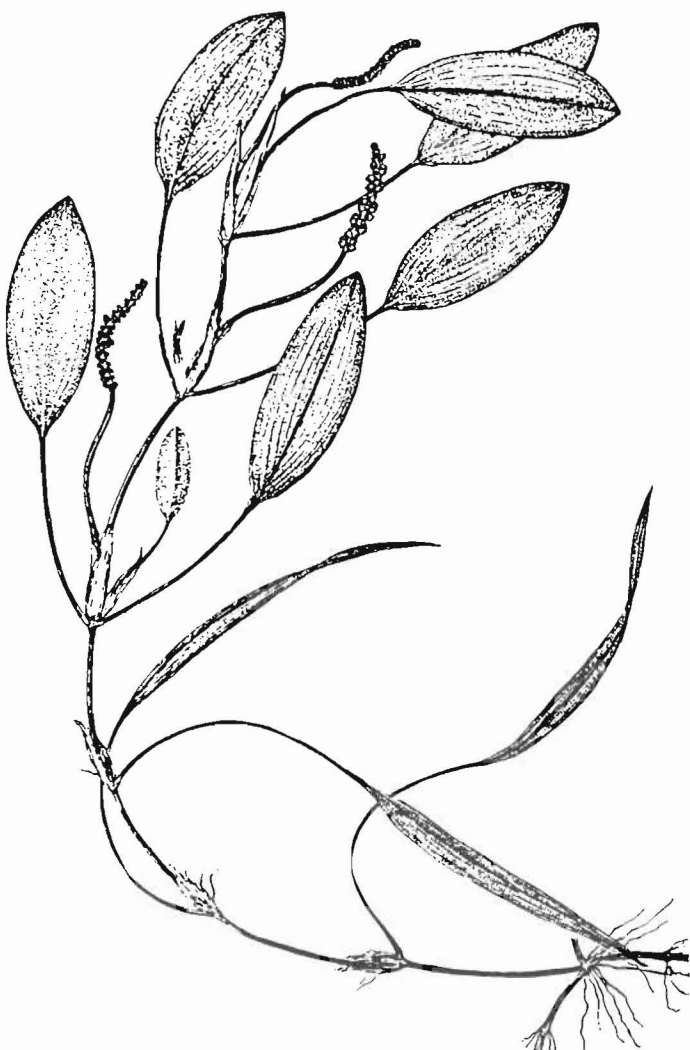
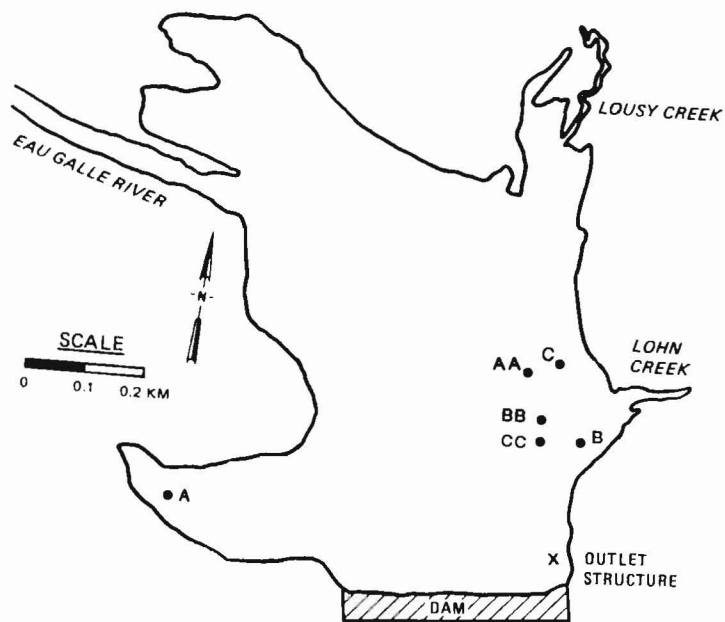
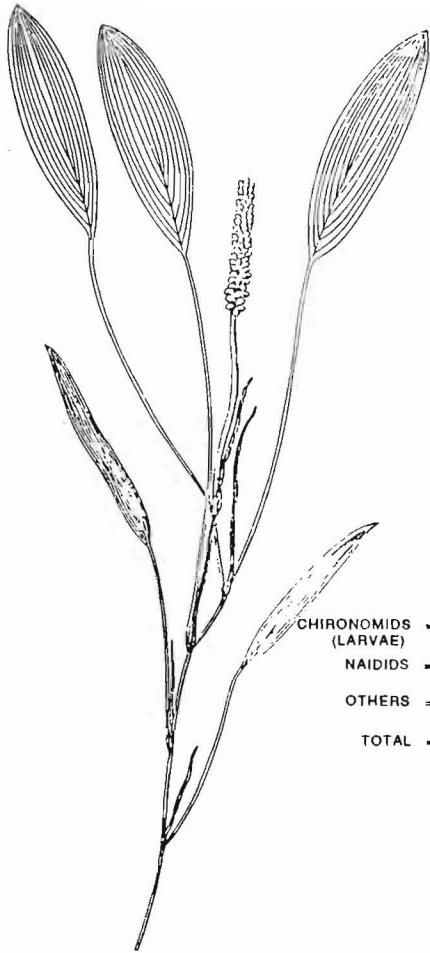
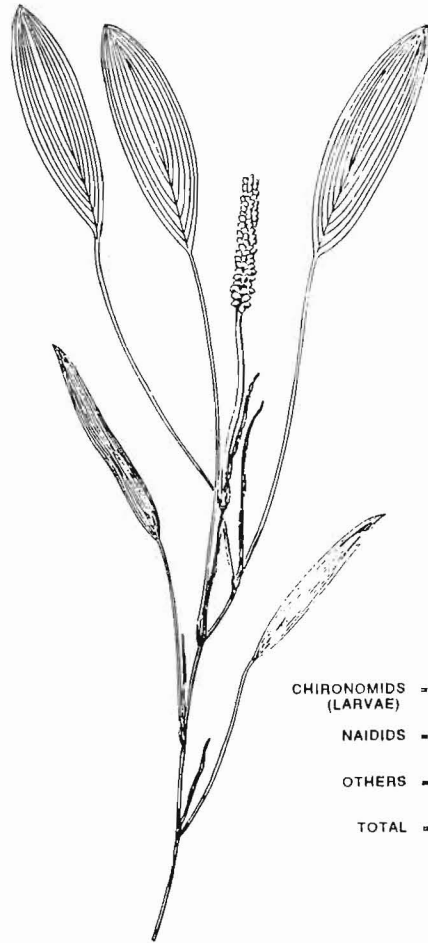


Figure 2. *Potamogeton nodosus*



CHIRONOMIDS	=	12 SPECIES
(LARVAE)	=	177 INDIVIDUALS
NAIDS	=	8 SPECIES
	=	143 INDIVIDUALS
OTHERS	=	16 SPECIES
	=	235 INDIVIDUALS
TOTAL	=	36 SPECIES
	=	555 INDIVIDUALS

Figure 3. Composition and number of invertebrates inhabiting a *P. nodosus* plant collected on 22 June 1987 at Site B in Eau Galle Reservoir. "Others" indicates invertebrates that were not chironomid larvae or naiddid worms

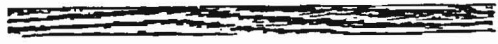


CHIRONOMIDS	=	7 SPECIES
(LARVAE)	=	52 INDIVIDUALS
NAIDS	=	3 SPECIES
	=	70 INDIVIDUALS
OTHERS	=	17 SPECIES
	=	199 INDIVIDUALS
TOTAL	=	27 SPECIES
	=	321 INDIVIDUALS

Figure 4. Composition and number of invertebrates inhabiting a *P. nodosus* plant collected on 5 August 1987 at Site B in Eau Galle Reservoir. "Others" indicates macroinvertebrates that were not chironomid larvae or naiddid worms

P. NODOSUS BED
AT SITE B

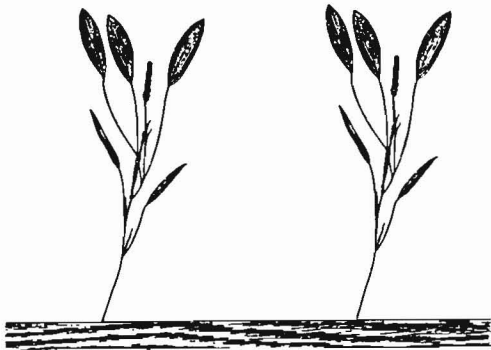
P. NODOSUS BED
AT SITE C



} 1,677

} 3,256

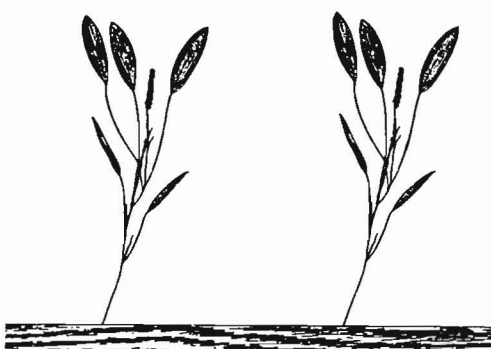
a. Number of benthic macroinvertebrates



} 19,143

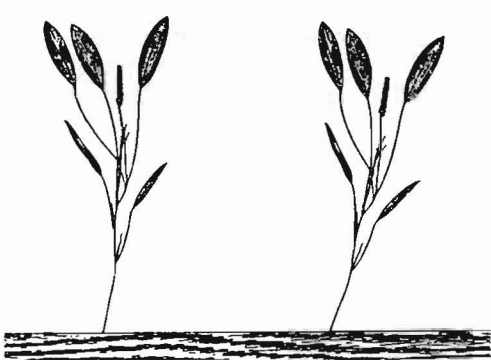
} 16,183

b. Number of epiphytic macroinvertebrates



} 24,618

} 18,275



} 43,761

} 34,458

c. Total macroinvertebrates (benthic plus epiphytic)

