ABSTRACT

ARE PLANT BEDS IN STREAMS HOT SPOTS OF MACROINVERTEBRATE DIVERSITY, ABUNDANCE AND BIOMASS?

By Michael P. Shupryt

Macroinvertebrates are known to exhibit habitat preferences for macrophytes in lakes and large rivers where macrophyte beds are abundant. It is less understood if these preferences will hold true in low order streams where macrophyte beds are less abundant and sporadic. I examined the ability of small sporadic macrophyte beds to be hot spots of macroinvertebrate diversity, abundance and biomass in a Central Wisconsin sand plain stream. I sampled eight discrete macrophyte beds and 4 sand/gravel patches monthly from March through October 2007. Overall mean invertebrate diversity (Shannon-Weiner Index), abundance and biomass in the macrophyte beds was significantly greater than in sand/gravel patches (paired t-test p < 0.05). Mean invertebrate diversity in the macrophyte beds had a non-significant time (Repeated Measures ANOVA p=0.057) and a significant bed effect (p<0.05). Although there was a significant difference in mean diversity the difference was small and not a likely indication of a biodiversity hot spot. Mean invertebrate abundance and biomass had significant time (p<0.001) and bed effects (p<0.01). I scaled the results of the summer invertebrate abundance and biomass results using a substrate survey in a 400m stream reach. Although sand/gravel outnumbered macrophytes as a habitat nearly 3:1 they contributed equally to macroinvertebrate abundance and biomass and the whole reach level. I concluded that macrophyte beds were hot spots of macroinvertebrate abundance and biomass. These results show that even when macrophyte beds are isolated and sporadic in small streams they may be major contributors to invertebrate biomass and production at the whole stream level.
ARE PLANT BEDS IN STREAMS HOT SPOTS OF MACROINVERTEBRATE DIVERSITY, ABUNDANCE AND BIOMASS?

by

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Chapter I

Habitat complexity is often defined as an ecosystem with many intricate and interconnecting habitats. Ecologists have long studied the effects of habitat complexity on animal populations and communities. One of the most famous studies was conducted by MacArthur & MacArthur (1961) who examined the relationship between habitat complexity and species diversity. MacArthur & MacArthur found that in the tropics as tree foliage complexity increased so did bird species diversity. Since this paper numerous others have studied the relationship between habitat complexity and species diversity (Williams et al. 2002, Harper et al. 1997). It is believed the mechanism behind this association is that as habitat complexity increases there is a creation of more niches within the environment. These niches are filled by increasing number of organisms specialized to exploit these new resources.

Other studies have shown the association between habitat complexity and secondary production on populations and communities (Benke et al. 1984, O’Conner 2004). Secondary production is the heterotrophic accumulation of biomass through time (Benke & Huryn 2007). The two important components of production are abundance and biomass. Secondary production can increase through the growth of individuals within a population or the recruitment of new individuals. When determining the importance of habitat complexity it is not entirely obvious whether increased production is driven by habitat complexity or increased species diversity. To understand the importance of habitat complexity, community diversity, abundance and biomass must all be examined.

Habitat complexity leads to more niches in the environment but these areas are not always evenly distributed. Some niches/habitats may contain a higher number of species and a greater number of individuals. Habitats that are small in area compared to the surrounding
environment and contain a much greater diversity or productivity are known as hotspots. Hotspots are created when there are a number of available habitats in an ecosystem and the life history traits of the organisms in the community cause a large number of species to occupy the same habitat. This leads to uneven distributions of organisms because of individual species habitat preferences (Roper et al. 1994). If the habitat is in relatively small abundance compared to the surrounding landscape then this habitat can be a hot spot of animal abundance and production.

An interesting and less studied way to examine habitat complexity and hot spots is to determine the importance of one unique habitat to organismal diversity and production. Aquatic environments often have varied and distinct habitats such as wood, boulders, sand, gravel, silt, aquatic plants (macrophytes) etc. These habitats are colonized by a wide range of habitat generalist and specialist organisms. In this study I will examine the importance of one unique habitat, aquatic macrophytes, to macroinvertebrate diversity and production in a low-order groundwater fed stream.

Invertebrates are found in nearly every freshwater system and are important components of the food web. Aquatic invertebrates are good organisms to study in order to assess the importance of a single habitat as a hot spot because many invertebrate species exhibit habitat preferences (Merrit & Cummins 1996). Many aquatic invertebrate taxa also show a strong preference for macrophyte beds (Phillips 2003). Macrophyte beds are often found in lakes, large rivers, and low-gradient low-order streams where they serve as important habitat for macroinvertebrates (Warfe & Barmuta 2006). I will study the importance of macrophytes as a single unique habitat in stream ecosystems.
Macrophytes are not uniformly distributed throughout all streams because they cannot colonize or become established in streams prone to large, unpredictable discharge fluctuation (Riis & Biggs 2003). Macrophytes are rarely found in low order streams with water velocities above 1 m/s (Chambers et al. 1991) and discharges above 1 m$^3$/s (Maltchik & Pedro 2001). Even in streams with thalweg velocities too high for macrophyte growth macrophyte beds may be found in small backwater patches where velocity and discharge are low. Although the energy in low-order streams are known is often driven by allochthons inputs (i.e. terrestrial leaf decomposition) areas where sunlight reaches the stream macrophytes can be abundant. The sporadic distribution of macrophytes within and among streams may be one reason they are commonly ignored in macroinvertebrate habitat preference studies and macroinvertebrate surveys (Andrews & Minshall 1979).

