ABSTRACT

Title of Document: MACROINVERTEBRATE PREDATORS AND THEIR ROLE IN SHAPING FRESHWATER COMMUNITIES IN CONSTRUCTED WETLANDS

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The recent increase in the number of wetland construction projects has led to numerous studies investigating the response of the macroinvertebrate community in wetlands. Little is known, however, about the factors structuring these communities and how predation may shape community development. Here, I analyze two years of macroinvertebrate community data collected from 9 constructed wetlands at the Jackson Lane Preserve on the Eastern Shore of Maryland. Results suggest that abiotic factors may be less important than previously thought in structuring the macroinvertebrate community, and biotic factors such as predation may be more important. I then investigate the role of two larval dytiscid beetles in structuring the primary consumer community. These predators exert strong pressure on the community and, therefore, I conclude that predation is an important factor shaping freshwater communities in

constructed wetlands. I offer several suggestions for wetland management with the goal of constructing wetlands with high ecological value.

MACROINVERTEBRATE PREDATORS AND THEIR ROLE IN SHAPING FRESHWATER COMMUNITIES IN CONSTRUCTED WETLANDS

By

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Abstract

With the growing number of wetland construction projects, the importance of understanding how animal communities respond to these activities is imperative for informing future construction efforts. Most studies focusing on the response of whole aquatic macroinvertebrate communities find no clear patterns with differing habitat characteristics. Focusing analysis on smaller functional groups may lead to a better interpretation of the factors structuring these communities. I used two years of biomonitoring data collected from 9 constructed wetlands on the Eastern Shore of Maryland to determine which and to what extent abiotic factors structure both the predator and primary consumer macroinvertebrate communities. Both communities were found to be relatively homogenous throughout all of the wetlands, however, the primary consumers showed more of a response to habitat characteristics than the predators. Biotic factors may be more important in structuring both predator and primary consumer communities in constructed wetlands, but more focused studies are needed to determine the extent to which these factors influence community structure.

Introduction

Growing awareness by the public of essential wetland functions such as support of biodiversity, improvement of water quality, and flood control is providing support for their restoration and construction (Brinson and Malvarez 2002, Zedler 2006). Biomonitoring of restoration and construction projects is important because success of wetland management is determined and reflected by the abundance and taxonomic composition or organisms that colonize and establish populations (Rader et al. 2001, Batzer et al. 2005). Information derived from monitoring programs can then be used to identify the most effective strategies and inform future restoration and construction efforts.

Biomonitoring of macroinvertebrates is a popular way to evaluate the success of freshwater restoration projects. Reasons for monitoring macroinvertebrates include their ubiquitous occurrence, high species richness, and compatibility with inexpensive sampling equipment (Bonada et al. 2006). Further, macroinvertebrates play a crucial role in the functioning of wetland ecosystems as food for other organisms, predators of nuisance species, and decomposers of plant and animal material. Knowledge about what taxa are present can serve as an indicator of ecosystem function (Sharitz and Batzer 1999).

With the growing number of wetland construction projects (USEPA 2003), numerous studies have examined how aquatic macroinvertebrate communities respond to differing habitat gradients created by these activities (Spieles and Mitsch 2000, Tangen et al. 2003, Batzer et al. 2004, Balcombe et al. 2005, Villagren-Mella et al. 2006, Kratzer and Batzer 2007, Stewart and Downing 2008). Abiotic habitat characteristics are likely

to exert a strong influence over macroinvertebrate community composition, however, the studies examining this assumption often find no clear relationship between composition and abiotic factors, or find that macroinvertebrates are ubiquitous across wetland complexes, despite large variation in water quality, hydrology, geomorphology, and plant communities (Tangen et al. 2003, Batzer et al. 2004, Kratzer and Batzer 2007). One likely explanation is that no single abiotic factor will affect all macroinvertebrates equally because they are such a diverse group of organisms. A study by McNeely et al. (2008) examined feeding group richness across water quality gradients. They found that primary consumers responded to changing nutrient levels and turbidity in wetlands, but predators showed no response to these same variables. Weak or undetectable effects of nutrient levels or turbidity on macroinvertebrate richness may occur if considering the whole macroinvertebrate community, when in fact these factors are very important in structuring certain groups (McNeely et al. 2008). Therefore, focusing on smaller functional groups of macroinvertebrates may lead to a better interpretation of how abiotic factors structure the community, and thus how macroinvertebrates respond to the differing abiotic factors in constructed wetlands.

Primary consumers and predators are two broad classifications for wetland macroinvertebrates. Primary consumers eat live vascular plants, detritus from dead plants, or algae (Batzer and Wissinger 1996). Abiotic factors such a nutrient levels, dissolved oxygen levels, and pH are likely to affect these basal food resources, which may be reflected by the structure of the primary consumer community (Mizuno et al. 1982, Campeau et al. 1994, Gabor et al. 1994, Batty and Younger 2007). Macroinvertebrate predators rely on other organisms for food, and may be affected by

these abiotic factors, however, few studies have examined relationships among abiotic factors and predators (Wilcox 2001). Alternatively, biotic factors have been suggested as important controls on community composition in wetlands (Zimmer et al. 2000, Tangen et al. 2003), but are rarely considered in studies of macroinvertebrate communities in constructed wetlands.

I examined broad patterns in these two distinct functional groups in constructed freshwater wetlands to determine which and to what extent abiotic habitat characteristics were important in structuring these communities. By doing this, I also determined how biotic factors may or may not be more important in structuring communities. Nine constructed wetlands on the Eastern Shore of Maryland were monitored for physical, chemical, and biological conditions during years 2 and 3 post-construction. Each wetland had unique physical characteristics and water chemistry and, therefore, together they provided a range of habitat conditions for macroinvertebrates. Data collected from biomonitoring were analyzed with the following specific objectives in mind: 1) to determine how taxa richness and density of predator and primary consumer communities vary seasonally (by month) and spatially (by wetland), 2) to determine what abiotic habitat characteristics explain these patterns, 3) to determine if wetland abiotic habitat characteristics or distance between sites explains community similarity for predators and primary consumers, and 4) to compare and contrast patterns in the predator communities with patterns in the primary consumer communities.

Methods

Study Area

The Jackson Lane Restoration Site is located in the Choptank River watershed in Caroline County, Maryland (39°03'11.9''N, 75°44'50.2''W). Aerial photography revealed that prior to conversion to agriculture in the 1970's, this site consisted of several seasonal depressional wetlands. In 2003, The Nature Conservancy, U.S. Fish & Wildlife Service, Maryland Department of the Environment, and the Natural Resource Conservation Service partnered to reconstruct approximately 30 wetland "cells" at this site. Restoration activities began in August 2003 and included plugging drainage ditches and construction of 23 earthen ditch plugs. Coarse woody debris was placed in the wetlands to provide microhabitat and straw was added to deter establishment of cattails, an invasive wetland plant. The overall goal of the restoration was to recreate natural geomorphology and hydrology to provide suitable habitat for wetland plants, animals, and microorganisms.

Sampling Methods

In 2005 and 2006, nine of the constructed wetlands (Figure 1) were sampled in March, April, May, June, July, and August, as long as they were not dry (in 2005, wetlands 10 and 11 were dry in August; in 2006, wetlands 10, 11 and 19 were dry in June, and wetland 10 was dry in August). In each wetland during each sampling month, temperature (°C), pH, and specific conductivity (µS/cm) were measured using a handheld YSI Model 63 Probe (YSI Inc., Yellow Springs, Ohio) and dissolved oxygen (% and mg/L) was measured with a handheld YSI Model 55 Probe.

Water samples were collected in acid washed bottles and returned in a cooler to the lab of Ken Staver at the Wye Research and Education Center. Each sample was filtered through a 0.45 micron filter and analyzed for nitrogen (NH_4-N, NO_3-N, NO_2-N, TN, TDN) and phosphorus (PO_4-P, TP, TDP). Nitrate analysis was performed on a higher pressure liquid chromatograph, and followed EPA Method 300 (USEPA 1979). Phosphorus in water samples was determined colorimetrically using a spectrophotometer following procedures outlined in Parsons et al. (1984). All sample runs included blanks, as well as standards that spanned the range of sample values.