Figure 5. Means of benthic, epifaunal, and total number of invertebrates present in and above a square meter of reservoir bottom in two *P. nodosus* beds in Eau Galle Reservoir during August 1987



Figure 6. *Ceratophyllum demersum*



Figure 7. Zooplankton traps used in Eau Galle Reservoir, 1986

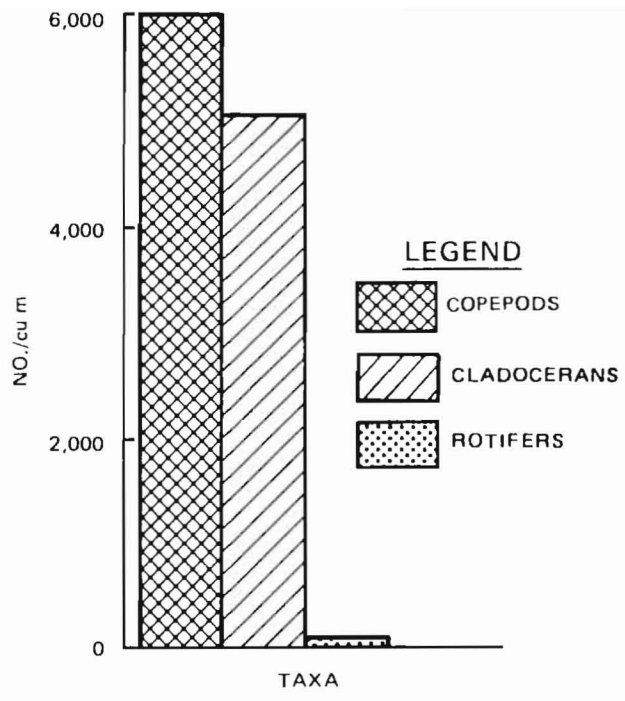


Figure 8. Zooplankton community at two limnetic sites, Eau Galle Reservoir

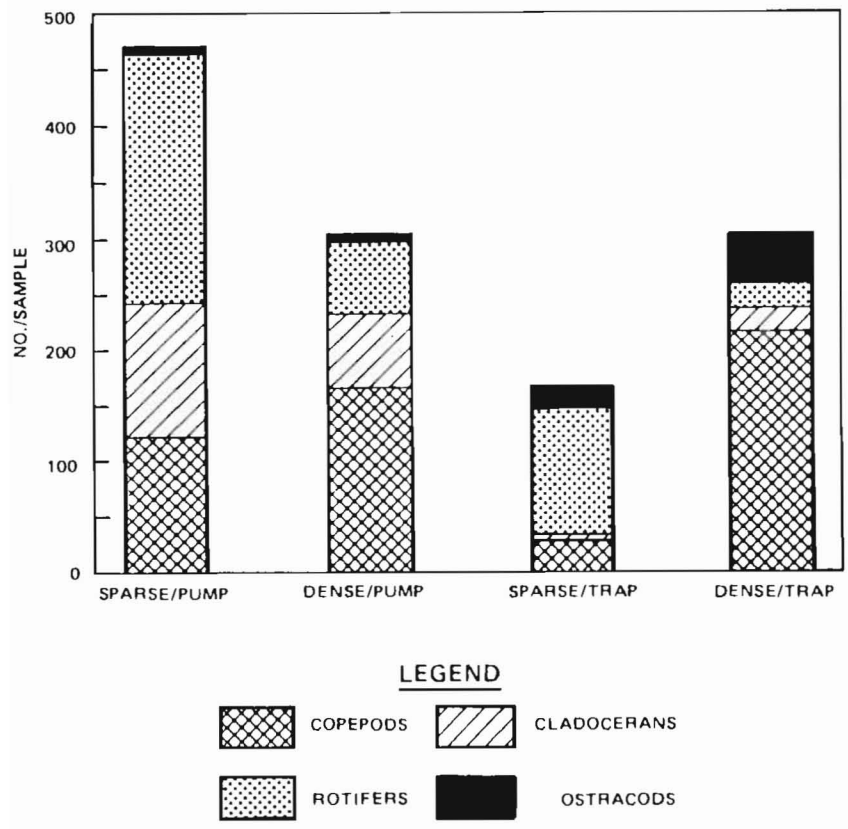


Figure 9. Comparison of zooplankton communities in sparse and dense vegetation determined from samples collected by pumping 20 l of water and by using zooplankton traps, Eau Galle Reservoir, August 1986

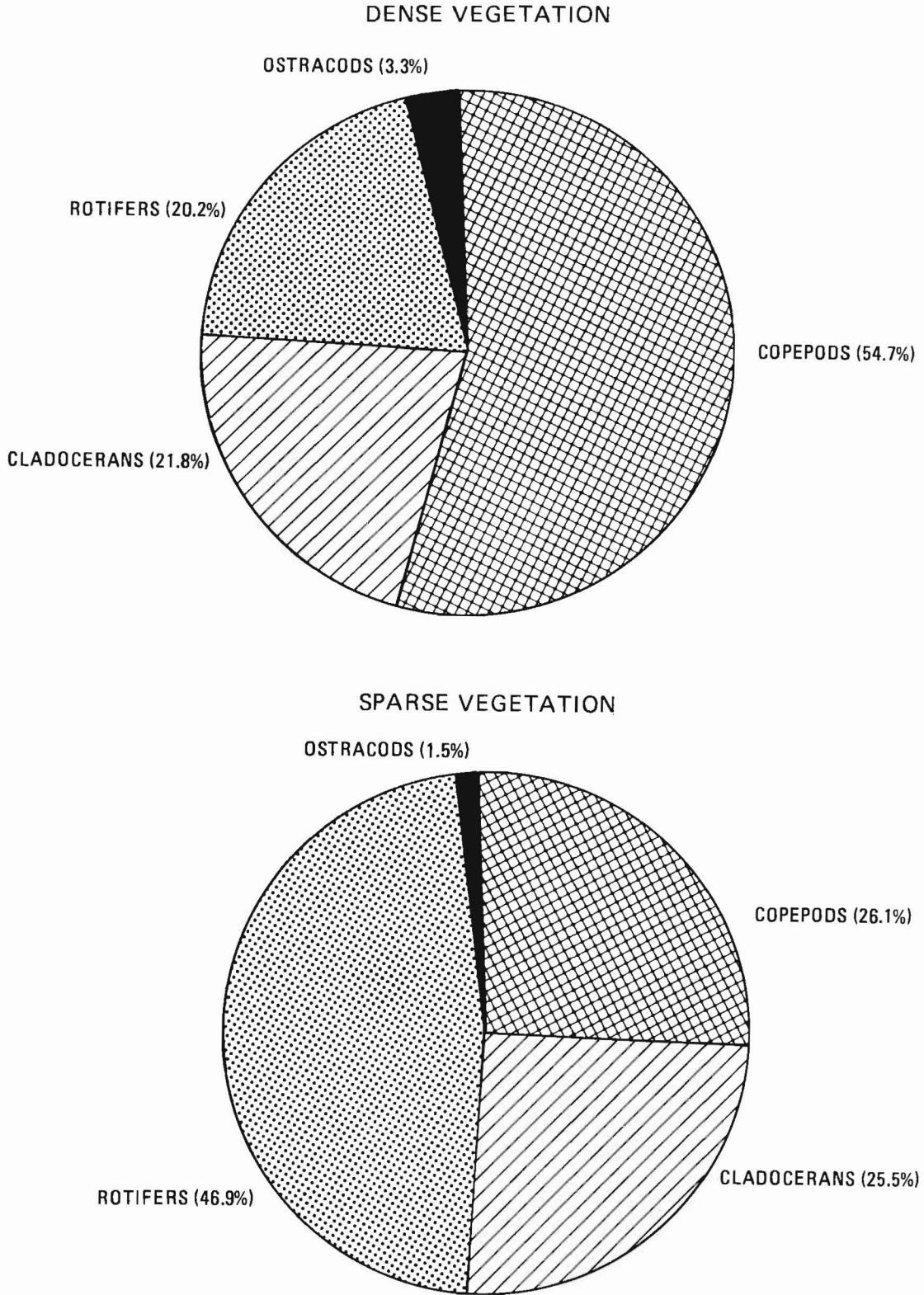


Figure 10. Zooplankton community composition from areas with dense and sparse *Ceratophyllum*, determined with samples collected by pumping 20 l of water, Eau Galle Reservoir, August 1986