In this study I will 1) Determine invertebrate diversity, abundance and biomass in macrophyte beds compared to the dominant stream habitat, sand\gravels. 2) Scale-up the results to the whole stream level to determine the system wide importance of macrophytes as invertebrate habitat. 3) Examine the temporal changes in macrophyte bed aerial size and biomass and examine the effects on invertebrate diversity, abundance and biomass.
Chapter II

Introduction

Hot spots have recently been used to explain a number of uneven distributions of ecosystem measures such as; biodiversity, erosion and secondary productivity (Myers 1988, Payne & Moore 2006, Benedet et al. 2007). Hot spots are defined as localized areas that have an increased rate of an ecological process compared to the surrounding landscape. When explaining uneven distributions of animals within ecosystems the main factors to consider include: 1) The influence of available habitats on the distribution of organisms and, 2) Life history traits of the organisms in the community. These drivers often lead to uneven distributions of organisms because of individual species habitat preferences (Roper et al. 1994). A number of species may share the same habitat preference and create an uneven distribution within the ecosystem. If the habitat is in relatively small abundance compared to the surrounding landscape then this habitat can be a hot spot of animal abundance and production.

Habitat preferences are an important factor in shaping macroinvertebrate communities in aquatic ecosystems. Many aquatic invertebrate taxa show a strong preference for macrophyte beds (Phillips 2003). Macrophyte beds are often found in lakes, large rivers, and low-gradient low-order streams where they serve as important habitat for macroinvertebrates (Heck & Crowder 1991, Warfe & Barmuta 2006). In lotic systems macrophyte beds have been shown to be important for organic matter retention and nutrient processing (Cotton et al. 2006, Forshey 2007). In lakes and rivers, macroinvertebrate diversity and production within plant beds are often higher than that of other habitats (Thorp et al. 1997, Richardson et al. 1998, Hutchens et al. 2004). The role of macrophyte beds in shaping macroinvertebrate communities in low-order
streams is much less clear. In low-order streams macroinvertebrate habitat preferences are well studied for other habitats such as woody debris (Benke et al. 1984, Magoulik 1998) leaf packs (France 1998, Moffet 1998) and inorganic substrates (Smock et al. 1985, Benoy & Kalff, 1999). Much of the recent research on invertebrate-macrophyte interactions has focused on a subset of a lotic invertebrate community, such as a single functional feeding group (Underwood et al. 1992, Fritz et al. 2004). While this research is important in explaining how certain groups of organisms utilize macrophytes as a resource it fails to capture the role of macrophytes in structuring macroinvertebrate communities.

Macrophytes are not uniformly distributed throughout all streams because they cannot colonize or become established in streams prone to large, unpredictable discharge fluctuation (Riis & Biggs 2003). Macrophytes are rarely found in low order streams with water velocities above 1 m/s (Chambers et al. 1991) and discharges above 1 m³/s (Maltchik & Pedro 2001). Even in streams with thalweg velocities too high for macrophyte growth macrophyte beds may be found in small backwater patches where velocity and discharge are low. The sporadic distribution of macrophytes within and among streams may be one reason they are commonly ignored in macroinvertebrate habitat preference studies and macroinvertebrate surveys (Andrews & Minshall 1979, Krueger & Waters 1983).

Phillips (2003) conducted one of the few comprehensive macroinvertebrate habitat preference studies that include macrophytes. He found in a predominately sandy stream that macroinvertebrates associated with macrophytes had the second-highest taxa richness and the highest invertebrate abundance (per unit area) relative to other habitat types. Phillips suggested that macrophytes had the highest invertebrate abundance because they provide a more stable substrate to colonize than do sand, silt or leaf packs. This conclusion is in agreement with
previous studies which show that streams with stable substrates (macrophytes, cobble, CWD) have increased invertebrate production and different invertebrate communities than in streams with unstable substrates (Benke et al. 1984, Smock et al. 1985).

There have been a small number of studies that have attempted to determine the causes of relationships between macrophytes and macroinvertebrates in streams and some investigators have attributed increased invertebrate abundance to the ability of macrophytes to increase sedimentation of particulate organic matter, an important food source for detritivores (Sand-Jensen & Mebus 1996, Fritz et al. 2004). Other ecologists have suggested that macrophytes benefit invertebrates by providing stable substrate for epiphytic algal growth (utilized by grazers) (Chantha et al. 2000, Riis & Biggs 2000), by providing refuge from predators (Warfe & Barmuta 2006) and by increasing colonization space (Losee and Wetzel 1988, Huryn & Wallace 2000).

In many ecosystems habitat complexity is positively correlated with biodiversity (Kohn & Walsh 1994, Downes et al. 1998) and production (Wiens 1973, Cardinale et al. 2002). Habitats in streams that cover a small percentage of the wetted or active channel (macrophytes, wood and boulders) have been shown on some occasions to have higher invertebrate diversity and productivity than more abundant substrate types (Kaenel, et al., 1998, Negishi & Richardson 2003, Hutchens et al. 2004, Lester et al. 2007). The contribution of these relatively rare habitats to whole stream invertebrate diversity and productivity is much less understood.

The few studies describing invertebrate productivity in macrophyte beds have tended to treat macrophytes as static entities rather than living substrates that change throughout a growing season (Phillips 2003, Hutchens et al. 2004). Because macrophyte beds in temperate streams are morphologically dynamic (aspects such as total area, plant biomass, and shape change throughout the season) the importance of macrophytes for invertebrates will likely change
throughout the year. I measured invertebrate abundance, biomass and diversity in the two most abundant habitats, macrophyte beds and sand/gravel patches, of a Central Wisconsin sand plain stream from March to October. I also measured plant bed morphology (bed area and plant biomass per unit area) during this period. I estimated the contributions of macrophyte beds and sand/gravel to reach-scale invertebrate abundance and biomass at peak macrophyte biomass. I hypothesized that: 1) Macr invertebrate diversity, abundance and biomass are considerably greater in macrophyte beds than in benthic sand/gravel patches. 2) Macroinvertebrate diversity, abundance and biomass in macrophyte beds will vary temporally as beds change in size and plant density throughout the year 3) Macrophyte beds and sand/gravel patches will contribute similarly to overall invertebrate abundance and biomass even though macrophyte habitat is much less abundant.