Physical characteristics such as depth at the center of the wetland and habitat types were determined for each wetland during each sampling month. Approximate wetland size was calculated in GIS using GPS boundary data from Towson University, and modified by Dr. Doug Samson (The Nature Conservancy). Hydroperiod was also determined by Dr. Doug Samson, by estimating the percent of sample dates (January 2005 to February 2007) when the wetland water levels were at or above half the maximum level.

Macroinvertebrates were sampled using 20 sweeps of a 500μm D-net in each wetland during each sampling month. The 20 sweeps were allocated by habitat type to obtain a representative sample of the macroinvertebrate community in the entire wetland. The habitat types considered were open water, vegetation, shallow edge, and coarse woody debris. For instance, if a given wetland was approximately 50% open water, 30% coarse woody debris, and 20% shallow edge, 10, 6, and 4 sweeps, respectively, were allocated to each area. A sweep consisted of using the D-net to disturb the bottom for approximately one meter, and then passing back through the disturbed area with the net

to capture dislodged macroinvertebrates. All 20 sweeps were combined in a pan, passed through a 500μm sieve in the field, added to a 3.8 L sample jar and preserved in 80% ethyl alcohol.

Samples were returned to the lab, and washed to remove large debris and vegetation. Each sample was subsampled in a manner that allowed the most effective means of obtaining community data. For wetland bioassessment, the subsampling approach of using fixed counts of ≥ 200 individuals from a composite sample most effectively provides quality macroinvertebrate community data (King and Richardson 2002). A 7 x 7 square gridded tray was constructed (each square was $16cm^2$; Figure 2A) into which an entire sample was dumped and randomly distributed. A single square was selected by using a random number generator in SAS (SAS v.9.1), and the sample debris from that square was removed and place into a sorting tray (Figure 2B). Sample debris was sorted under a microscope, and all macroinvertebrates were removed and counted to reach a total of 300 individuals.

If a total of 300 macroinvertebrates was not reached after sorting the first square, a second randomly selected square was removed and sorted. This process continued until at least 300 macroinvertebrates were removed. In the case where a count of 300 was reached in the middle of sorting a given square, the remainder of that square was sorted to reach a total of > 300 macroinvertebrates. In some instances, the entire sample was sorted and a count of 300 macroinvertebrates could not be reached. Microcrustaceans (Subclass Copepoda, Order Cladocera, and Class Ostracoda) were only counted and removed from the first square, and were not included in the total count of macroinvertebrates because their high numbers would overwhelm macroinvertebrate

data. Microcrustaceans were considered an important part of the primary consumer community however, and were included in the analysis. All macroinvertebrates were identified to the lowest practical taxonomic level (genus in most cases) using local and regional keys. Each taxon was classified as a predator or primary consumer according to the classification in Merritt et al. (2008).

Data Analysis

Variation in taxa richness and density- For each month and each wetland, taxa richness and density of the predator and primary consumer communities were calculated. Taxa richness was calculated as the number of taxa in each sample. Density was calculated by taking the count data for each taxon from the subsampled portion, multiplying to determine the total sample count, and dividing by the total area sampled. The total area sampled was approximately 6.0 m^2 (each of 20 sweeps covered 0.3 m^2 of wetland).

Preliminary analysis was done using two-way ANOVA to test for the effects of month and year and of wetland and year, on predator and primary consumer taxa richness and density. Interactions of year with month and year with wetland were not significant, so data from 2005 and 2006 were combined for analysis. This provided more replicates for each month and each wetland. Wetland 10 was dry in August for both 2005 and 2006, resulting in an incomplete factorial design. Therefore, wetland 10 was not included in the analysis of predator and primary consumer taxa richness and density.

Separate two-way repeated measure ANOVA's were used to test for the effect of month and wetland on taxa richness and density of predators and primary consumers (Proc Mixed SAS v.9.1). Density data were log (n + 1) transformed before analysis to

meet the assumptions of normality and homogeneity of variances. Fisher's Least Significant Difference test (LSD test) was used to compare individual months or wetlands if the interaction term was not significant and the main effects were significant.

Abiotic factors- Linear regression analysis was used to determine the relationships between the measured abiotic habitat characteristics versus taxa richness and density of predators and primary consumers (Proc Reg SAS v.9.1). Habitat characteristics included temperature, pH, dissolved oxygen (mg/L), specific conductivity, TN (total nitrogen), TP (total phosphorus), size, hydroperiod, depth, percent algae, percent coarse woody debris, and percent vegetation. Other measured habitat characteristics were left out of analyses because of strong collinearity between % and mg/L dissolved oxygen, TN and NH_4-N, TN and NO_3-N, TN and NO_2N, TN and TDN, TP and PO_4-P, TP and TDP. A relationship between the abiotic factor and the dependent variable (predator or primary consumer taxa richness or density) was considered significant at $\alpha = 0.05$ and $R^2 \geq 0.25$.

Community similarity-To determine the degree that wetlands were similar in terms of their predator and primary consumer communities, the beta diversity, β_T, between each wetland pair was calculated. Beta diversity measures the amount of taxa turnover, or taxa change along a habitat gradient. A low value for β_T indicates high similarity between sites, and a high value indicates the number of taxa increases rapidly with additional sampling sites along a gradient, or low similarity between sites. Beta diversity was calculated as,

$$\beta_T = [g(H) + l(H)] / 2\overline{\alpha}$$

where g(H) is the number of taxa newly encountered along the habitat gradient, l(H) is the number of taxa lost along the habitat gradient, and $\bar{\alpha}$ is the average sample richness (Wilson and Shmida 1984).

A distance matrix of the β_T values between all wetland pairs was created, and the program PHYLIP was used to cluster cells based on these distance measures using the UPGMA method (Felsenstein 2005). Briefly, this method involves the following procedure. The two most similar wetlands were combined to form a cluster, and then treated as a single "composite" wetland. From among the new group of composite and single wetlands, the pair with the highest similarity was clustered. This process was continued until all wetlands were included. TreeView was used to create the actual cluster diagram, which displayed the results of the UPGMA clustering (Page 2001).

To determine differences in abiotic habitat characteristics between wetland pairs, distance matrices of temperature, pH, dissolved oxygen (mg/L), specific conductivity, TN, TP, size, depth, hydroperiod, percent algae, percent vegetation, and percent coarse woody debris were created by taking the difference between the values for each wetland pair. Distance between each wetland pair was measured using ImageJ software, and these values were also placed into a distance matrix (Rasband 2007). These values provided several habitat gradients for which to test the hypothesis that as wetlands become more different in terms of habitat, or the distance between them becomes greater, taxa turnover (β_T) will increase. Linear regression analysis was used to test this hypothesis for both predators and primary consumers (Proc Reg SAS v.9.1).

Predator versus primary consumer communities- Results from objective 1 were used to compare broad patterns in the primary consumer community with broad patterns

in the predator community. No statistical analysis was done for this objective, rather general conclusions based on observed patterns were made.

Results

Variation in taxa richness and density

Overall, 19,684 macroinvertebrates were sorted and identified in 2005, and 18,862 were sorted and identified in 2006 (Appendix A- Table 1). Representatives of 7 insect orders and 41 insect families were found in the 9 Jackson Lane wetlands sampled. Additionally, freshwater snails (Gastropoda), annelid worms, nematodes, copepods, cladocera, and ostracods made up a portion of the macroinvertebrate community. In total, 124 taxa were considered in the analysis, with 65 predator taxa and 59 primary consumer taxa. A reference collection of these taxa has been created and stored in the Department of Entomology Insect Museum at the University of Maryland.

Predator communities - The interaction between month and wetland, and the main effect of wetland were not significant for predator taxa richness or predator density (Table 2). However, the main effect of month was significant for predator taxa richness and predator density.