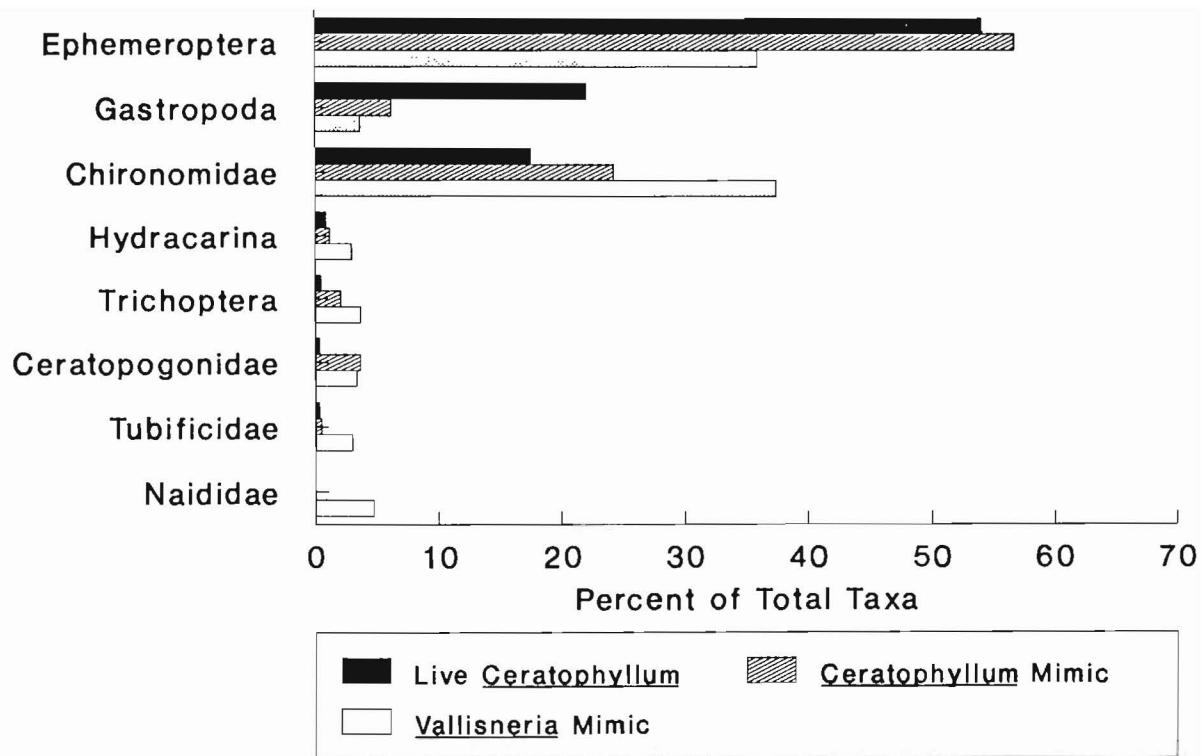


Figure 11. Percent abundance of common macroinvertebrate taxa colonizing live *C. demersum*, plastic *Ceratophyllum*, and plastic *Vallisneria* from a borrow pit lake in Louisiana, 1987

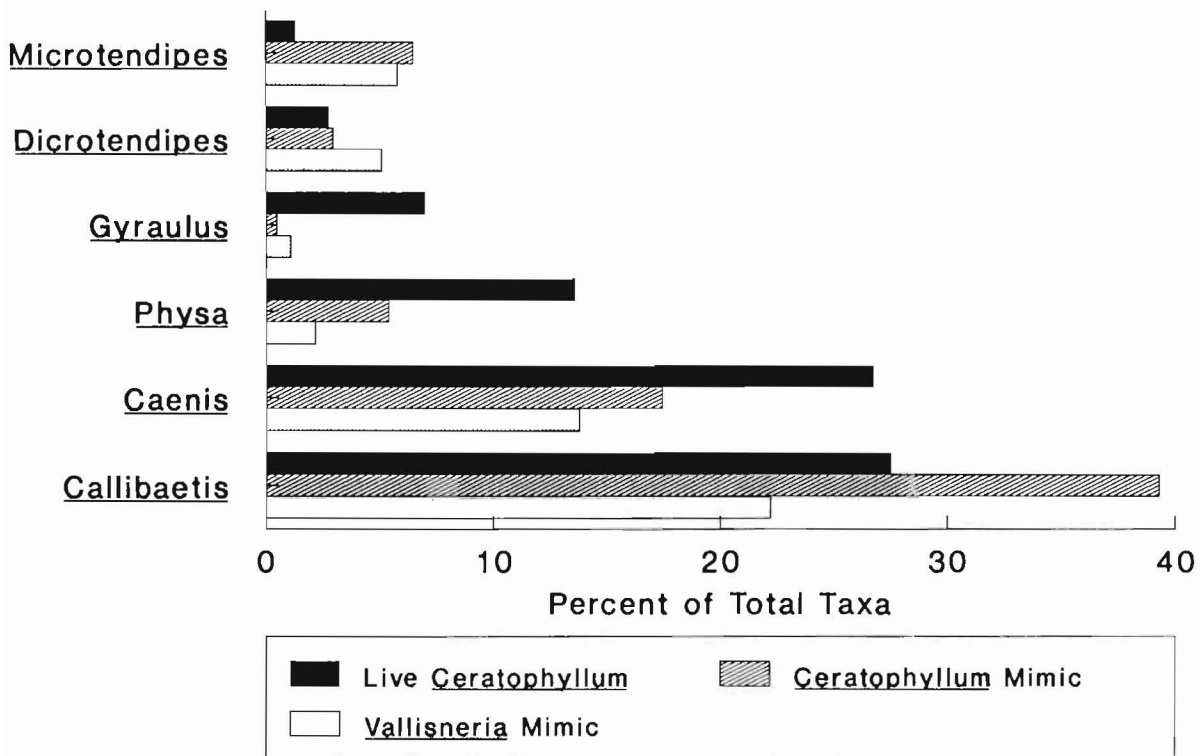


Figure 12. Percent abundance of common macroinvertebrate genera colonizing live *C. demersum*, plastic *Ceratophyllum*, and plastic *Vallisneria* from a borrow pit lake in Louisiana, 1987

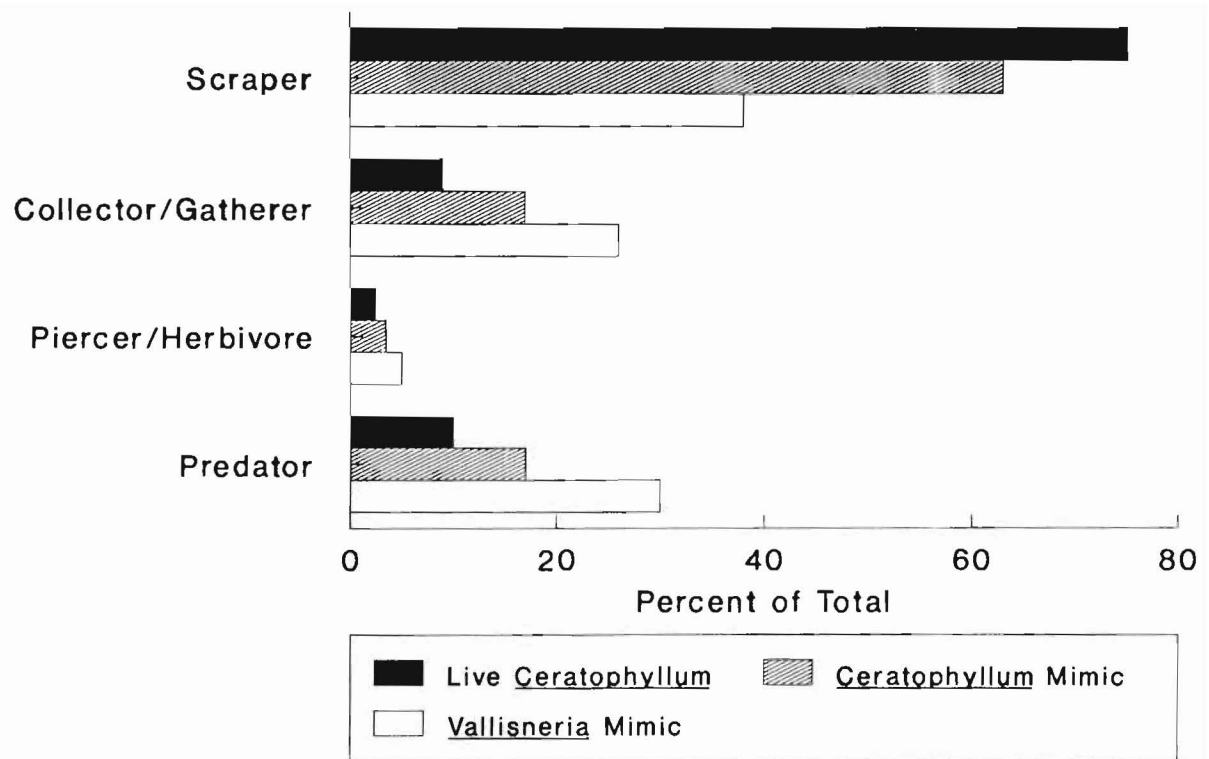


Figure 13. Percent abundance of feeding guilds (adapted from Merritt and Cummins 1984) on live *C. demersum*, plastic *Ceratophyllum*, and plastic *Vallisneria* from a borrow pit Lake in Louisiana, 1987

APPENDIX A: SUMMARY DATA ON MACROINVERTEBRATES ASSOCIATED WITH
AQUATIC MACROPHYTES

Table A1

Densities (Mean Number/sq m) for Invertebrate Taxa Collected from Eau Galle Reservoir, Wisconsin