Methods

Study Area

The study was conducted in a 400 meter stretch of the West Branch of the White River (hereafter referred to as the West Branch) in Waushara County, WI (Fig 1, 44.08036N 89.35247W). The West Branch is a groundwater-fed trout stream located in the Central Sand Plains region of Wisconsin that is known for its sandy soils and stable stream flows. The reach has an average stream velocity of 0.4 m/s with little seasonal variation. The wetted channel is 3 to 5 meters wide in most areas with daily average water temperature varying between a low of 4\(^\circ\) and a high of 20\(^\circ\) C during the study period. A substrate survey conducted in July 2007 showed that the predominant substrate in the West Branch is a sand/gravel mixture which covers 57% of
that the predominant substrate in the West Branch is a sand/gravel mixture which covers 57% of the stream bottom. Macrophytes are the second most abundant benthic substrate covering 18% at peak growth. Macrophyte beds in the reach were predominantly composed of *Veronica Anagalis-aquatica* L. followed by *Ranunculus* sp. Other aquatic plant species comprised less than 1% of the macrophyte community within the study reach. The West Branch drains a watershed of mixed deciduous–coniferous forest, grassland and agriculture.

Fig 1. Location of the study site on the West Branch of the White River in Waushara County, WI. Site begins just east of County Highway T crossing.
Sampling

Eight discrete macrophyte beds were identified before the study began and were sampled monthly from March to November 2006 for benthic invertebrates and plant bed attributes (Fig 2). The same beds were sampled each month except one bed was dropped from the sample population between March and April due to sampling difficulties. The dropped bed was not included in the March calculations therefore March only had seven plant beds sampled while the rest of the months had eight included in the calculations. Four sand/gravel areas were sampled for benthic invertebrates from March to November directly upstream from four of the macrophyte beds. The sampling locations had similar water depths and velocities compared to the adjacent plant beds (Fig 2). Macrophytes and sand/gravel patches were sampled using a 15-cm diameter 16-gauge stainless steel stovepipe corer. One core sample was collected for

Fig 2. Arial photograph showing the locations of macrophyte beds (circles) and sand/gravel (triangles) sampling locations along the West Branch of the White River. Bed numbers are labeled right to left (#1 on the far right) and water flows left to right.
invertebrates from each plant bed (or sand/gravel patch). Core locations were determined by dividing each plant bed into eight equal quadrats and by choosing a quadrat with a list created by a random number generator. Plant stems were cut along the inside edge of the corer and all of the plant material inside the corer was removed from the sediment and placed into a sample jar. The top two centimeters of benthic sediment were collected and sieved through a 0.6mm mesh and all invertebrates were collected. I did not distinguish between macrophyte-dwelling invertebrates and invertebrates inhabiting sediment within the macrophyte beds. Samples for invertebrates were preserved in the field with 95% ethanol. Each macrophyte bed was measured monthly for aerial bed size. Bed size was mapped in the field and seasonal growth or retreat was calculated for each bed. A second stovepipe core sample was taken from each macrophyte bed to determine plant bed biomass $\text{m}^2$. Plant biomass samples were collected in the same manner as invertebrate samples except they were not preserved in ethanol. Plant samples were then dried at $60^\circ$C for a minimum of three days and weighed. Water velocity was measured at the upstream edge of each plant bed with an acoustic Doppler system on three separate occasions throughout the year. Water temperature was recorded throughout the sampling period with two HOBO temperature loggers submerged at the upstream and downstream portions of the study.

Sample Processing and Analysis

All invertebrates collected were enumerated and most were identified to genus (Merrit & Cummings 1996, Thorp & Covich 2001) although some groups (e.g., Chironomidae, Oligocheates) were identified only to family. These data were used to calculate biodiversity using the Shannon-Weiner Diversity Index per habitat patch (plant bed or sand/gravel area) per sample date. Invertebrate density was expressed as number of individuals per $\text{m}^2$ of stream
bottom. For macrophytes and sand/gravel patches the values for each habitat type were averaged to determine a monthly invertebrate density per habitat. The total length of each invertebrate was measured with an ocular micrometer (to 0.01 mm) and published length-dry mass regressions were used to determine individual dry masses (Benke et al. 1999). In cases where no length-dry mass regressions were published or individuals were too small and numerous to measure (Chironimidae) individuals were dried at 60°C for 48 hours and weighed on a microbalance to 0.01 mg. Dry masses measured directly were corrected for losses due to preservation in ethanol (Leuven et al. 1985). Individual dry masses were then summed across all taxa for a sampling period to determine total sample biomass. The invertebrate biomasses from each of the eight macrophyte and four sand/gravel samples were then averaged to estimate monthly invertebrate biomass for each habitat.

I conducted a substrate survey of the West Branch on July 20th 2006 to assess the abundances of macrophytes and sand/gravel patches in the stream. The survey was conducted using a point intercept method where transects were measured out in the stream channel every 10m. At every 0.4m across each transect the habitat type was determined and recorded creating a 10m by 0.4m grid. At each point the dominant habitat type was recorded. The points were used to determine a percentage of stream bottom occupied by each habitat type. Reach area was determined by calculating reach length which is the number of lengthwise transects multiplied by the distance between each transect (10m). The transects were also used to determine stream width every 10 meters and the points were connected with a straight line to determine channel shape and total area. Those data were used to scale-up the abundance and biomass data in order to compare the contributions of the most abundant habitat types (sand/gravel and macrophytes)
to invertebrate abundance and biomass in the whole reach. I used the following equations to calculate whole reach invertebrate abundance and biomass:

\[ A_H = R \times H \]  
\[ R_A = A_H \times I_A \]  
\[ R_B = A_H \times I_B \]  

Where:
- \( A_H \) = Area of a specific habitat type within the reach (m\(^2\))
- \( R \) = Reach area (m\(^2\))
- \( H \) = Percent of stream bottom per habitat type
- \( R_A \) = Reach scale invertebrate abundance per habitat type
- \( I_A \) = Mean Invertebrate abundance (per m\(^2\)) per habitat type
- \( R_B \) = Reach scale invertebrate biomass per habitat type
- \( I_B \) = Mean Invertebrate biomass (mg/m\(^2\)) per habitat type

I only used invertebrate data from June, July and August to scale up to the whole reach because macrophyte bed area is dynamic and the mid summer substrate survey would not be applicable to early and late season macrophyte stream bottom coverage.