Fisher's Least Significant Difference (LSD) test revealed significant differences in numbers of predator taxa between months (Figure 3A), with generally an increase in taxa with time. Samples in July and August had significantly higher numbers of predator taxa than samples in March, April, May, and June, which averaged 41% fewer taxa. March had the lowest number of predator taxa (mean = 5.0), which was significantly lower than May, June, July, and August (mean = 10.6).

The majority of taxa found in March were present throughout the year, and new taxa were added each month (Figure 3B). There was a trend of a greater density of predators as the season progressed from March through August (mean densities (# individuals / m^2): March = 14.8, April = 26.4, May = 54.9, June = 155.3, July = 132.1, and August = 337.4). A LSD test revealed significant differences between months, with August having the highest density, and March the lowest density (Figure 3C).

Primary consumers communities - For the taxa richness and density of the primary consumer community, the interaction between month and wetland was not significant, but the main effects of month and wetland were significant (Table 2). Taxa richness was greatest for July and August, followed by March and June, averaging 14% fewer taxa, and April and May, averaging 25% fewer taxa (Figure 4A). Some of the taxa present in March were present throughout the year, but several new taxa were added (Figure 4B). April, May, and June had significantly higher densities of primary consumers (mean = 2111.5) than March, July, and August (mean = 628.9; Figure 4C).

Wetlands 2, 6 and 17 had 25% more taxa than the wetlands with the fewest number of taxa, 11 and 19 (Figure 4D). The average density of primary consumers in wetlands 7, 15, 17, and 19 (mean = 1997.4) was almost three times the average density found in wetlands 2, 3, 6, and 11 (mean = 728.9; Figure 4E).

Abiotic factors

Habitat characteristics varied across months and across the wetlands at the site (Appendix B- Tables 3A, 3B, 3C). Linear regression analysis of the measured habitat characteristics with taxa richness and density of predators and primary consumers revealed several significant relationships, although the maximum R^2 value was 0.44

(Table 4). There was a weak positive relationship between predator taxa richness and temperature ($R^2 = 0.37$, $p < 0.0001$) and predator density and temperature ($R^2 = 0.44$, $p < 0.0001$; Figure 5A). There was also a weak negative relationship between predator taxa richness and dissolved oxygen ($R^2 = 0.25$, $p < 0.0001$), predator taxa richness and specific conductivity ($R^2 = 0.31$, $p < 0.0001$), and predator density and dissolved oxygen ($R^2 = 0.26$, $p < 0.0001$). Variation in dissolved oxygen and specific conductivity (Figures 5B, 5C) explained 25% and 31% of the variation in predator taxa richness respectively. Dissolved oxygen explained 26% of the variation in predator density.

No abiotic factors explained greater than 25% of the variation in the primary consumer communities (Table 4).

Community similarity

Overall, the average β_T value across wetlands was higher for predator communities than for primary consumer communities (0.29 and 0.25, respectively). For predator communities, values of β_T varied from 0.18 to 0.43 (Table 5). The cluster dendogram (Figure 6A) showed wetlands 10 and 11 clustering together indicating community similarity, but these two clustered the furthest from the other wetlands. Wetlands 2 and 3 clustered, 6 and 7 clustered, and 15 and 17 clustered; this indicates similarity between these pairs. Wetland 19 is similar to wetlands 6, 7, 15, and 17.

Results from the regression analysis of predator beta diversity with habitat gradients showed that only the gradient of vegetation coverage had a weak positive relationship with taxa turnover ($R^2 = 0.14$, $p = 0.02$; Table 6). All other habitat gradients and distance between wetlands had no relationship to predator beta diversity ($p > 0.05$; Table 6).

For the primary consumer community, values of β_T varied from 0.16 to 0.35 (Table 5). The cluster dendogram (Figure 6B) showed wetland 10 being the most dissimilar from all other wetlands. Wetlands 11 and 19 clustered, 2, 6, and 17 clustered, and 3, 7, and 15 clustered.

Regression analysis of primary consumer beta diversity with habitat gradients and distance showed that primary consumer communities were related to gradients of pH ($R^2 = 0.20$, $p = 0.0065$) and specific conductivity ($R^2 = 0.12$, $p = 0.037$), though these regressions were not strong (Table 6). All other habitat gradients and distance between wetlands had no relationship to primary consumer beta diversity ($p > 0.05$; Table 6).

Predator versus primary consumer communities

The most notable pattern found was a peak in density of primary consumers in the months of April, May, and June (Figure 4C), and a subsequent peak in density of predators in June, July, and August (Figures 3C). The second pattern worthy of discussion is a decrease in primary consumer richness from March to April (Figure 4A), and an increase in primary consumer density (Figure 4C).

Discussion

Overall Macroinvertebrate Community - Two years post-construction, aquatic macroinvertebrates colonized all of the constructed wetlands at the Jackson Lane site, suggesting rapid ecological improvement. This is consistent with previous studies that suggest macroinvertebrates are often the earliest colonizers of newly constructed wetlands (Batzer et al. 2005, Stewart and Downing 2008).

Predator Communities – Taxa richness and density of the predator communities varied by month, but not by wetland. Both taxa richness and density increased from March to August, but were not strongly correlated with any of the habitat characteristics. Throughout the Jackson Lane site, a total of 28 predator taxa were found in March, and the majority of these taxa were found in the wetlands throughout the year (Figure 3B). Each month, a few new predator taxa were found which resulted in the observed increase in taxa richness. The pattern of a seasonal increase in taxa richness is common in freshwater systems, and wetlands with a longer hydroperiod tend to have more taxa (Brooks 2000, Williams 1996). In these constructed wetlands, there was no relationship between hydroperiod and taxa richness. This is likely because the wetlands were only sampled from March through August, even though some remained wet for the entire year. Continued sampling of the wetlands with a longer hydroperiod would have likely added more taxa, and thus resulted in more of a relationship between hydroperiod and taxa richness.

The predator taxa present during all months must be able to tolerate a wide range of habitat conditions, considering variables such as water temperature, dissolved oxygen, specific conductivity and depth vary greatly over the year (Figures 5A, 5B, 5C). Though no strong correlations were found, there was a general trend of more taxa later in the year with increasing water temperatures, decreasing levels of dissolved oxygen, decreasing specific conductivity, and decreasing water levels. The new taxa found later in the year may be more adapted for these habitat conditions. For example, many of the later season predator taxa use atmospheric sources of oxygen for respiration, e.g., Dolichopodidae

(Diptera), Hydrophilidae, Dytiscidae, Gyrinidae (Coleoptera), and Nepidae, Naucoridae (Hemiptera) (Merritt et al. 2008).

The increase in density of predators through the season was related to the density of prey, or primary consumers. There was a peak in density of primary consumers in the months of April, May, and June, and a subsequent peak in density of predators in June, July, and August. Predator populations may initially be limited by the numbers of available prey, but as more prey are available in late spring, populations of predators may be able to grow, thus resulting in a greater density of predators. Interactions between aquatic predators and primary consumers, however, are poorly understood in freshwater systems (Batzer and Wissinger 1996, Batzer 1998), and no causal relationship was established in this study. The overall increase in density could be a result of both the increase in the number of taxa, and the ability of the predator populations to grow when food is abundant.

Primary Consumer Communities - Primary consumer taxa richness and density varied both by month and by wetland. The highest taxa richness was found in July and August, similar to the predator community. If primary consumers were sensitive to changes in habitat, the expectation would be that community composition would change completely as the wetlands became warmer, had lower dissolved oxygen, lower specific conductivity and lower water levels. Most of the taxa present in March were present all year, and new taxa were added in the later months, resulting in greater taxa richness. Certain taxa, such as limnephilid and phyrganeid caddisflies complete the aquatic stage of their life cycle early in the season, and these taxa were absent from the wetlands by April. This may have partially caused the decrease in taxa richness from March to May.

No relationships were found between the measured abiotic habitat characteristics and primary consumer taxa richness. The seasonal changes in community composition could have resulted from the addition or removal of taxa with differing life histories or tolerances to wetland conditions in late summer. Primary consumer taxa richness also varied by wetland. Wetlands 2, 6, and 17 had the greatest number of primary consumer taxa for unknown reasons. These wetlands varied in size, depth, and percent vegetation, yet contained similar numbers of primary consumer taxa.