Taxa	<i>Ceratophyllum</i> Bed				<i>Potamogeton</i> Bed				No-Plant Zone			
	AA	BB	CC	Mean*	AA	BB	CC	Mean	AA	BB	CC	Mean
Larval chironomids												
<i>Ablabesmyia peleenis</i>	395	99	--	164.7	--	--	--	0.0	--	--	--	0.0
<i>Chironomus</i> sp.	888	2,072	197	1,052.3	99	99	--	66.0	--	--	--	0.0
<i>Cladopelma</i> sp.	99	--	--	33.0	99	99	--	66.0	197	99	--	98.7
<i>Cladotanytarsus</i> sp.	--	--	--	0.0	--	--	99	33.0	--	--	--	0.0
<i>Cricotopus intersectus</i> gr.	--	--	--	0.0	--	--	99	33.0	--	--	--	0.0
<i>Cryptochironomus</i> sp.	--	--	--	0.0	--	--	197	65.7	197	--	--	65.7
<i>Dicrotendipes</i> sp.	296	395	197	296.0	--	99	--	33.0	99	--	--	33.0
<i>Glyptotendipes dreisbachi</i>	99	99	--	66.0	--	--	--	0.0	--	--	--	0.0
<i>G. lobiferus</i>	296	296	--	197.3	--	--	296	98.7	--	--	99	33.0
<i>Guttipelopia guttipennis</i>	197	888	296	460.3	--	--	--	0.0	--	--	--	0.0
<i>Labrundinia neopilosella</i>	99	--	--	33.0	--	--	--	0.0	--	--	--	0.0
<i>Lauterborniella agrayliodes</i>	197	99	--	98.7	99	--	--	33.0	--	--	--	0.0
<i>Parachironomus hirtalatus</i>	99	99	99	99.0	99	--	--	33.0	99	--	--	33.0
<i>Paratanytarsus</i> sp.	--	99	--	33.0	--	--	99	33.0	691	--	--	230.3
<i>Polypedilum bergi</i>	--	--	99	33.0	--	--	--	0.0	--	--	--	0.0
<i>Larsia</i> sp.	--	--	--	0.0	--	--	99	33.0	--	--	--	0.0
<i>P. halterale</i> gr.	--	--	99	33.0	--	1,973	1,381	1,118.0	99	99	--	66.0
<i>Procladius</i> sp.	296	296	789	460.3	99	99	395	197.7	197	--	197	131.3
<i>Tanytarsus</i> sp.	--	--	--	0.0	--	--	--	0.0	296	--	--	98.7
Chironomini ei**	00	--	--	0.0	--	197	296	164.3	--	--	--	0.0
Total larval chironomid densities	2,961	4,442	1,776	3,059.6	495	2,566	2,961	2,007.4	1,875	198	296	789.7
Percent of total invertebrates	7.3	11.3	6.8	8.7	3.1	12.9	15.5	10.9	57.6	6.1	17.6	28.9
Oligochaetes												
Tubificidae												
<i>Aulodrilus limmobius</i>	395	99	--	164.7	99	--	--	33.0	--	--	--	0.0
<i>A. piqueti</i>	691	--	--	230.3	197	197	--	131.3	--	--	--	0.0
<i>Limnodrilus hoffmeisteri</i>	99	296	197	197.3	592	493	197	427.3	--	197	--	65.7
<i>L. uedekianus</i>	99	197	99	131.7	99	592	--	230.3	--	--	--	0.0
<i>Guistadrilus multisetosus</i>	888	1,184	691	921.0	--	--	--	0.0	--	--	--	0.0
<i>T. without caps.</i> †	4,539	2,862	5,032	4,144.3	1,974	7,499	6,611	5,361.3	493	888	395	592.0

(Continued)

Note: Five cores were taken in each of three (AA, BB, CC) *Ceratophyllum* beds, three *Potamogeton* beds, and three no-plant zones. Densities include invertebrates collected from 0 to 15 cm. No entry in the table indicates that the taxon was not collected.

* Some mean values may differ slightly from the means of the values given for the three sites, due to arithmetical rounding.

** Early instar, not identifiable to genus.

† Immature tubificids without capilliform chaeta.

(Sheet 1 of 3)

Table A1 (Continued)

Taxa	<i>Ceratophyllum</i> Bed				<i>Potamogeton</i> Bed				No-Plant Zone			
	AA	BB	CC	Mean	AA	BB	CC	Mean	AA	BB	CC	Mean
Oligochaetes (Continued)												
Tubificidae (Continued)												
T. with caps.*	888	888	592	789.3	--	789	395	394.7	--	197	296	164.3
Newly hatched tubificids	888	493	296	559.0	99	1,480	296	625.0	--	197	--	65.7
Naididae												
<i>Dero digitata</i>	1,184	592	789	855.0	296	493	--	263.0	99	99	99	99.0
<i>D. nivea</i>	197	395	691	427.7	197	197	--	131.3	--	--	--	0.0
<i>Nais simplex</i>	99	--	--	33.0	--	--	--	0.0	--	--	--	0.0
<i>Ophidonais serpentina</i>	493	--	--	164.3	--	--	--	0.0	--	--	--	0.0
<i>Pristina leidyi</i>	--	--	--	0.0	--	--	296	98.7	--	--	--	0.0
<i>Stylaria lacustris</i>	888	197	--	361.7	--	--	--	0.0	--	--	--	0.0
Enchytraeidae	--	--	--	0.0	--	--	197	65.7	--	--	--	0.0
Total oligochaete densities	11,348	7,203	8,387	8,979.3	3,553	11,740	7,992	7,761.6	592	1,578	790	986.7
Percent of total invertebrates	28.0	18.4	32.2	25.5	21.9	59.2	41.7	42.2	18.2	48.5	47.1	36.1
Other macroinvertebrates												
Turbellaria												
<i>Dugesia tigrina</i>	1,381	592	99	690	--	--	--	--	99	--	--	33.0
Nematoda												
	789	493	395	559.0	3,355	2,467	4,243	3,355.0	197	1,085	197	493.0
Hirundinea												
<i>Helobdella</i> sp.	--	--	--	0.0	99	--	--	33.0	--	--	--	0.0
Cladocera												
	1,085	691	--	592.0	99	--	--	33.0	--	--	--	0.0
Copepoda												
Cyclopoid copepods	592	592	888	690.7	--	--	--	0.0	99	--	99	66.0
Harpacticoid copepods	888	888	197	657.7	197	987	197	460.3	--	--	--	0.0
Ostracoda	--	296	--	98.7	99	--	296	131.7	--	--	--	0.0
Amphipoda												
<i>Hyalella azteca</i>	1,875	888	--	921.0	99	--	--	33.0	--	--	--	0.0
Hydracarina	493	987	493	657.7	296	197	197	230.0	197	296	197	230.0
Collembola	--	--	99	33.0	--	99	--	33.0	--	--	--	0.0
Ephemeroptera												
<i>Caenis</i> sp.	--	395	197	197.3	--	--	197	65.7	--	--	--	0.0
Odonata												
Libellulidae ei	--	--	--	0.0	--	--	99	33.0	--	--	--	0.0
Coenagrionidae ei	395	691	--	362.0	--	--	99	33.0	--	--	--	0.0
<i>Enallagma</i> sp.	--	--	--	0.0	--	--	99	33.0	--	--	--	0.0
Hemiptera												
Mesoveliidae	99	--	--	33.0	--	197	--	65.7	--	--	--	0.0

(Continued)

* Immature tubificids with capilliform chaeta.

(Sheet 2 of 3)

Table A1 (Concluded)

Taxa	<i>Ceratophyllum</i> Bed				<i>Potamogeton</i> Bed				No-Plant Zone			
	AA	BB	CC	Mean	AA	BB	CC	Mean	AA	BB	CC	Mean
Other macroinvertebrates (Continued)												
Trichoptera												
<i>Leptocerus americanus</i>	1,974	5,526	2,960	3,486.7	888	99	99	362.0	--	--	--	0.0
<i>Oecetis</i> sp.	--	296	--	98.7	--	--	--	0.0	--	--	--	0.0
<i>Orthotrichia</i> sp.	--	197	--	65.7	--	--	99	33.0	--	--	--	0.0
Trichoptera pupae	--	--	197	65.7	99	--	--	33.0	--	--	--	0.0
Lepidoptera												
<i>Munroessa, Synclita,</i> <i>etc., complex</i>	99	--	--	33.0	--	--	--	0.0	--	--	--	0.0
Coleoptera												
<i>Berosus</i> sp.	--	--	--	0.0	99	99	--	66.0	--	--	--	0.0
Hydrophilidae ei	--	--	--	0.0	197	--	--	65.7	--	--	--	0.0
<i>Donacia</i> sp.	--	--	--	0.0	99	99	99	99.0	--	--	--	0.0
Dipterans other than chironomids												
<i>Psychoda</i> sp.	--	--	--	0.0	--	99	99	66.0	--	--	--	0.0
Heleidae ei	--	--	296	98.7	--	--	--	0.0	--	--	--	0.0
<i>Bezzia, Falpomyia,</i> <i>Probezzia</i> sp.	--	--	99	33.0	99	99	99	99.0	--	--	--	0.0
<i>Chrysops</i> sp.	--	--	--	0.0	99	--	--	33.0	--	--	--	0.0
Ephydriidae	--	--	--	0.0	--	--	99	33.0	--	--	--	0.0
Dipteran pupae	--	99	--	33.0	--	99	--	33.0	99	--	--	33.0
Unidentified insect pupae	99	--	--	33.0	99	--	--	33.0	--	--	--	0.0
Gastropoda												
<i>Ammicola limosa</i>	12,631	10,953	8,585	10,723.0	6,019	493	1,283	2,598.3	--	99	99	66.0
<i>Gyraulus parvus</i>	1,776	2,368	592	1,578.7	99	296	296	230.3	99	--	--	33.0
Immature gastropods	1,480	1,283	789	1,184.0	--	--	--	0.0	--	--	--	0.0
Pelecypoda												
Sphaeriidae	99	296	--	131.7	99	99	592	263.3	--	--	--	0.0
Immature pelecypods	493	--	--	164.3	--	99	--	33.0	--	--	--	0.0
Total other macroinvertebrates	26,248	27,531	15,886	23,222	12,140	5,528	8,192	8,620	790	1,480	592	954
Percent of total macroinvertebrates	64.7	70.3	61.0	65.9	75.0	27.9	42.8	46.9	24.3	45.5	35.3	34.9
Total macroinvertebrate density*	40,556	39,174	26,050	35,260	16,183	19,834	19,143	18,387	3,256	3,256	1,677	2,730

* Some total density values may differ slightly from the totals produced by adding the columns, due to arithmetical rounding of mean values given in columns.