**Data Analysis**

I used a paired t-test to assess differences in monthly mean invertebrate diversity, abundance and biomass between macrophyte beds and sand/gravel samples. Significance was set at \( p=0.05 \). I also assessed temporal trends for invertebrate diversity, abundance and biomass within the macrophyte beds. I used a Repeated Measures ANOVA to determine the effect of time, macrophyte bed and time x bed interactions on invertebrate diversity, abundance and biomass.
Results

Overall mean invertebrate diversity (Shannon-Weiner Diversity Index), abundance and biomass were higher in the plant beds than in the sand/gravel (Paired t-tests p<0.05, Figs 3, 4 & 5). Invertebrate diversity was higher in plant beds in every month except June and October. Mean invertebrate Shanon-Weiner diversity ranged from 1.25 to 1.84 (SD = 0.21, grand mean = 1.66) in the plants and 0.84 to 1.83 (SD = 0.31, grand mean = 1.39) in the sand/gravel. Mean monthly invertebrate diversity tended to be lower in the spring months and slightly higher and more consistent during the rest of the year in the plant beds (repeated measures ANOVA time effect p=0.057, Fig 3). Mean invertebrate diversity varied significantly among beds (p=0.02, Fig 6) and a bed x time interaction (p=0.02) indicated the change in diversity over time depended on the plant bed under consideration.

In every month during the sampling period mean invertebrate abundance and biomass was greater in plant beds than in sand/gravel patches (Fig. 4, 5). Mean invertebrate abundance (individuals/m²) ranged from 1297 to 5175 (SD= 1201, grand mean = 2552) in the plant beds and 477 to 1238 (SD= 274, grand mean = 893) in the sand/gravel patches. Macrophytes and sand/gravel habitats ranged in mean invertebrate biomass (mg/m²) from 802 to 2890 (SD= 693, grand mean = 1693) and from 308 to 747 (SD=132, grand mean = 521), respectively.
Fig 3. Mean invertebrate diversity (Shannon-Weiner Index) in plant beds and sand/gravel patches. Mean diversity between plant beds and sand/gravel patches are significantly different. There is a significant bed and bed x time effect and a nonsignificant time effect. Error bars indicate standard deviation.

Fig 4. Mean invertebrate abundance/m$^2$ in plant beds and sand samples. Mean abundance for plant beds and sand/gravel patches are significantly different. There is a significant bed and time effect but no time x bed interaction. Error bars indicate standard deviation.
There were strong temporal trends in invertebrate abundance and biomass associated with the plant beds. Mean invertebrate abundance was highest in early spring and tended to decrease throughout the year (repeated measures ANOVA time effect $p<0.001$, Fig 4). Invertebrate abundances varied strongly by bed ($p=0.001$, Fig 7) but the time effect did not depend on bed (time x bed interaction, $p=0.13$). Mean invertebrate abundance in the plant beds was nearly 4 fold higher in the first month of the study, March, than in the final month of the study, October. For the most part beds that were the highest in invertebrate abundance were consistently that way throughout the year and as overall invertebrate abundance decreased throughout the year it also decreased proportionally in each bed. Unlike the plant beds invertebrate abundance in the sand/gravel habitats was highest during the latter months of the sampling period (Fig 4).

Fig 5. Mean invertebrate biomass (dry mass) in plant beds and sand samples. Mean invertebrate biomass in plant beds and sand/gravel patches are significantly different (paired t-test: $p=0.001$). There is a significant bed and time effect but no time x bed interaction. Error bars indicate standard deviation.
Mean invertebrate biomass in the macrophyte beds was also highest in spring and early summer with a general decreasing trend throughout the year (repeated measures ANOVA time...

**Fig 6.** Mean invertebrate diversity (Shannon-Weiner Index) March through October for each plant bed. Error bars indicate standard deviation.

**Fig 7.** Mean invertebrate abundance (Individuals/m²) March through October for each plant bed. Error bars indicate standard deviation.

Mean invertebrate biomass in the macrophyte beds was also highest in spring and early summer with a general decreasing trend throughout the year (repeated measures ANOVA time...
effect $p<0.001$, Fig 5). There were a few anomalies to this trend as invertebrate biomass in April was greater than in March and there was a large reduction of biomass in May that quickly recovered. There was a significant difference in invertebrate biomass among beds ($p=0.01$, Fig 8) but no significant bed x time interaction for invertebrate biomass ($p=0.08$). There was a large decrease between April and May when invertebrate biomass was essentially halved but recovered quickly in June. Biomass then steadily decreased for the rest of the year with a small spike in October, the last sampling date (Fig 5). There was high variation among the plant beds within any given month. In June, for example, invertebrate biomass varied from 1164 mg/m$^2$ to 4703 mg/m$^2$ and as for abundance the beds that were highest in invertebrate biomass stayed that way throughout the sampling period and declined proportionally throughout the year.

Fig 8. Mean invertebrate biomass (mg/m$^2$) during March through October for each plant bed. Error bars indicate standard deviation.

The substrate survey conducted in late July showed that sand/gravel was the most prominent habitat covering 57% of the stream bottom within our 400 meter reach (Fig 9).
Macrophyte beds were the second most common habitat covering 18% of the stream bottom. Other habitats in the West Brach comprised 25% of the stream bottom and are made up of boulders (10%), woody debris (7%), cobble (4%) and silt (4%, Fig 9). At the whole reach scale (1,580 m²) invertebrate abundance in sand/gravel was 6.93E+05 individuals while in macrophyte beds there were 7.31E+05. Invertebrate biomass associated with sand/gravel and macrophyte beds was 505 and 494 g dry mass respectively, for the whole reach (Table 1). Plants beds and sand/gravel contributed about equally to whole reach invertebrate abundance and biomass in the West Branch even though plant beds are much less common than sand/gravel habitat.