Primary consumer density rapidly increased from March through June. This could have resulted from low numbers of predators present early in the season allowing primary consumer populations to escape. By June however, macroinvertebrate predators increased in numbers, and primary consumers decreased. This pattern in the primary consumer community could be explained by differences in predator density or some other factor not considered in this study.

A second pattern did emerge from the primary consumer data. In March, primary consumer richness was high, but density was low. By April, richness had decreased, but density had increased. This could have resulted from selective predation by early season predators. Selective predation could have eliminated certain prey taxa from the community, while allowing other prey populations to escape predation and increase in density. This would result in decreased taxa richness and an increased density.

Primary consumer density varied by wetland, with wetlands 7, 15, 17 and 19 having the greatest density of primary consumers. These wetlands were generally shallower and more vegetated than the other wetlands, however regression analysis did not show any of these abiotic habitat characteristics to be related with primary consumer

density. Differences in primary consumer density could result from differences in predators in these wetlands, however, no significant differences were found in terms of macroinvertebrate predator communities in these wetlands. One possible explanation for differences in primary consumer density in the Jackson Lane wetlands could be the effect of fish predation on primary consumers. The effect of fish predation on macroinvertebrate communities has been examined and results suggest that fish may or may not preferentially feed on smaller aquatic invertebrates (Gilinsky 1984, Morin 1984). Fish were often present in some of the wetlands, though were difficult to detect during monthly macroinvertebrate sampling.

Similarity - At the Jackson Lane site, nine constructed wetlands provided a range of habitat conditions in terms of temperature, pH, dissolved oxygen, specific conductivity, total nitrogen, total phosphorus, size, depth, hydroperiod, percent algae cover, percent vegetation cover, and percent containing coarse woody debris. I expected to see higher taxa turnover in wetlands that were more different in terms of habitat, or located further apart on the landscape.

The predator cluster dendogram provides insight into which wetlands were more similar in terms of predator communities. Several explanations exist for why certain wetland predator communities were clustered, however, there is no general explanation for the layout of this dendogram. Wetlands 10 and 11 were clustered together and considered similar, or to have low taxa turnover. This meant that wetlands 10 and 11 shared many taxa, and there were few taxa found in 10 that were not in 11 (and vice versa). These two wetlands were unique in that they generally had the shortest hydroperiod, and dried down before the other wetlands. The predators found in wetlands

10 and 11 may have been taxa that were able to complete their life cycle before dry down, though more focused analysis of the communities is needed to determine if this is true. The location of these wetlands at almost opposite ends of the landscape (Figure 1) suggests that distance was not important for the similarity of these predator communities. High similarity between wetlands 2 and 3 was likely due to the fact that they were in close proximity and connected during high water levels. Wetlands 6 and 7 clustered but there were no clear reasons why their communities were similar. Wetlands 6 and 7 were not located close to one another on the landscape, and the abiotic habitat characteristics between the two were extremely variable. Wetland 6 was deep with very little vegetation, while wetland 7 was shallow, with almost 100% vegetation coverage. Wetlands 15 and 17 were clustered as well. These wetlands were in relatively close proximity, though did not connect, and did not share any common habitat characteristics. Wetland 15 had lower dissolved oxygen and specific conductivity and was much deeper than wetland 17. Finally, wetland 19 was equally similar to wetlands 6, 7, 15, and 17. The clustering of these wetlands in terms of their predator communities suggests that predators are not regulated by abiotic habitat characteristics.

The clustering of primary consumers was quite different from the predators, but again, the abiotic habitat characteristics did not explain the layout of the dendogram. Wetland 10 had the shortest and most unpredictable hydroperiod, which may have caused the community in wetland 10 to be the most dissimilar from the other wetlands. Distance also did not explain the clustering in the primary consumer dendogram.

The results of the regression analyses supported the interpretation of both the predator and primary consumer dendograms. Regression of predator beta diversity with

the habitat gradients of distance from one another, temperature, pH, dissolved oxygen, specific conductivity, total nitrogen, total phosphorus, size, depth, hydroperiod, percent algae cover, percent vegetation cover, and percent containing coarse woody debris revealed that taxa turnover was not strongly related to any of these habitat features. There was a weak relationship with percent vegetation cover, but overall the predator community was remarkably similar in all of the wetlands. At such a small scale, predator distributions may be less regulated by abiotic habitat characteristics and more regulated by biotic factors. Many wetland predator taxa are highly mobile as adults, especially Odonates and Coleoptera, and, therefore, have the ability to disperse and readily colonize new habitats. Dispersal to a "preferred" wetland in terms of abiotic habitat characteristics may not necessarily lead to successful colonization, if the density of predators in the preferred wetland is already high. Competition for prey and antagonistic interactions between predators are common in freshwater wetlands (Van Buskirk 1989, Batzer and Wissinger 1996), and may be more important in structuring the community than specific habitat requirements. This could explain the overall similarity of the predator community at the Jackson Lane Preserve. This is also supported by the fact that densities of predators do not differ significantly among wetlands, which suggest that there may be some maximum carrying capacity in wetlands for predator populations.

The lack of mobility for some primary consumer taxa might cause taxa turnover to be greater than predators, and might lead to a relationship between beta diversity and differences in wetland habitat. However, the overall primary consumer community was similar, and regression of primary consumer beta diversity with the habitat gradients revealed that taxa turnover was not strongly related to any of the habitat features or to

distance between wetlands. There were weak positive correlations between pH and specific conductivity with beta diversity, meaning as pH or specific conductivity became more different between wetlands, so did the primary consumer community. The distribution of primary consumers was more regulated by habitat characteristics than the predator communities, but abiotic habitat characteristics were a weak predictor overall. Biotic factors such as predation may be important for how the primary consumer communities are structured.

Summary - The predator communities in the wetlands at the Jackson Lane Preserve varied seasonally, but were generally similar among all of the wetlands. There were no abiotic habitat characteristics that related strongly to the predator communities, suggesting that predators may have been regulated less by habitat characteristics and more by biotic interactions within wetlands. Predator communities were found to be more similar in wetlands with similar amounts of vegetation cover, so this habitat characteristic could be important for predators. A more quantitative analysis of how vegetation structure relates to predator communities could provide useful information for management of constructed wetlands. The primary consumer community varied seasonally and spatially, but was not strongly related to habitat characteristics. However, there was a general trend that primary consumer communities were more similar in wetlands exhibiting similar habitat characteristics, although no significant patterns emerged. Patterns in the richness and density of predators and primary consumers suggested biotic interactions affected community structure, though no causal relationship was identified in this study.

Overall, the lack of a relationship between abiotic factors and the predator and primary consumer community could be due to the scale at which this study was performed. These wetlands are situated on approximately 80 ha, so their close proximity, occasional connectivity, and relatively high similarity in terms of habitat could explain the lack of significant relationships. More focused studies are needed to address how predator and primary consumer communities are structured in freshwater wetlands, and experimental manipulations of communities could help establish the causal relationships lacking from this study. An improved understanding of macroinvertebrate community structure and the effects of abiotic and biotic factors can contribute to management strategies aimed at enhancing wetland function (Stewart and Downing 2008).

Table 2 Analysis of variance table for taxa richness and density of predators and primary consumers.

	Predator					
	Taxa Richness			Density		
Effect	df	*F*	*p*	df	*F*	*p*
Wetland	7, 40	1.1	0.38	7, 40	1.25	0.3
Month	5, 40	13.28	<0.0001	5, 40	18.1	<0.0001
Wetland X Month	35, 40	0.78	0.77	35, 40	0.55	0.96
	Primary Consumer					
	Taxa Richness			Density		
Effect	df	*F*	*p*	df	*F*	*p*
Wetland	7, 40	2.56	0.028	7, 40	2.51	0.019
Month	5, 40	3.7	0.0076	5, 40	9.29	0.0003
Wetland X Month	35, 40	0.4	0.99	35, 40	0.38	0.99

Table 4 Results from regression analysis of measured habitat characteristics with predator and primary consumer taxa richness and density. Temp is in °C. DO is dissolved oxygen in mg/L. SpC is specific conductivity in µS/cm. TN is total nitrogen in parts per million. TP is total phosphorus in parts per million. Size is approximate wetland acreage. Hydro is hydroperiod. % Alg is percent of wetland covered by algae. % CWD is percent of wetland containing coarse woody debris. % Veg is percent of wetland containing vegetation.