Table A2

Numbers of Macroinvertebrates Present on *Potamogeton nodosus* Samples Collected from Eau Galle Reservoir

Taxon	August 1986				June 1987					August 1987				
	1	2	T	%	A	B	C	T	%	A	B	C	T	%
Larval chironomids														
<i>Ablabesmyia peleensis</i>	36	12	48	2.71	--	4	2	6	0.53	2	18	11	31	6.37
<i>Corynoneura taris</i>	8	8	16	0.90	8	52	35	95	8.38	--	2	3	5	1.03
<i>Cricotopus elegans</i>	--	--	--	0.00	1	1	1	3	0.26	--	3	--	3	0.62
<i>Cricotopus ornatus-laetus</i>	--	--	--	0.00	--	--	--	--	0.00	--	--	2	2	0.41
<i>Cricotopus sylvestris</i>	4	--	4	0.23	6	12	2	20	1.76	--	--	--	--	0.00
<i>Dicrotendipes</i> sp.	8	33	41	2.31	17	25	13	55	4.85	11	6	17	34	6.98
<i>Endochironomus nigricans</i>	124	85	209	11.78	1	2	--	3	0.26	1	47	22	70	14.37
<i>Glyptotendipes dreisbachi</i>	112	180	292	16.46	7	10	20	37	3.26	4	15	6	25	5.13
<i>Glyptotendipes lobiferus</i>	8	16	24	1.35	--	1	--	1	0.09	--	--	--	--	0.00
<i>Labrundinia neopilosella</i>	4	8	12	0.68	--	--	1	1	0.09	--	--	--	--	0.00
<i>Larsia</i> sp.	12	8	20	1.13	--	--	--	--	0.00	5	--	--	19	3.90
<i>Nanocladius</i> sp.	--	--	--	0.00	--	--	--	--	0.00	1	10	4	1	0.21
<i>Parachironomus abortivus</i> gr.	--	--	--	0.00	4	--	--	4	0.36	--	--	--	--	0.00
<i>Paratanytarsus</i> sp.	8	8	16	0.90	41	306	244	591	52.12	12	3	--	15	3.08
<i>Polypedilum bergi</i>	--	--	--	0.00	1	--	--	1	0.09	--	1	--	1	0.21
<i>Polypedilum illinoense</i>	476	586	1,062	59.86	26	28	11	65	5.73	74	76	47	197	40.45
<i>Polypedilum halterale</i> gr.	--	--	--	0.00	--	2	--	2	0.18	--	--	--	--	0.00
<i>Polypedilum</i> nr. <i>tritum</i>	--	--	--	0.00	--	--	--	--	0.00	--	1	--	1	0.21
<i>Pseudochironomus</i> sp.	--	--	--	0.00	--	3	--	3	0.26	--	--	--	--	0.00
<i>Psectrocladius</i> sp.	--	--	--	0.00	--	--	1	1	0.09	--	--	--	--	0.00
<i>Tanytarsus</i> sp.	--	--	--	0.00	--	--	--	--	0.00	1	--	--	1	0.21
<i>Thienemanniella</i> nr. <i>fusca</i>	4	--	4	0.23	--	81	43	124	10.93	1	--	--	1	0.21
<i>Thienemanniella</i> nr. <i>xena</i>	4	--	4	0.23	--	--	--	--	0.00	--	--	--	--	0.00
<i>Thienemannimyia</i> gr.	--	4	4	0.23	--	--	--	--	0.00	--	--	--	--	0.00
Tanypodinae ei*	4	--	4	0.23	12	7	11	30	2.65	5	24	17	46	9.45
Chironomini ei	--	14	14	0.79	8	38	44	90	7.94	9	13	13	35	7.19
Orthocladinae	--	--	--	0.00	--	1	1	2	0.18	--	--	--	--	0.00
Total larval chironomids	812	962	1,774	100.00	132	573	429	1,134	100.00	126	219	142	487	100.00
% of total invertebrates	35.2	31.8	33.3		37.5	45.7	59.8	48.8		29.3	19.9	37.2	25.5	

(Continued)

Note: August 1986 data show invertebrate abundances in two large samples of *P. nodosus*; numbers listed for the June and August 1987 collections are summary data indicating the totals of invertebrates present on five *P. nodosus* plants collected at each of three sampling sites (A, B, and C) on each of the two sampling dates.

Percentage abundance of chironomid taxa, oligochaetes, and "other macroinvertebrates" (not chironomid larvae or oligochaetes) is based on total numbers of individuals in that major taxonomic group.

* Early instar, not identifiable to genus.

Table A2 (Continued)

Taxon	August 1986				June 1987					August 1987				
	1	2	T	%	A	B	C	T	%	A	B	C	T	%
Oligochaetes														
<i>Aeolosoma</i> sp.	--	--	--	0.00	--	1	--	1	0.27	--	1	--	1	0.70
<i>Chaetogaster diaphanus</i>	10	9	19	1.70	14	14	6	34	9.02	--	10	--	10	7.04
<i>Chaetogaster limmaei</i>	--	--	--	0.00	--	--	4	4	1.06	--	--	--	--	0.00
<i>Dero digitata</i>	--	--	--	0.00	0	1	--	1	0.27	--	--	--	--	0.00
<i>Dero nivea</i>	3	--	3	0.27	1	6	--	7	1.86	9	--	1	10	7.04
<i>Nais communis</i>	--	--	--	0.00	2	6	--	8	2.12	5	2	--	7	4.93
<i>Nais pardalis</i>	--	--	--	0.00	10	136	83	229	60.74	--	--	--	--	0.00
<i>Nais simplex</i>	6	16	22	1.97	7	2	17	26	6.90	--	1	--	1	0.70
<i>Pristina aequisetata</i>	--	--	--	0.00	--	1	--	1	0.27	--	--	1	1	0.70
<i>Pristina leidy</i>	273	631	904	80.93	3	8	--	11	2.92	8	96	5	109	76.76
<i>Stylaria lacustris</i>	40	129	169	15.13	10	22	16	48	12.73	--	3	--	3	2.11
T. without caps.*	--	--	--	0.00	7	--	--	7	1.86	--	--	--	--	0.00
Total oligochaetes	332	785	1,117	100.00	54	197	126	377	100.00	22	113	7	142	100.00
% of total invertebrates	14.4	25.9	20.9		15.3	15.7	17.6	16.2		5.1	10.3	1.8	7.4	
Other macroinvertebrates														
Cnidaria														
<i>Hydra</i> sp.	5	--	5	0.20	64	66	4	134	16.48	--	6	--	6	0.47
Turbellaria														
<i>Dugesia tigrina</i>	26	31	57	2.33	--	4	2	6	0.74	--	--	--	--	0.00
Nematoda	1	--	1	0.04	13	129	76	218	26.81	57	25	14	96	7.49
Hirudinea														
<i>Helobdella triserialis</i>	2	101	103	4.22	--	--	--	--	0.00	--	--	--	--	0.00
Cladocera	76	112	188	7.70	13	64	16	93	11.44	4	31	6	41	3.20
Copepoda	62	134	196	8.02	12	13	--	25	3.08	14	51	14	79	6.16
Ostracoda	111	35	146	5.98	25	33	15	73	8.98	12	64	47	123	9.59
Amphipoda														
<i>Hyalella azteca</i>	13	32	45	1.84	--	--	--	--	0.00	4	6	2	12	0.94
Hydracarina**														
Group A	324	193	517	21.16	6	14	--	20	2.46	13	41	35	89	6.94
Group B	150	128	278	11.38	2	19	4	25	3.08	8	77	58	143	11.15
Group C	9	10	19	0.78	6	13	7	26	3.20	1	9	3	13	1.01
Collembola	1	1	2	0.08	--	2	--	2	0.25	--	1	--	1	0.08
Ephemeroptera														
<i>Caenis</i> sp.	39	27	66	2.70	--	2	2	4	0.49	1	11	--	12	0.94
Early instar nymphs	--	12	12	0.49	1	1	--	2	0.25	1	--	--	1	0.08

(Continued)

* Immature turbidicids without capilliform chaeta.

** Group A - small, brown, hard-bodied mites with no long abdominal hairs; B - small, brown, hard-bodied mites with long abdominal hairs; C - soft-bodied mites.