![Fig 9. Substrate relative abundance in summer, based on a survey using the point intercept method, in the 400m study reach of the West Branch of the White River.](image)

| Table 1. Scaled up total invertebrate abundance and biomass for macrophytes and sand/gravel habitats in the West Branch of the White River. Habitat area for macrophytes and sand/gravel patches were based on habitat survey conducted in July. Mean invertebrate abundance and biomass was calculated from data collected in June, July and August. |
|-----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| Reach Area (m²) | Proportion of Total Habitat | Reach Habitat Area (m²) | Mean Invertebrate Abundance (per m²) | Reach Scale Mean Invertebrate Abundance (mg/m²) | Reach Scale Invertebrate Biomass (g) |
| Macrophytes     | 1,580          | 18%            | 284            | 2437           | 6.93E+05        | 1739           | 494            |
| Sand/Gravel     | 1,580          | 57%            | 900            | 813            | 7.31E+05        | 561            | 505            |
In early spring the plant beds were dominated by insect taxa and Chironomidae was by far the most dominant group (Appendix A, Fig A-1). Insects made up almost all of the major taxa except for one genus of amphipods (Gammarus). At this point of the year gastropods were rare comprising only a small percentage of the total individuals; the majority of which were Physidae (Physa). The relative abundance of chironomids decreased from spring to summer resulting in a more even taxa distribution. While in the plant beds many insect taxa (Simulium, Baetis) fluctuated in terms of relative abundance and biomass non-insects such as Gammarus and Lumbriculidae, an aquatic annelid became increasingly abundant. By fall the only insect taxon that had high relative abundance in the plant beds was Chironomidae (Appendix A, Fig A-1). Invertebrate relative biomass in the late summer and fall samples were dominated by the non-insects such as Gammarus and Lumbriculidae. By this time two gastropod taxa increased in terms of relative biomass in the plant beds (Physa and Planorbidae). Throughout the year the major trend in community composition of the plant beds was the decrease in relative abundance and biomass of insects and the increase in relative abundance and biomass of non-insect detritivores and grazers.

Community composition here after reported is representative of three distinct seasons throughout the year, spring, summer and fall (Appendix A Figs A-1 & A-2). In March the macroinvertebrate community was dominated by chironomids comprising 60% of all individuals in macrophyte beds. The rest of the macroinvertebrate community within the plant beds was comprised mainly of Simulium (Simulidae, 7%), Lumbriculidae (4%), Gammarus (Gammaridae, 4%), and Baetis (Baeitidae, 3%). In June macroinvertebrate community composition had changed considerably. In the macrophyte beds the major taxa were Chironomidae (30%), Gammarus (23%), Baetis (11%), Simulium (5%), Lepidostoma (Lepidostomatidae, 7%) and
Optioservus (Elmidae 6%). In the fall, September, chironomids and amphipods continued to be the dominant taxa in terms of abundances (Appendix A). Macroinvertebrates in the macrophyte

![Graph A](image1)

![Graph B](image2)

![Graph C](image3)

Fig. 10. Scatterplot of mean water velocity (grand mean of three sampling dates in m/s) and invertebrate diversity (H', A), abundance (individuals/m², B) and biomass (mg/m², C). Mean invertebrate diversity (r² = 0.131, p = 0.004), abundance (r² = 0.234, p < 0.001) and biomass (r² = 0.220, p < 0.001) were all significantly correlated to water velocity.
beds consisted of Chironomidae (35%), *Gammarus* (27%), *Baetis* (7%), *Physa* (6%) and *Cheumatopsyche* (4%).

In March the macroinvertebrate community in the sand/gravel patches was dominated by Chironomidae at 70% if all individuals. The rest of the community was comprised of Lumbriculidae (8%), *Gammarus* (7%), *Optioservus* (4%) and Sphaeridae (3%). While Lumbriculidae made up a small percentage of the overall abundance it was the dominant taxa in the sand/gravel patches in terms of biomass. In the June sand/gravel samples the macroinvertebrate community was made up of Chironomidae (39%), *Gammarus* (19%), *Optioservus* (14%), *Protoptila* (Glossosomatidae, 8%) and *Baetis* (6%). In September in the sand/gravel patches Chironomids comprised 40% of all individuals followed by *Gammarus* (36%), *Optioservus* (8%), *Baetis* (4%) and Lumbriculidae (3%).

I attempted to determine the driving force behind this variation by measuring plant bed aerial size (m²), plant biomass (mg/m², Appendix B, Fig B-1) and water velocity (Appendix C, Fig C-1). I found that there was a weak, but significant trend between water velocity and mean invertebrate diversity (p=0.004, r²=0.131), abundance (p=<0.001, r²=0.274) and biomass (p=<0.001, r²=0.220, Fig 10). Although there was a pattern of certain beds always having higher or lower invertebrate abundance and/or biomass there was not a strong relationship. There was no relationship between either macrophyte bed aerial size or plant biomass and invertebrate diversity, abundance and biomass (Appendix D, Fig D-1).