	Predator			
	Taxa Richness		Density	
Effect	R^2	*p*	R^2	*p*
Temp	0.37	<0.0001	0.44	<0.0001
pH	0.067	0.015	0.028	0.12
DO	0.25	<0.0001	0.26	<0.0001
SpC	0.31	<0.0001	0.092	0.004
TN	0.0009	0.78	0.066	0.016
TP	0.03	0.11	0.071	0.012
Size	0.0025	0.64	0.0003	0.88
Hydro	0.0057	0.49	0.0068	0.45
Depth	0.072	0.012	0.13	0.0005
% Alg	0.0073	0.43	0.0028	0.62
% CWD	0.026	0.14	0.011	0.34
% Veg	0.049	0.039	0.039	0.066

	Primary Consumer			
	Taxa Richness		Density	
Effect	R^2	*p*	R^2	*p*
Temp	0.081	0.0071	0	0.96
pH	0.051	0.034	0.0038	0.57
DO	0.018	0.22	0.0072	0.43
SpC	0.0072	0.43	0.0025	0.65
TN	0.0022	0.66	0.031	0.099
TP	0.0025	0.65	0.0062	0.47
Size	0.0043	0.54	0.014	0.28
Hydro	0.041	0.059	0.0009	0.78
Depth	0.0015	0.72	0.0051	0.51
% Alg	0.021	0.18	0.09	0.0044
% CWD	0	1	0.027	0.12
% Veg	0.0084	0.4	0.023	0.16

Table 5 Values of β_T for predator and primary consumer communities for each wetland pair. Top half of matrix contains values for primary consumer communities, and bottom half contains values for predator communities.

β Predator \ β Primary Consumer	2	3	6	7	10	11	15	17	19
2		0.23	0.23	0.23	0.35	0.29	0.29	0.17	0.29
3	0.21		0.23	0.16	0.26	0.33	0.17	0.18	0.20
6	0.22	0.24		0.28	0.26	0.29	0.24	0.21	0.29
7	0.31	0.27	0.23		0.26	0.33	0.21	0.22	0.29
10	0.40	0.41	0.35	0.32		0.32	0.23	0.32	0.27
11	0.43	0.38	0.39	0.35	0.21		0.26	0.31	0.21
15	0.35	0.30	0.26	0.24	0.25	0.21		0.27	0.21
17	0.29	0.27	0.23	0.26	0.27	0.31	0.18		0.22
19	0.39	0.27	0.34	0.26	0.33	0.26	0.21	0.29	

Table 6 Regression results of β_T for predators and primary consumers. Distance is in meters. Temp is in °C. DO is dissolved oxygen in mg/L. SpC is specific conductivity in µS/cm. TN is total nitrogen in parts per million. TP is total phosphorus in parts per million. Size is approximate wetland acreage. Hydro is hydroperiod. % Alg is percent of wetland covered by algae. % CWD is percent of wetland containing coarse woody debris. % Veg is percent of wetland containing vegetation.

	β			
	Predator		Primary Consumer	
Effect	R^2	*p*	R^2	*p*
Distance	0.0002	0.94	0.012	*0.53*
Temp	0.0005	0.9	0.0029	0.75
pH	0.054	0.18	0.2	0.0065
DO	0.0005	0.9	0.014	0.5
SpC	0.042	0.23	0.12	0.037
TN	0.0047	0.69	0.027	0.34
TP	0.0028	0.76	0.037	0.26
Size	0.049	0.2	0.035	0.28
Hydro	0.029	0.32	0.0085	0.59
Depth	0.061	0.15	0.0086	0.59
% Alg	0.025	0.36	0.062	0.14
% CWD	0.001	0.86	0.043	0.23
% Veg	0.14	0.023	0.023	0.38

Figure 1 Map of Jackson Lane Preserve, Caroline County, Maryland. Arrows point to the location of the nine wetlands sampled in this study.

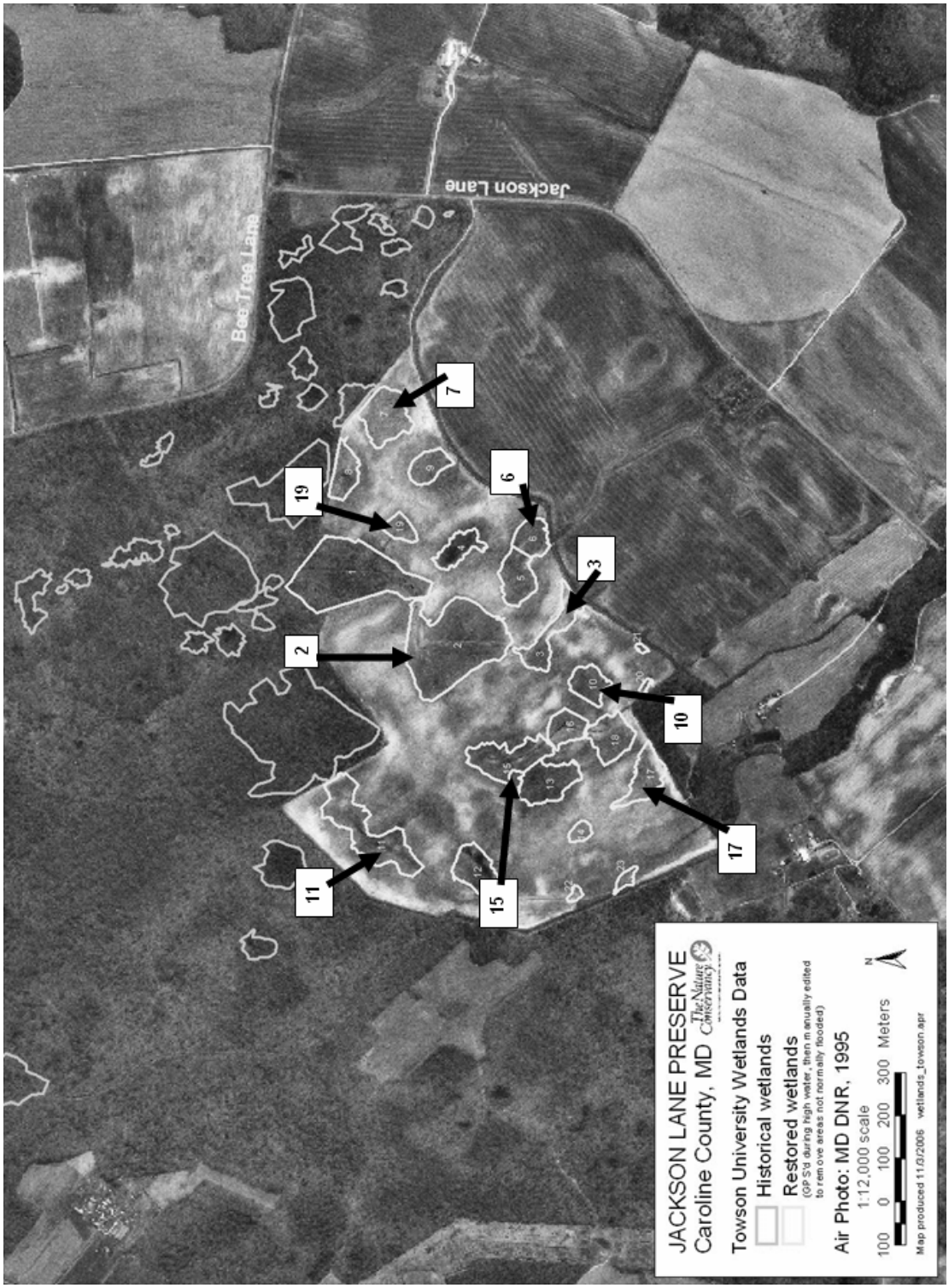
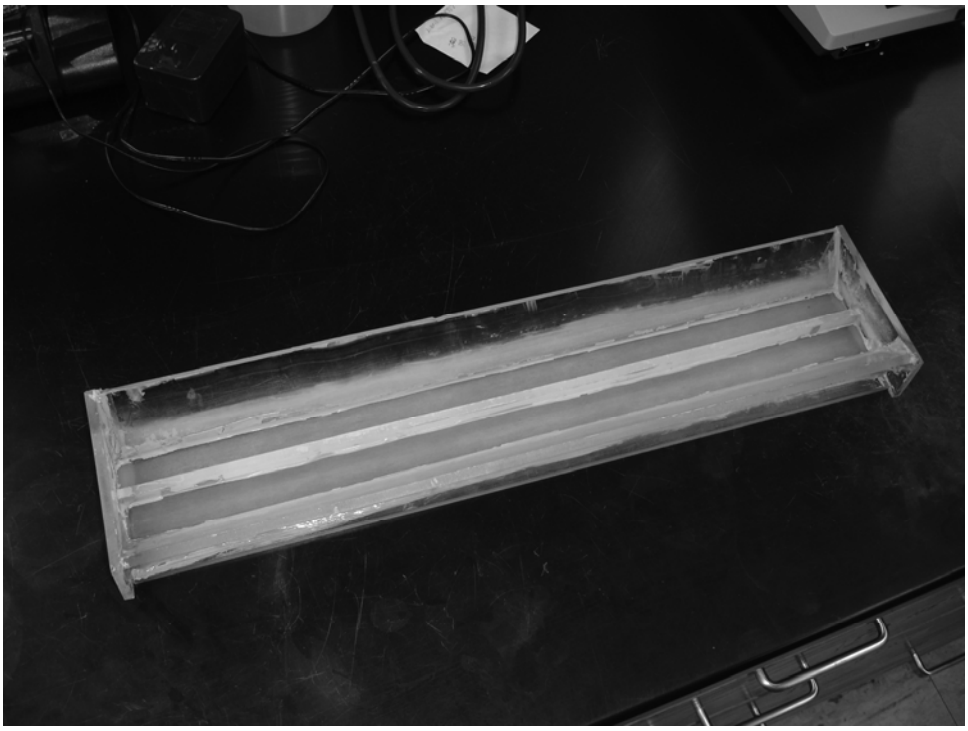