(Sheet 2 of 4)

Table A2 (Continued)

Taxon	August 1986				June 1987					August 1987				
	1	2	T	%	A	B	C	T	%	A	B	C	T	%
Other macroinvertebrates (Continued)														
Odonata														
Anisoptera ei	--	1	1	0.04	--	--	1	1	0.12	--	--	--	--	0.00
Libellulidae ei	1	--	1	0.04	--	--	--	--	0.00	--	--	--	--	0.00
Coenagrionidae ei	23	44	67	2.74	--	1	--	1	0.12	--	5	1	6	0.47
<i>Ischnura/Anomalagrion/ Enallagma</i>	30	33	63	2.58	--	1	1	2	0.25	--	29	4	33	2.57
Hemiptera														
<i>Merragata</i> sp.	1	1	2	0.08	--	--	--	--	0.00	--	--	--	--	0.00
<i>Mesovelia amoena</i>	17	20	37	1.51	2	--	--	2	0.25	--	1	1	2	0.16
<i>Mesovelia mulsanti</i>	2	--	2	0.08	--	--	--	--	0.00	0	--	--	1	0.08
<i>Microvelia</i> sp.	1	--	1	0.04	--	--	--	--	0.00	--	--	--	--	0.00
<i>Neoplea striola</i>	5	6	11	0.45	--	1	--	1	0.12	--	2	--	2	0.16
<i>Belostana</i> sp.	--	1	1	0.04	--	--	--	--	0.00	--	--	--	--	0.00
Megaloptera														
<i>Chauliodes rastricornis</i>	--	--	--	0.00	--	1	--	1	0.12	--	--	--	--	0.00
Trichoptera														
<i>Agraylea</i> sp.	--	--	--	0.00	--	--	--	--	0.00	--	2	--	2	0.16
<i>Leptocerus americanus</i>	33	52	85	3.48	1	--	--	1	0.12	--	--	3	3	0.23
Leptoceridae ei	--	--	--	0.00	--	3	--	3	0.37	--	--	--	--	0.00
<i>Nectopsyche</i> sp.	--	4	4	0.16	--	--	--	--	0.00	--	--	--	--	0.00
<i>Orthotrichia</i> sp.	--	2	2	0.08	--	--	--	--	0.00	--	1	--	1	0.08
<i>Polycentropus</i> sp.	--	4	4	0.16	--	--	--	--	0.00	--	--	--	--	0.00
Trichoptera ei	--	--	--	0.00	--	--	--	--	0.00	--	2	--	2	0.16
Trichoptera pupae	2	4	6	0.25	--	--	2	2	0.25	--	--	--	--	0.00
Lepidoptera														
<i>Munroessa, Synclita</i> complex	23	16	39	1.60	2	--	--	2	0.25	12	5	5	22	1.72
<i>Paraponyx</i> sp.	--	--	--	0.00	--	1	--	1	0.12	--	--	--	--	0.00
Lepidoptera larvae ei	8	58	66	2.70	1	--	--	1	0.12	1	24	--	25	1.95
Lepidoptera pupae	--	2	2	0.08	--	--	--	--	0.00	--	--	--	--	0.00
Coleoptera														
<i>Haliphus</i> sp.	--	1	1	0.04	--	--	--	--	0.00	--	--	--	--	0.00
<i>Eerosus</i> sp.	3	12	15	0.61	--	--	--	--	0.00	2	--	2	4	0.31
Coleoptera larvae ei	--	--	--	0.00	--	--	--	--	0.00	--	--	--	--	0.00
Hymenoptera														
Hymenoptera pupae	1	--	1	0.04	--	--	--	--	0.00	128	148	--	276	21.53

(Continued)

(Sheet 3 of 4)

Table A2 (Concluded)

Taxon	August 1986				June 1987					August 1987				
	1	2	T	%	A	B	C	T	%	A	B	C	T	%
Other macroinvertebrates (Continued)														
Diptera other than chironomid larvae														
Chironomini pupae	4	13	17	0.70	--	1	1	2	0.25	2	1	1	4	0.31
Tanypodinae pupae	1	--	1	0.16	--	--	--	--	0.00	1	2	--	3	0.23
<i>Alluaudomyia</i> sp.	--	2	2	0.04	--	--	--	--	0.00	--	--	--	--	0.00
<i>Bezzia</i> , <i>Probezzia</i> complex	60	78	138	5.65	2	18	7	27	3.32	14	43	9	66	5.15
<i>Dasyhelea</i> sp.	--	--	--	0.00	--	--	--	--	0.00	2	--	--	2	0.16
Heleidae pupae	3	1	4	0.16	--	--	--	--	0.00	--	--	--	--	0.00
<i>Hydrellia</i> sp.	7	10	17	0.70	--	3	--	3	0.37	2	5	3	10	0.78
<i>Hydrellia</i> pupae	4	--	4	0.16	--	--	--	--	0.00	2	--	--	2	0.16
Anthomyiidae	--	1	1	0.04	--	--	--	--	0.00	--	--	--	--	0.00
Unidentified dipteran larvae	1	--	1	0.04	--	2	--	2	0.25	--	--	--	--	0.00
Unidentified dipteran pupae	--	--	--	0.00	--	2	6	8	0.98	--	1	--	1	0.08
Unidentified insect larvae	1	--	1	0.04	--	--	1	1	0.12	--	5	2	7	0.55
Unidentified insect pupae	--	--	--	0.00	--	--	--	--	0.00	--	1	--	1	0.08
Gastropoda														
<i>Ammicola limosa</i>	92	71	163	6.67	5	56	5	66	8.12	--	51	21	72	5.62
<i>Gyraulus parvus</i>	15	19	34	1.39	6	27	10	43	5.29	--	41	2	43	3.35
<i>Physella</i> sp.	--	--	--	0.00	--	--	2	2	0.25	--	--	--	--	0.00
Immature gastropods	5	9	14	0.57	5	8	--	13	1.60	--	76	--	76	5.93
Total other macroinvertebrates	1,162	1,281	2,443	100.00	166	485	162	813	100.00	282	767	233	1,282	100.00
% of total macroinvertebrates	50.4	42.3	45.8		47.2	38.6	22.6	35.0		66.6	69.8	61.0	67.1	
Total macroinvertebrates	2,306	3,028	5,334		352	1,255	717	2,324		430	1,099	382	1,911	
Mean individuals/plant					70	251	143			86	220	76		
Standard deviation					12	175	38			72	140	67		

* Immature tubificids without capilliform chaeta.

** Group A - small, brown, hard-bodied mites with no long abdominal hairs; B - small, brown, hard-bodied mites with long abdominal hairs; C - soft-bodied mites.

Table A3
 Numbers of Invertebrates Present on *Ceratophyllum demersum* Samples Collected from Eau Galle Reservoir

Taxon	August 1986				June 1987					August 1987							
	1	2	Total	%	A	B	C	Total	%	A	As	B	Bs	C	Cs	Total	%
Larval chironomids*																	
<i>Ablabesmyia</i>																	
<i>peleensis</i>	32	48	80	6.25	13	21	21	55	7.43	2	11	1	10	1	10	35	14.77
<i>Cladopelma</i> sp.	--	--	0	0.00	1	--	--	1	0.14	--	--	--	--	--	--	0	0.00
<i>Corynoneura taris</i>	4	--	4	0.31	2	3	4	9	1.22	--	--	--	1	--	2	3	1.27
<i>Cricotopus</i>																	
<i>intersectus</i> gr.	--	--	0	0.00	--	--	--	0	0.00	1	--	--	--	--	--	1	0.42
<i>C. ornatus-laetus</i> gr.	--	--	0	0.00	16	4	--	20	2.70	1	--	--	--	--	--	1	0.42
<i>C. sylvestris</i>	--	--	0	0.00	--	1	--	1	0.14	1	--	1	--	--	--	2	0.84
<i>Dicrotendopes</i> sp.	48	8	56	4.38	83	16	9	108	14.59	1	1	--	1	--	7	10	4.22
<i>Endochironomus</i>																	
<i>nigricans</i>	4	4	8	0.63	1	--	--	1	0.14	--	--	2	11	--	17	30	12.66
<i>Glyptotendipes</i>																	
<i>dreisbachi</i>	4	4	8	0.63	2	5	1	8	1.08	--	--	--	--	1		1	0.42
<i>G. lobiferus</i>	12	--	12	0.94	--	--	--	0	0.00	--	--	1	16	--	32	49	20.68
<i>Guttipelopia</i> sp.	8	--	8	0.63	--	--	--	0	0.00	--	--	--	--	--	--	0	0.00
<i>Labrundinia</i>																	
<i>neopilosella</i>	8	--	8	0.63	7	--	1	8	1.08	1	1	--	8	--	2	12	5.06
<i>Larvia</i> sp.	--	4	4	0.31	3	1	1	5	0.68	--	--	--	--	--	1	1	0.42
<i>Nanocladius</i> sp.	--	4	4	0.31	--	--	1	1	0.14	--	--	--	--	--	--	0	0.00
<i>N. nr.</i>																	
<i>alternantherae</i>	--	--	0	0.00	1	--	1	2	0.27	--	--	--	--	--	--	0	0.00
<i>Parachironomus</i>																	
<i>abortivus</i> gr.	4	--	4	0.31	--	--	--	0	0.00	--	1	--	--	--	--	1	0.42
<i>Paratanytarsus</i> sp.	580	404	984	76.88	184	47	153	384	51.89	1	--	--	--	--	3	4	1.69
<i>Polypedilum bergi</i>	8	8	16	1.25	14	20	41	75	10.14	2	2	4	1	3	6	18	7.59
<i>Psectrocladius</i> sp.	--	--	0	0.00	2	1	2	5	0.68	--	--	--	--	--	--	0	0.00
<i>Tanytarsus lugens</i> gr.	--	--	0	0.00	9	1	--	10	1.35	--	--	--	--	--	--	0	0.00
<i>Thienemanniella</i> nr.																	
<i>fusca</i>	44	36	80	6.25	--	2	1	3	0.41	1	--	--	20	--	30	51	21.52
<i>Tanyodinae</i> ei**	--	--	0	0.00	4	1	1	6	0.81	--	--	--	--	--	2	2	0.84
<i>Chironominae</i> ei	--	4	4	0.31	17	9	12	38	5.14	4	2	1	--	3	6	16	6.75
Total chironomids	756	524	1,280	100.00†	359	132	249	740	100.00	15	18	10	68	8	118	237	100.00
Naidids																	
<i>Chaetogaster</i>																	
<i>diaphanus</i>	10	8	18	0.68	30	3	11	44	14.24	--	--	--	--	--	2	2	3.57
<i>Dero nivea</i>	--	--	0	0.00	3	--	--	3	0.97	--	--	--	--	--	--	0	0.00

(Continued)

Note: August 1986 data show invertebrate abundance in two large samples of *C. demersum*; numbers listed for the June and August 1987 collections are summary data indicating the totals of invertebrates present on five *C. demersum* samples collected at each of three sampling sites (A, B, and C).