**Discussion**

Mean invertebrate diversity was significantly different between plant bed and sand/gravel patches although the differences varied temporally. Mean invertebrate abundance and biomass
were much higher in the plant beds than in the sand/gravel patches. I anticipated that diversity would increase throughout the year as macrophyte beds continued to grow and more colonization space became available. More colonization space would likely lead to increased habitat complexity with more niches to be occupied by a diverse community of invertebrates. Although there was a statistical difference between mean invertebrate diversity in the plant beds and sand/gravel patches it was not large enough to be considered strong evidence for macrophytes being a diversity hot spot. The reason that the difference in invertebrate diversity was not as large as abundance and biomass may be because most of the taxa collected during the study were found in both macrophyte and sand/gravel samples. Macrophytes and sand/gravel patches were similar in community composition and that may have kept diversity similar between the two habitats. The similar community composition indicates that the difference in invertebrate abundance and biomass is likely not because of taxa-specific habitat preferences. When mean invertebrate abundance and biomass data were scaled to the whole reach macrophyte beds contributed as much to total invertebrate abundance and biomass as sand/gravel habitats (Table 1). This is surprising as sand/gravel is three times more abundant than macrophyte habitat in the West Branch. The scaled up results are only applicable to mid summer (June, July and August) because the habitat survey was conducted in July where macrophytes were thought to be at peak growth. Although mid summer macrophyte aerial bed sizes were not considerably larger than spring months (Fig 12A) for most beds mean invertebrate abundance and biomass were greatest during the early portions of the year. Macrophytes may contribute even more disproportionately to their substrate coverage during spring and early summer months. Macrophytes have been shown to contain high invertebrate abundances compared to other habitats in aquatic systems (Heck & Crowder 1991, Phillips 2003, Warfe & Barmuta 2006). This study shows that even
when macrophyte beds are isolated and sporadic in small streams they may be major contributors to invertebrate biomass and production at the whole stream level. This trend could signify that invertebrate production in almost any stream similar to the study stream (cold water, low-gradient) would benefit from the presence of macrophytes.

Hutchens *et al.* (2004) also showed that macrophytes are important to invertebrate communities at the whole-stream scale, base on an experimental study in a high-order river. Hutchens *et al.* measured invertebrate abundance and biomass in macrophyte beds and then partially or completely removed the plant beds from the river. The removal of macrophytes greatly reduced invertebrate abundance and biomass initially, and three and six weeks post treatment. They also found that there was reduction in abundance across all taxa but not an overall shift in community structure or functional feeding groups when compared across all dates. This study is consistent with my finding that macrophytes do not contribute to widely different invertebrate communities within a system. Macrophytes may be more important for invertebrate biomass and production than invertebrate diversity in lotic ecosystems.

Mean invertebrate diversity in the macrophyte beds was slightly lower in the early season samples (March, April, May) than during the rest of the year. One reason why diversity remained low during the early months was that the community was dominated by one taxon (Chironomidae). In the first three months of the study chironomids comprised 60%, 52% and 50% of all individuals present in the plant beds. The high relative abundance of one taxon resulted in a low value for taxa evenness which kept H’ low. For the remainder of the year chironomids comprised between 35% and 21% of all individuals, and community composition. The temporal fluctuation in chironomid relative abundances may be because chironomids are known to emerge often and sporadically from spring to fall in Midwestern streams (Berg &
Hellenthal 1991). Since chironomids were not identified to a lower classification in my study it is unknown if their summer decline and subsequent fluctuations were due to emergence of individual species or some other factor. The sand/gravel samples showed a fairly clear parabolic trend with low diversity in early spring and rising diversity until it peaked in June (just above $H' = 1.8$) and slowly decreased throughout the rest of the year. In October diversity unexpectedly spiked to the second highest value of any month. The increase in diversity in October is likely a result of increased taxa richness.

Mean invertebrate abundance showed a clear trend of decreasing abundance throughout the season in the plant beds. The first month of the study, March, far exceeded any other month in terms of abundance. In March there were nearly 2,000 more individuals/m$^2$ in the plant beds than during any other month. At first it may seem that much of this difference between months can be attributed to the decline of Chironomidae with their abundances in March being almost twice the number of total individuals per m$^2$ than the next month, April. The decline in chironomid abundance was approximately 1,200 individuals but the change in overall invertebrate abundance cannot solely be explained by the decline in chironomid density because their relative abundances are similar between the two months (60% in March and 56% in April). There were large decreases in the absolute abundances of *Simulium*, *Gammarus* and Lumbriculidae between March and April accounting for a combined 300 individuals/m$^2$. The decline in the abundance of the *Simulium* can be explained by the possibility of early emergence but *Gammarus* and Lumbriculidae are non-insects and their decline must be attributed to either mortality or habitat shift. Between April and October there was a steady increase in the relative and absolute abundances of *Gammarus* and other noninsects (i.e. *Physa* & Planorbidae). Insects did not follow a clear temporal trend in relative abundances and some of the major groups
fluctuated month to month. Chironomidae, *Baetis* and *Simulium* decreased, with few exceptions, throughout the year. *Simulium* and *Baetis* are known to have up to six and two or more generations per year, respectively. (Pearson & Franklin 1968, Smock 1987). Because each taxon may have numerous generations per year in the West Branch it is plausible that the fluctuating abundances each month were due to emergence and recruitment events. I expected to see a decline in abundance during spring and early summer followed by an increase of small early instar individuals. This pattern only held true for one Trichopteran genera, *Cheumatopsyche*. *Cheumatopsyche* has been shown to be univoltine in northern coldwater streams and is likely the reason I was able to detect a clear emergence and recruitment pattern (Mackay 1986).

Invertebrate abundance between macrophytes and sand/gravel showed two opposite temporal trends. While invertebrate abundance in macrophyte beds declined during the course of the study abundance in the sand/gravel patches increased (Fig 5). Abundance in the two habitats nearly converge in the last two months of the study. One possible explanation for this trend may be a habitat shift by mobile taxa out of the macrophyte beds.