Figure 2 Illustrations of sample processing apparatuses: (**A**) Gridded tray used for subsampling, and (**B**) tray used for sorting.



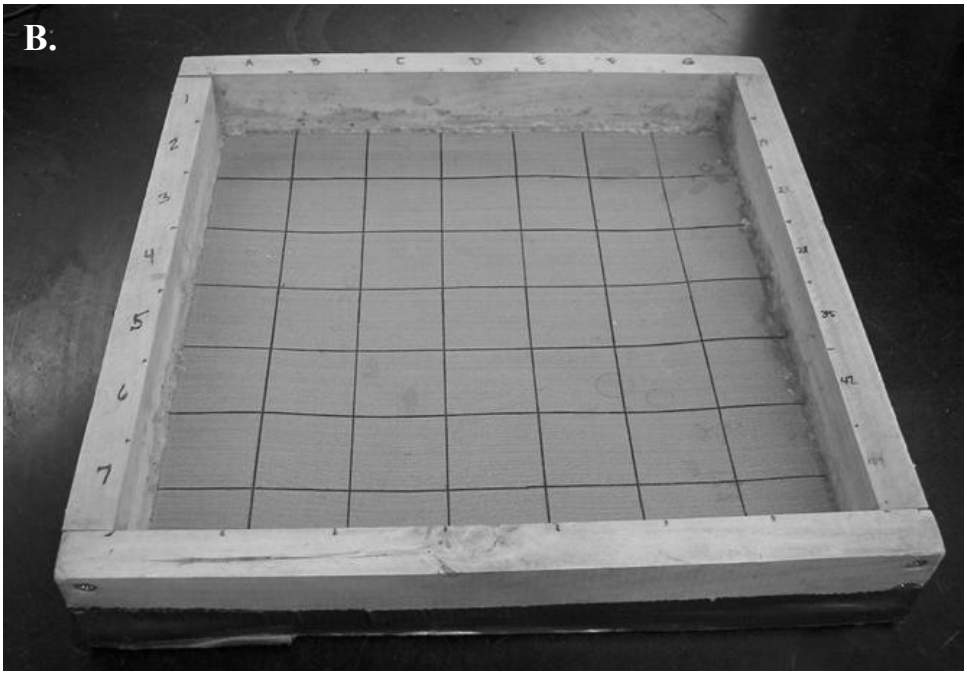


Figure 3 Predator community comparisons in relation to sample month: (**A**) Average number of predator taxa per month, (**B**) composition of predator taxa in relation to sampled month, and (**C**) density of predators per month. Bars in A and C represent means +/- SE. Comparisons with different letters indicate significant LSD differences at α=0.05.

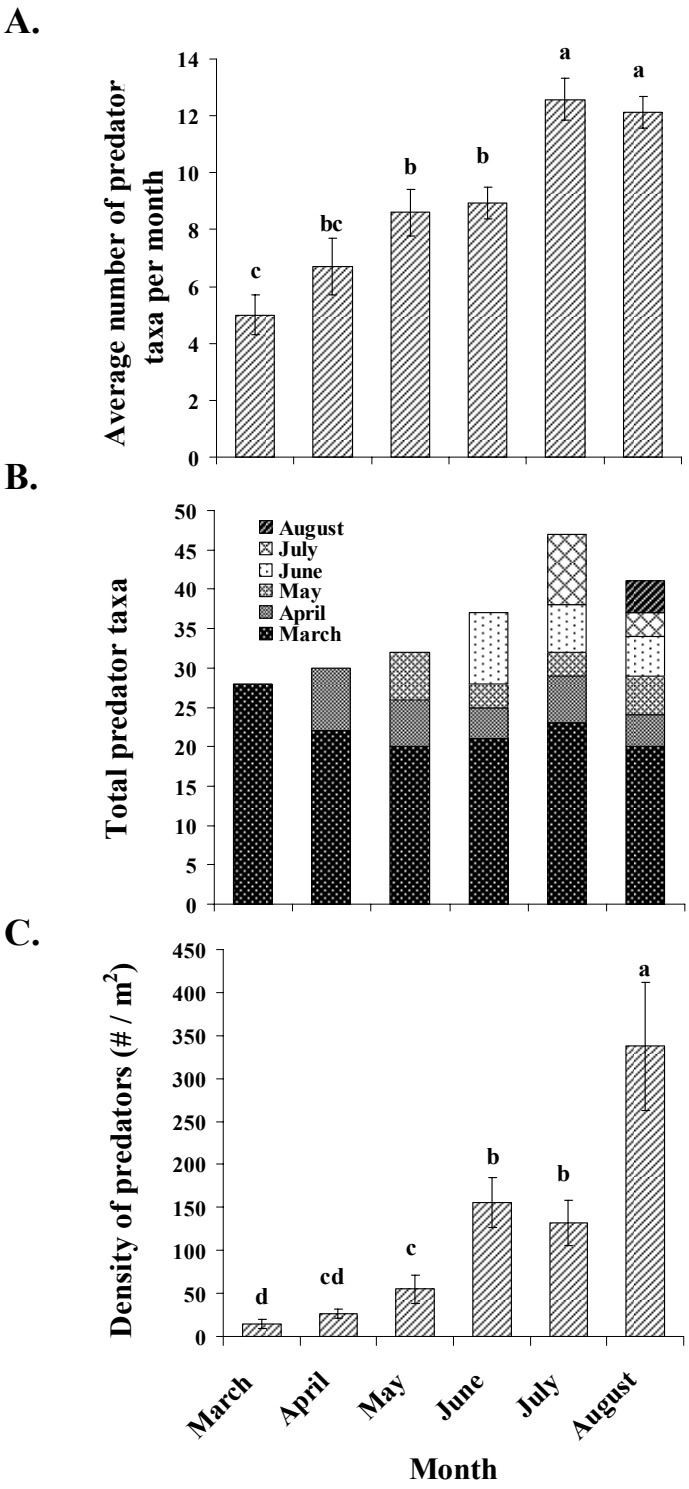


Figure 4 Primary consumer comparisons in relation to sample month or wetland: (**A**) Average number of primary consumer taxa per month, (**B**) composition of primary consumer taxa in relation to sampled month, (**C**) density of primary consumers per month, (**D**) average number of primary consumer taxa per wetland, and (**E**) density of primary consumers per wetland. Bars in A, C, D, and E represent means +/- SE. Comparisons with different letters indicate significant LSD differences at α=0.05.