Numbers of invertebrates in the supplementary samples (As, Bs, and Cs) of August 1987 are also shown.

* Organisms in this group were all immatures (larvae or nymphs) except for those listed as being in another stage (i.e., pupae).

** Early instar, not identifiable to genus.

† Totals may differ slightly from 100.00 due to arithmetical rounding.

Table A3 (Continued)

Taxon	August 1986				June 1987					August 1987							
	1	2	Total	%	A	B	C	Total	%	A	As	B	Bs	C	Cs	Total	%
Naidids (Continued)																	
<i>Nais simplex</i>	25	8	33	1.25	9	2	2	13	4.21	--	--	--	--	--	--	0	0.00
<i>N. pardalis</i>	520	584	1,104	41.91	30	16	6	52	16.83	--	--	--	--	--	--	0	0.00
<i>Ophidonais</i>																	
<i>serpentina</i>	107	--	107	4.06	--	--	--	0	0.00	--	--	--	--	--	--	0	0.00
<i>Fristina leidy</i>	--	--	0	0.00	--	1	--	1	0.32	--	--	--	--	--	--	0	0.00
<i>Stylaria lacustris</i>	816	556	1,372	52.09	115	23	58	196	63.43	3	6	--	16	1	28	54	96.43
Total naidids	1,478	1,156	2,634	100.00	187	45	77	309	100.00	3	6	0	16	1	30	56	100.00
Other invertebrates																	
Cnidaria																	
<i>Hydra</i> sp.	34	8	42	1.56	320	4	8	332	14.05	2	--	--	30	--	--	32	1.47
Turbellaria																	
<i>Ducesia tiprina</i>	14	1	15	0.56	4	--	--	6	0.25	--	--	--	21	--	1	22	1.01
Nematoda																	
		1	1	0.04	1	2	1	4	0.17	--	--	--	--	--	1	1	0.05
Cladocera																	
	69	34	103	3.83	42	31	45	118	4.99	7	9	17	16	42	44	135	6.22
Copepoda																	
	194	706	900	33.44	17	6	22	45	1.90	2	4	3	5	9	23	46	2.12
Ostracoda																	
	169	328	497	18.47	275	102	109	486	20.57	17	162	33	136	11	142	501	23.07
Amphipoda																	
<i>Hyaella azteca</i>	18	1	19	0.71	20	6	18	44	1.86	15	7	1	10	1	27	61	2.81
Hydracarina*																	
Group A	15	19	34	1.26	13	3	4	20	0.85	5	1	--	21	3	22	52	2.39
Group B	1	1	2	0.07	2	1	--	2	0.08	--	--	--	3	--	2	5	0.23
Group C	151	158	309	11.48	44	15	30	89	3.77	--	3	--	7	2	13	25	1.15
Collembola																	
	--	--	0	0.00	--	--	2	2	0.08	--	--	--	--	--	--	0	0.00
Ephemeroptera**																	
<i>Baetidae</i> ei	2	3	5	0.19	2	1	1	4	0.17	--	--	--	--	--	--	0	0.00
<i>Caenis</i> sp.	63	55	118	4.38	19	--	1	20	0.85	2	3	--	--	--	--	5	0.23
<i>Callibaetis</i> sp.	--	1	1	0.04	1	--	--	1	0.04	--	--	--	--	--	--	0	0.00
Ephemeroptera ei	--	3	3	0.11	3	4	3	10	0.42	--	--	--	--	--	2	2	0.09
Odonata**																	
<i>Anisoptera</i> ei	--	--	0	0.00		1	--	1	0.04	--	--	--	--	--	--	0	0.00
<i>Coenagrionidae</i> ei	35	17	52	1.93	66	36	6	108	4.57	29	--	6	--	10	2	47	2.16
<i>Ischnura/</i>																	
<i>Anomalagrion/</i>																	
<i>Enallagma</i>	7	5	12	0.45	3	4	2	9	0.38	12	--	--	--	--	15	27	1.24
Hemiptera																	
<i>Mesovelia amoena</i>	--	1	1	0.04	4	1	--	5	0.21	1	--	1	--	--	--	2	0.09
<i>Microvelia</i> sp.	--	--	0	0.00	1	--	--	1	0.04	--	--	--	--	--	--	0	0.00
<i>Neoplea striola</i>	1	--	1	0.04	3	2	1	6	0.25	--	--	--	--	1	--	1	0.05
Trichoptera**																	
<i>Agraylea</i> sp.	1	--	1	0.04	--	--	--	0	0.00	--	--	--	--	--	--	0	0.00

(Continued)

* Group A - small, brown, hard-bodied mites without long abdominal hairs; B - small brown, hard-bodied mites with long abdominal hairs; C - soft-bodied mites.
 ** Organisms in this group were all immatures (larvae or nymphs) except for those listed as being in another stage (i.e., pupae).

(Sheet 2 of 4)

Table A3 (Continued)

Taxon	August 1986				June 1987						August 1987							
	1	2	Total	%	A	B	C	Total	%	A	As	B	Bs	C	Cs	Total	%	
Other invertebrates (Continued)																		
Trichoptera (Continued)																		
<i>Leptocerus americanus</i> (Instar II-V)	97	22	119	4.42	--	--	--	0	0.00	52	127	17	252	13	211	672	30.94	
<i>L. americanus</i> (Instar I)	12	7	19	0.71	16	20	19	55	2.33	--	--	--	--	--	--	1	0.05	
<i>L. americanus</i> pupae	--	--	0	0.00	29	5	7	41	1.74	--	2	--	--	--	--	2	0.09	
<i>Oecetis cinarescens</i>	--	--	0	0.00	1	--	--	1	0.04	--	--	--	--	--	--	0	0.00	
<i>Oecetis</i> sp. (not <i>O. cinarescens</i>)	33	3	36	1.34	--	--	--	0	0.00	--	--	--	6	--	4	10	0.46	
<i>Orthotrichia</i> sp.	1	--	1	0.04	1	--	--	1	0.04	--	5	1	14	--	4	24	1.10	
<i>Orthotrichia</i> pupae	--	--	0	0.00	--	--	--	0	0.00	--	--	--	2	--	--	2	0.09	
<i>Oxyethira</i> sp.	--	--	0	0.00	--	--	--	0	0.00	--	--	--	--	--	1	1	0.05	
<i>Triaenodes injustus</i>	1	1	2	0.07	--	--	--	0	0.00	--	--	--	--	--	--	0	0.00	
Trichoptera ei	5	1	6	0.22	79	--	--	79	3.34	--	1	--	--	--	--	1	0.05	
Trichoptera pupae	1	1	2	0.07	--	--	--	0	0.00	--	--	--	--	--	--	0	0.00	
Lepidoptera*																		
<i>Munroessa, Synclita, Neocataclysta</i>	--	--	0	0.00	12	--	1	13	0.55	--	--	--	--	--	--	0	0.00	
<i>Paranonyx</i> sp.	--	--	0	0.00	--	--	--	0	0.00	--	--	--	--	--	--	1	0.05	
Lepidoptera ei	--	--	0	0.00	--	2	4	6	0.25	--	--	--	--	--	--	0	0.00	
Lepidoptera pupae	--	--	0	0.00	--	--	--	0	0.00	--	--	--	--	--	1	1	0.05	
Ceoloptera*																		
<i>Berosus</i> sp.	1	2	3	0.11	--	--	--	0	0.00	1	--	--	--	--	--	1	0.05	
Bidessina complex	2	3	5	0.19	--	--	--	0	0.00	--	--	--	--	--	--	1	0.05	
<i>Haliphus</i> sp.	2	--	2	0.07	--	--	--	0	0.00	--	--	--	--	--	--	0	0.00	
Hymenoptera	--	--	0	0.00	--	--	1	1	0.04	--	--	--	--	--	--	0	0.00	
Diptera other than chironomid larvae*																		
<i>Bezzia, Palpomyia Probezzia</i> sp.	53	29	82	3.05	19	26	34	79	3.34	4	--	--	2	5	9	23	1.06	
Heleidae pupae	--	3	3	0.11	--	--	--	0	0.00	--	--	--	--	--	--	0	0.00	
Chironomidae pupae	10	2	12	0.45	3	--	1	4	0.17	--	--	--	--	--	3	3	0.14	
Unidentified dipteran pupae	--	--	0	0.00	--	--	--	0	0.00	--	--	--	--	--	1	1	0.05	
Unidentified insect larvae*	--	--	0	0.00	3	--	5	8	0.34	--	--	--	3	--	6	9	0.41	

(Continued)

* Organisms in this group were all immatures (larvae or nymphs) except for those listed as being in another stage (i.e., pupae).