Mean invertebrate biomass in macrophyte beds showed some similar trends to abundance, as biomass was greatest in the early months and declined throughout the year. Through most of the year invertebrate biomass in macrophyte beds and sand/gravel habitats was dominated by Lumbriculidae, an aquatic oligocheate. The lumbriculids do not live on the plants but are found in the first few centimeters of sediment. The ability for macrophyte beds to trap particulate organic matter (Koetsier & McArthur 2000) may be advantageous to the lumbriculids as they are known to be indiscriminating detritivores and algavores (Alexander *et al.* 2007). In the spring samples I often found more lumbriculids in the plant beds than the sand/gravel samples but later in the year their abundances were similar among the two habitats. In March
and April chironomids, lumbriculids and *Gammarus* were important in terms of biomass in each habitat due to their large early season abundances. In April *Baetis* and *Brachycentrus* both increased in biomass in the plant beds though they did not increase in overall abundance (245 to 233 combined individuals/m²). An increase in combined biomass from 87 to 201 mg/m² suggest that *Baetis* and *Brachycentrus* individuals were growing substantially during this period. By May some of the early emerging insects are important in relative biomass but noninsects (Lumbriculidae, *Gammarus* and *Physa*) are the most dominant taxa and continue so until October.

Mean invertebrate biomass in the sand/gravel patches did not show a clear trend (Fig 6). Biomass was high in March and declined through June. Biomass began to rise again and peaked in July before another decline in the following months. Chironomids contribute substantially to invertebrate biomass in the sand/gravel patches in March, April and May. Chironomids showed high biomass because during these months they were by far the most abundant taxa (Appendix A, Fig A-1). For most of the year lumbriculids and *Gammarus* were a major group because of their large body size. Oddly, *Brachycentrus* comprised 24% and 22% of the total biomass in May and June. It was surprising to see such a large amount of *Brachycentrus*, a known filter feeder, on an unstable substrate like sand. I have also observed *Brachycentrus* on sand/gravel habitat in the thalweg of Emmons Creek, another stream in the Central Sand Plains. Because abundances were low in the sand/gravel habitats biomass was dominated by large bodied taxa throughout most the year.

The ability of macrophyte beds to harbor large abundances and biomass of aquatic invertebrates has major implications for stream management and conservation. The West Branch of the White River is a popular trout stream in central Wisconsin. It is only one of two
streams in the state of Wisconsin containing naturally reproducing populations of brown (*Salmo trutta*), brook (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*, personal communication John Lyons, Wisconsin Department of Natural Resources). This stream, like many others across the Midwestern United States, is a candidate for extensive stream rehabilitation to increase the value of this fishery (personal communication Scott Bunde, Wisconsin Department of Natural Resources). The prevailing method of restoration for many managers is narrowing the stream channel in order to deepen runs and to increase water velocity. Increasing water velocity leads to more scour, eroding away silt and creating more spawning areas (Hunter 1991). This is an effective method for creating more spawning grounds but at the same time this creates a poor environment for macrophyte colonization. As mentioned previously macrophytes are rarely found in water velocities above 1 m/s and discharges above 1 m³/s (Chambers *et al.* 1991, Maltchik & Pedro 2001). Deeper and narrower channels are good for holding trout and creating spawning habitat but they are poor habitat for macrophytes. Based on the results of my study, decreasing habitat for macrophytes could substantially decrease invertebrate abundances and biomass in low gradient streams.

Previous studies have shown a correlation between habitat heterogeneity and diversity for plant species (Kohn & Walsh 1994), stream fishes (Gorman & Karr 1978) and stream invertebrates (Downes *et al.* 1998, Taniguchi, *et al.*, 2003). Current rehabilitation practices for streams may actually damage a healthy invertebrate community by removing high-quality low-quantity habitats, such as macrophytes, and decreasing overall habitat heterogeneity (Hunter 1991, Moukta *et al.* 2002). The ability of macrophytes, as a relatively rare habitat, to contain such high abundances of invertebrates compared to the surrounding substrate confirms the need to consider them in any stream rehabilitation plan where they are known to occur currently or
historically. The conservation of macrophytes and other patchy invertebrate habitats should become a commonly practiced management strategy.

The importance of small isolated habitats, such as macrophyte beds, to invertebrate diversity and productivity is far from a well-understood concept. Much of the work on small isolated habitats in streams is usually conducted on severely degraded stream systems where high quality habitats have already been lost (Larson et al. 2001, Moukta et al. 2002). Much can be learned about the importance of these habitats from studying them in relatively healthy systems. I was able to show that macrophyte beds contributed disproportionally to whole reach invertebrate abundance and biomass. It would be interesting to determine the importance of additional habitats in this system (macrophytes, wood, boulders and silt) to whole reach invertebrate diversity and biomass. The current study was only conducted in one stream and though the trends found here are likely to be seen in similar systems multiple sites are needed to fully understand the importance of macrophytes for macroinvertebrate communities in low-order streams.

The idea of hot spots is generally credited to Myers (1988) as a way to explain the uneven distribution of endemic biodiversity worldwide. This concept has currently been adopted by Conservation International as a way to promote conservation of areas with high endemic species and in danger of habitat loss. This should not be considered the only application of the idea of hot spots. Whether the idea of hot spots can be applied to small-scale approaches is relatively understudied. I have shown that there can be hot spots of invertebrate abundance and biomass on the scale of a 400m stream reach. Undoubtedly there are other hotspots in streams as they commonly contain isolated and patchy habitats. The hot spot approach may lead to
enhancements in our understanding that small areas play in the health and function of stream ecosystems.

Acknowledgements

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Overall mean invertebrate diversity (Shannon-Weiner Diversity Index), abundance (individuals\textsuperscript{m}\textsuperscript{2}) and biomass (mg\textsuperscript{m}\textsuperscript{2}) were significantly greater in the plant beds than in the sand/gravel patches (Paired t-tests $p<0.05$). Mean invertebrate diversity was the most similar between macrophytes and sand\textsuperscript{gravel} habitats. Although the mean values were significantly different because the means were similar it is not good evidence for macrophytes as an invertebrate diversity hot spot.