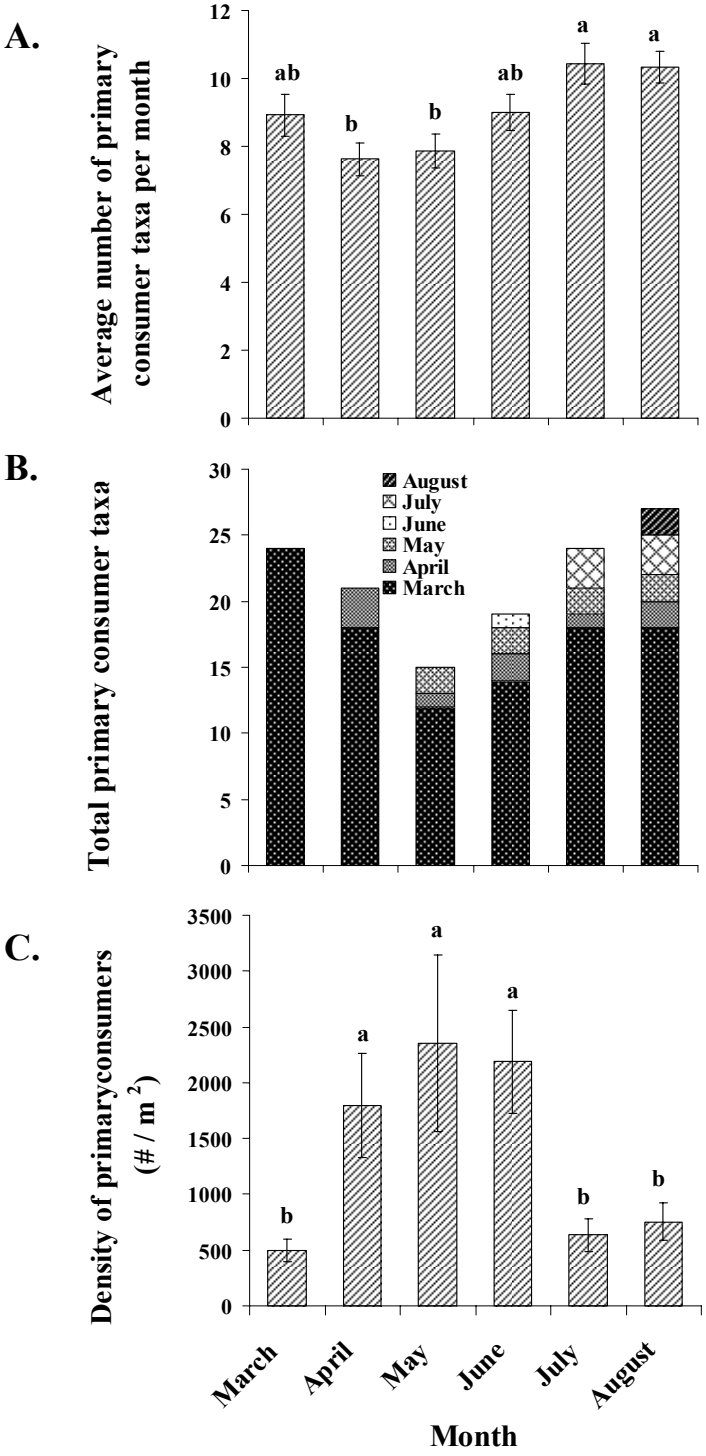


Figure 4 (Continued)

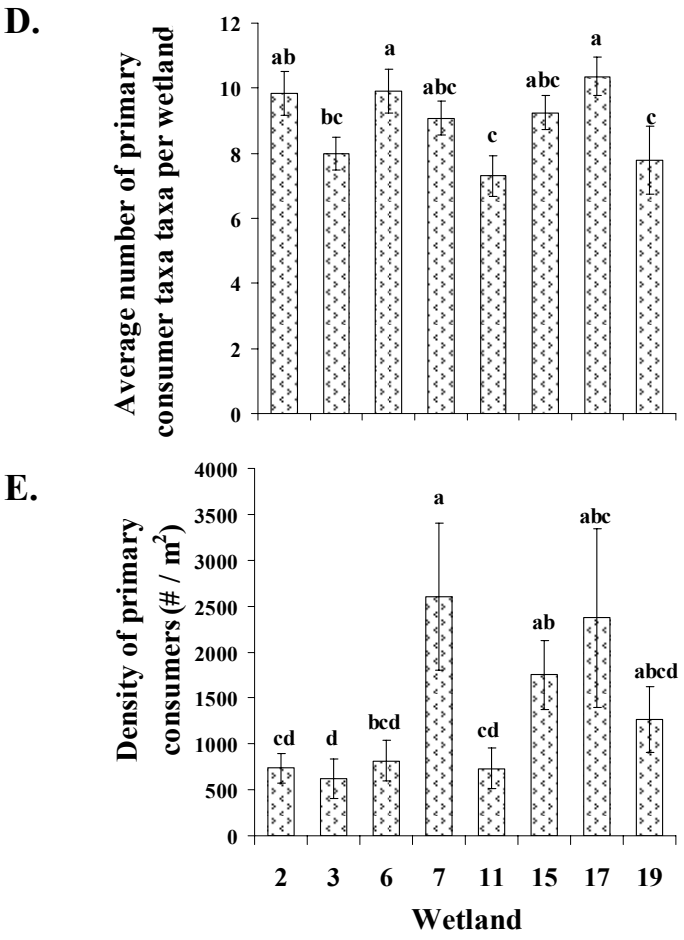


Figure 5 Variation in: (**A**) temperature (°C), (**B**) dissolved oxygen (mg/L), and (**C**) specific conductivity (µS/cm) during sampling in 2005 and 2006. Each line is an individual wetland in 2005 or 2006.