(Sheet 3 of 4)

Table A3 (Concluded)

Taxon	August 1986				June 1987					August 1987							
	1	2	Total	%	A	B	C	Total	%	A	As	B	Bs	C	Cs	Total	%
Other invertebrates (Continued)																	
Gastropoda																	
<i>Amnicola limnosa</i>	162	8	170	6.32	29	7	40	76	3.22	6	48		202	14	155	425	19.57
<i>Gyraulus parvus</i>	53	13	66	2.45	125	99	185	409	17.31	--	--	--	--	2	24	26	1.20
<i>Physella</i> sp.	--	--	0	0.00	5	1	8	14	0.59	--	--	--	1	--	--	1	0.05
Immature gastropods	47	--	47	1.75	35	62	166	263	11.13	1	--	--	--	--	2	3	0.14
Total other invertebrates	1,254	1,437	2,691	100.00	1,197	440	726	2,363	100.00	156	372	82	732	116	714	2,172	100.00
Total invertebrates	3,488	3,117	6,605		1,743	617	1,052	3,412		174	396	92	816	125	862	2,465	
Mean stem length (cm) of <i>C. demersum</i> per sample (N = 5)	--	--	--		224.5	201.8	203.9	210.1		59.3		75.5		82.8			
Total stem length (cm) of <i>C. demersum</i> in supplementary samples	--	--	--		--		--	--		--	1,472.1	--	2,198.1	--	2,162.7		

Table A4

A Summary of the Relative Abundance of Individual Taxa from a Borrow Pit
in Mississippi, 1987 (N = 8 for All Means)

Species	Live <i>Ceratophyllum</i>		Plastic <i>Ceratophyllum</i>		Plastic <i>Vallisneria</i>	
	Mean	SD	Mean	SD	Mean	SD
<i>Physa</i> sp.	37.4	13.8	4.3	2.7	0.6	0.5
<i>Gyraulus</i> sp.	19.3	13.6	0.4	0.5	0.3	0.4
<i>Somatogyrus</i> sp.	4.1	1.9	0.3	0.4	0.0	0.0
<i>Viviparous</i> sp.	0.0	0.0	0.0	0.0	0.1	0.3
<i>Dugesia tigrina</i>	0.6	1.0	0.3	0.4	0.0	0.0
<i>Planaria</i> sp.	1.1	1.0	0.3	0.4	0.4	0.5
<i>Hydra</i> sp.	1.0	1.2	0.3	0.4	0.3	0.4
<i>Hyallolela azteca</i>	7.4	3.7	1.5	1.5	0.6	1.0
<i>Palaemonetes kodiakensis</i>	0.0	0.0	0.0	0.0	0.0	0.0
<i>Neotrichia</i> sp.	0.0	0.0	0.1	0.3	0.4	0.5
<i>Orthotrichia</i> sp.	1.3	1.5	1.3	1.4	0.6	0.5
<i>Bagous</i> sp.	0.1	0.3	0.0	0.0	0.0	0.0
<i>Pleidae</i> (nymph)	0.0	0.0	0.1	0.3	0.0	0.0
<i>Hydrobiomorpha casta</i>	0.0	0.0	0.1	0.3	0.0	0.0
<i>Berosus</i> sp.	0.0	0.0	0.1	0.3	0.0	0.0
<i>Pelocoris</i> sp.	0.1	0.3	0.0	0.0	0.0	0.0
<i>Oecetis</i> sp.	0.0	0.0	0.1	0.3	0.0	0.0
<i>Caenis</i> sp.	73.6	26.7	13.9	9.8	3.8	1.8
<i>Callibaetis</i> sp.	75.6	45.6	31.1	24.1	6.1	3.3
<i>Enallagma</i> sp.	3.7	2.1	1.6	0.9	0.1	0.3
<i>Chironomidae</i> (pupae)	0.1	0.3	0.6	0.5	0.0	0.0
<i>Erythemis</i> sp.	0.0	0.0	0.1	0.3	0.1	0.3
<i>Dasyhelea</i> sp.	0.3	0.5	2.4	2.3	0.6	0.5
<i>Isotomurus fimentaria</i>	0.0	0.0	0.0	0.0	0.1	0.3
<i>Probezzia</i> sp.	0.0	0.0	0.1	0.3	0.0	0.0
<i>Alluadomyia</i> sp.	0.6	0.7	0.1	0.3	0.3	0.4
<i>Clinotanytus</i> sp.	0.0	0.0	0.1	0.3	0.0	0.0
<i>Cricotopus sylvestris</i>	4.4	2.3	0.1	0.3	0.0	0.0
<i>Cricotopus</i> sp.	0.4	0.7	0.1	0.3	0.1	0.3
<i>Nanocladius distinctus</i>	0.1	0.3	0.3	0.4	0.0	0.0
<i>Nanocladius alternathe</i>	8.3	5.8	2.6	2.9	0.6	0.5
<i>Nanocladius</i> sp.	0.1	0.3	0.0	0.0	0.1	0.3
<i>Orthocladius</i> sp.	0.0	0.0	0.0	0.0	0.3	0.4
<i>Dicrotendipes</i> sp. I	7.6	6.9	2.4	1.9	1.4	0.9
<i>Microtendipes</i> sp.	3.6	3.8	5.1	4.5	1.6	0.9
<i>Chironomus</i> sp.	0.1	0.3	0.1	0.3	0.0	0.0
<i>Parachironomus abortives</i>	5.6	4.1	1.6	3.1	0.6	0.5
<i>Parachironomus frequens</i>	0.1	0.3	0.0	0.0	0.0	0.0
<i>Parachironomus</i> sp.	1.0	1.8	0.0	0.0	0.0	0.0
<i>Endochironomus nigricans</i>	0.6	0.7	0.5	0.5	0.3	0.4
<i>Endochironomus subtends</i>	0.1	0.3	0.0	0.0	0.0	0.0

(Continued)

Table A4 (Concluded)

Species	Live <i>Ceratophyllum</i>		Plastic <i>Ceratophyllum</i>		Plastic <i>Vallisneria</i>	
	Mean	SD	Mean	SD	Mean	SD
<i>Pentaneura</i> sp.	0.1	0.3	0.1	0.3	0.0	0.0
<i>Polypedilum convictum</i>	0.0	0.0	0.1	0.3	0.0	0.0
<i>Polypedilum illinoense</i>	0.1	0.3	0.4	0.5	0.0	0.0
<i>Parakiefferiella</i> sp.	0.4	0.7	0.1	0.3	0.0	0.0
<i>Procladius</i> sp.	0.0	0.0	0.1	0.3	0.0	0.0
<i>Phaenopsectra</i> sp.	0.7	0.5	0.1	0.3	0.0	0.0
<i>Labrundinia pilosella</i>	0.0	0.0	0.1	0.3	0.1	0.3
<i>Labrundinia neopilosella</i>	8.9	8.8	2.4	3.2	0.9	0.3
<i>Ablabesmyia peleensis</i>	1.1	1.0	0.5	0.5	1.5	0.6
<i>Ablabesmyia annulata</i>	0.0	0.0	0.1	0.3	0.1	0.3
<i>Albabesmyia cinctipes</i>	0.0	0.0	0.0	0.0	0.3	0.4
<i>Albabesmyia mallochi</i>	0.0	0.0	0.0	0.0	0.1	0.3
<i>Ablabesmyia</i> sp.	0.0	0.0	0.0	0.0	0.1	0.3
<i>Ablabesmyia parajanta</i>	0.3	0.7	0.3	0.4	0.1	0.3
Tanypodinae (ei)*	0.0	0.0	0.0	0.0	0.8	0.4
<i>Tanytarsus</i> sp.	1.0	1.2	0.1	0.3	0.1	0.3
<i>Tanytarsus glabrescen</i>	1.1	2.4	0.4	0.5	0.5	0.5
<i>Tanytarsus guerlus</i>	0.1	0.3	0.5	0.7	0.3	0.4
<i>Macropelopia</i> sp.	0.0	0.0	0.5	0.9	0.3	0.4
<i>Cryptochironomus</i> sp.	0.0	0.0	0.0	0.0	0.1	0.3
<i>Rheotanytarsus</i> sp.	0.1	0.3	0.0	0.0	0.0	0.0
<i>Limnesia</i> sp.	0.1	0.3	0.3	0.7	0.0	0.0
<i>Arrenurus</i> sp.	0.4	0.7	0.3	0.4	0.0	0.0
<i>Tyrellia</i> sp.	0.6	1.4	0.0	0.0	0.0	0.0
<i>Larsia</i> sp.	0.0	0.0	0.0	0.0	0.1	0.3
<i>Mideopsis</i> sp.	0.1	0.3	0.1	0.3	0.3	0.4
<i>Forelia</i> sp.	0.0	0.0	0.0	0.0	0.1	0.3
<i>Sperchon</i> sp.	0.1	0.3	0.1	0.3	0.0	0.0
<i>Hydrachna</i> sp.	0.1	0.3	0.1	0.3	0.0	0.0
<i>Hydroma despiciens</i>	0.3	0.5	0.0	0.0	0.3	0.4
Naididae	0.0	0.0	0.0	0.0	2.1	1.5
Oligochaeta	0.7	1.7	0.4	0.5	0.0	0.0

* Early instar, not identifiable to genus.