Overall mean invertebrate abundance and biomass were considerably greater in the macrophyte beds than the sand\textsuperscript{gravel} patches ($p<0.05$). Mean invertebrate abundance was two to four times greater than the sand gravel patches for most of the year. Trends in mean invertebrate biomass were very similar to abundance. Invertebrate biomass was two to three times greater in macrophyte beds for most of the year. The large differences between invertebrate abundance and biomass in the macrophytes and sand\textsuperscript{gravel} patches are a strong indication that macrophyte beds are a hot spot of invertebrate production. This study indicates that macrophytes do not contribute to widely different and diverse invertebrate communities within the system but macrophytes are likely more important for invertebrate abundance and biomass in lotic ecosystems.

Whole Reach Scale

I scaled up the mean invertebrate abundance and biomass conclusions to the whole reach scale to determine the system wide effects of macrophyte beds on invertebrate productivity. I first conducted a substrate survey of a 400 meter stretch of the West Branch of the White River
to determine the percent coverage macrophytes and sand\ gravel habitats. I conducted the survey in midsummer because macrophyte coverage is dynamic and I wanted to capture them at peak growth. Because the habitat survey was conducted in midsummer only the June, July and August invertebrate data was used to scale up. I determined that sand\ gravel was the most dominant habitat covering 59% of the stream bottom while macrophytes only covered 17%.

On the whole reach scale macrophytes and sand\ gravel contribute nearly evenly to invertebrate abundance (7.31E+05 to 6.93E+05 individuals, respectively) and biomass (494 to 505 g, respectively) even though sand\ gravel outnumbers macrophytes as a habitat 3:1 (Table 1). Macrophytes have also been shown to contain high invertebrate abundances compared to other habitats in aquatic systems where they are more abundant (Phillips 2003, Warfe & Barmuta 2006). This study shows that even when macrophyte beds are isolated and sporadic in small streams they may be major contributors to invertebrate biomass and production at the whole stream level.

Temporal Trends

This study was conducted over eight-month (March-October) period to determine the importance of macrophytes on invertebrate diversity and productivity over the course of one growing season. Because both aquatic invertebrate communities and macrophyte growth varies considerably over the time it was important to examine temporal trends. I found that there was a strong but non-significant time effect for invertebrate diversity (Repeated Measures ANOVA p=0.057) and a significant time effect for invertebrate abundance (p=>0.001) and biomass (p=>0.001). The community composition within the plant beds varied monthly but there were some major trends. Mean invertebrate abundance and biomass were greatest early in the season
and declined consistently throughout the year. Invertebrate abundance and biomass were three to five times greater in the first two months of the study (March & April) than the last two (September & October). The most common taxon was Chironomidae, often called midges. Chironomid abundance declined steadily throughout the year but they were always one of the most abundant taxa. The major trend in community composition was an increasing relative abundance on non-insect invertebrates. While most aquatic insects emerge into terrestrial adults, the non-insect are entirely aquatic. The differences in life histories may be the cause for the increase in relative abundance of non-insects.

**Conclusions**

I found that macrophyte beds are an important habitat in stream ecosystems that contribute to the overall abundance and biomass of aquatic invertebrates. Macrophytes may be more important for invertebrate productivity rather than invertebrate diversity in lotic ecosystems. Although the current study was only conducted in one stream, the trends found here are likely to be seen in similar systems but multiple sites are needed to fully understand the importance of macrophytes for macroinvertebrate communities in low-order streams. I studied macrophytes to determine the effect of one habitat on invertebrate communities. As stated before, a positive relationship has been found between habitat complexity and invertebrate diversity and productivity (MacArthur & MacArthur 1961, Benke *et al.*, 1984, O’Conner 2004). I found that the presence of one relatively rare habitat greatly increased invertebrate productivity in this system.

The importance of one habitat for invertebrate productivity in low-order streams has major implications on natural resource management. Since 1977 the WI Department of Natural
Resources has restored over 750 stream miles on 400 different trout streams (www.wnrmag.org 2001). The current method of restoration for many managers is narrowing the stream channel in order to deepen runs and to increase water velocity. Increasing water velocity leads to more scour, eroding away silt and creating more spawning areas for trout (Hunter 1991). This is an effective method for creating spawning grounds but at the same time this creates a poor environment for macrophyte colonization. Current rehabilitation practices for streams may actually damage a healthy invertebrate community by removing high-quality low-quantity habitats, such as macrophytes, and decreasing overall habitat complexity (Hunter 1991, Moukta et al. 2002). Macrophyte bed protection should be considered in any stream rehabilitation plan where they are known to occur currently or historically. Based on the results of my study, decreasing habitat for macrophytes could substantially decrease invertebrate abundances and biomass in low gradient streams.

The nation’s streams are continually affected by human uses. Streams are under threats from straightening, channelization, bank erosion, riparian modification and sedimentation. These lead to a decreased habitat complexity, which substantially decreases the productivity of the stream. If we wish to keep streams in healthy condition for recreation and aesthetics it is important to protect the entire ecosystem. Preserving habitat complexity in healthy streams and restoring it in degraded streams should become a standard conservation principle.
APPENDIX A

Relative Invertebrate Abundance and Biomass
Fig A-1. Relative mean invertebrate abundances in plant beds for 3 chronologically representative months, March, June and September.

Fig A-2. Relative mean invertebrate biomass in plant beds for 3 chronologically representative months, March, June and September.
APPENDIX B

Seasonal Trends in Macrophyte Bed Size and Biomass
Fig B-1. Seasonal trends for plant bed size (A) and plant biomass (B) for all eight beds.
APPENDIX C

Mean Water Velocity at Individual Macrophyte Beds
Fig C-2. Mean water velocity at the upstream edge of each plant bed. Each point is the mean of three sampling dates. Error bars indicate standard deviation.
APPENDIX D

Invertebrate Abundance and Biomass Versus Macrophyte Bed Size
Fig D-1. Bed area vs mean invertebrate abundance (A) and Mean invertebrate biomass (B). There was no correlation between aerial bed size and invertebrate abundance or biomass.
Literature Cited