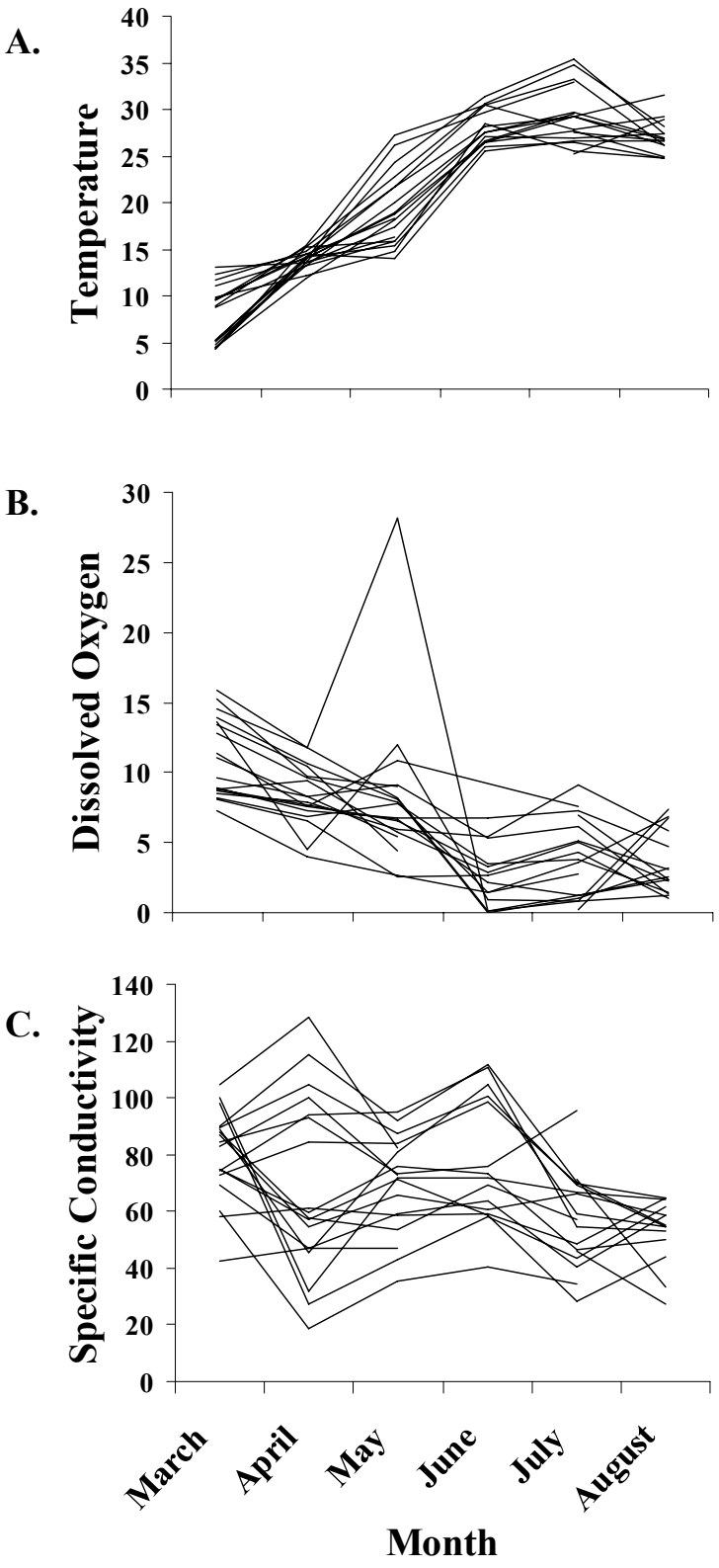
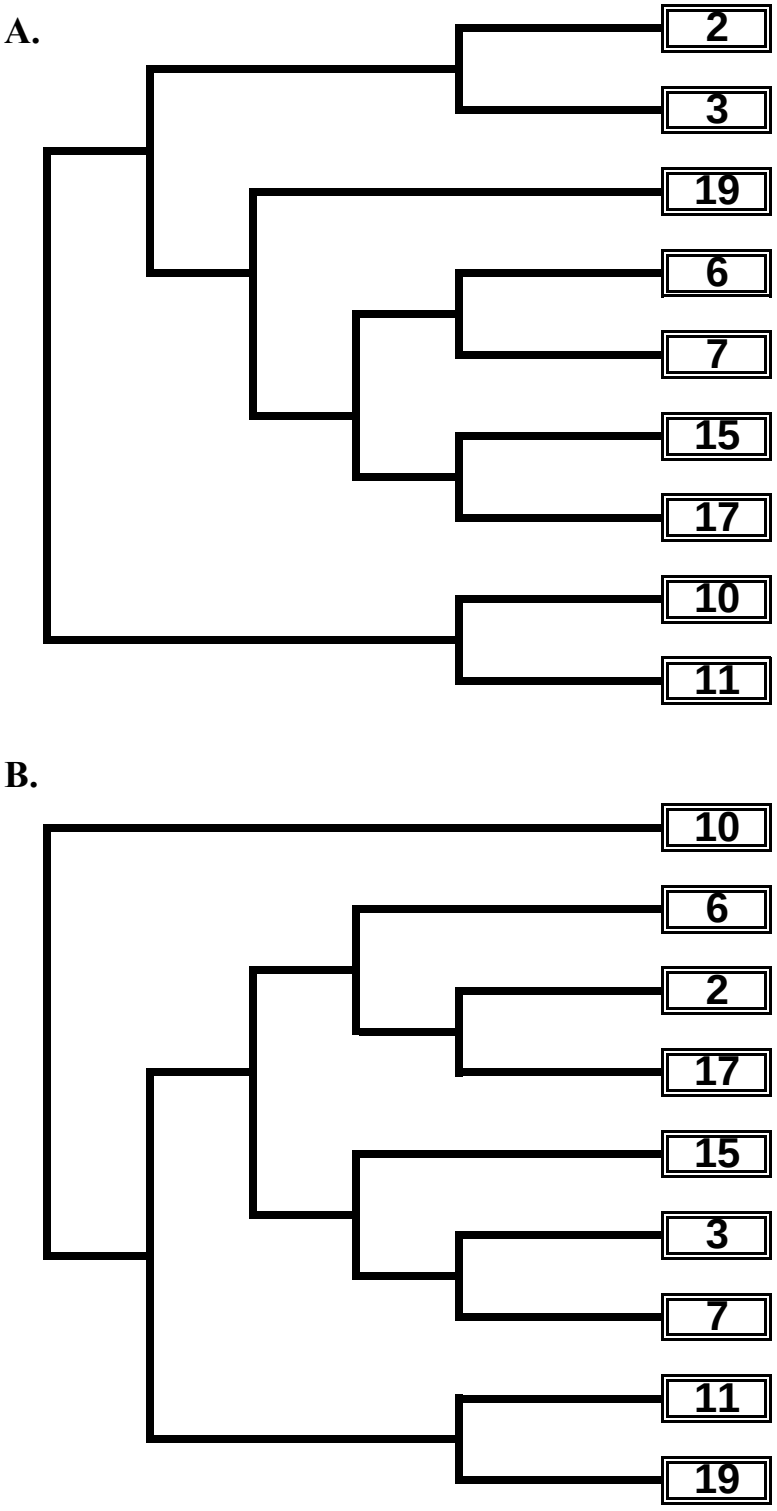


Figure 6 Cluster dendograms of: (**A**) predator communities, (**B**) primary consumer communities.



Chapter 2: Predation by larval *Agabus* (Coleoptera: Dytiscidae) on primary consumers in constructed freshwater wetlands

Abstract

As temporary freshwater wetlands become inundated, the macroinvertebrate community develops under strong predation pressure from the first predators to arrive. These predators can have an important impact on the abundance and structure of the primary consumer community by the direct effect of prey consumption, particularly if they select one type of prey over another. Larval dytiscid beetles (Coleoptera: Dytiscidae) are effective predators in temporary waters and are some of the first predators to arrive in recently inundated wetlands. I determined the potential impact of two species of these beetles, *Agabus punctatus* and *Agabus disintegratus*, on the primary consumer communities in constructed wetlands on the Eastern Shore of Maryland and used laboratory experiments to examine: (1) their ability to consume three different prey populations (copepods, ostracods, and mosquito larvae), (2) if prey selection occurs, (3) beetle performance on different prey types, (4) behavioral components of the predator-prey interaction, and (5) the potential for antagonistic interactions between predators. Results indicate that dytiscid beetle larvae do exert a strong predation force on the primary consumer community, and that when given a choice, mosquito larvae were selected over microcrustaceans. Performance and behavioral components may be the reason for this selection, because beetle larvae grew larger and were better at capturing mosquito larvae. Populations of beetles may be supported initially by high abundances of

microcrustaceans, but later switch to the preferred prey, mosquito larvae. This could be important in the suppression of mosquito populations in constructed wetlands, so future construction efforts should consider techniques aimed at attracting and maintaining a diverse predator complex.

Introduction

In temporary wetlands, the early season macroinvertebrate community consists of taxa with desiccation resistance (Wiggins et al. 1980, Wissinger and Gallagher 1999, Dietz-Brantley et al. 2002, Batzer et al. 2005) or those that are able to reach wetlands as soon as they become inundated, such as mosquitoes, midges, dragonflies, and beetles (Streever et al. 1996, Brown et al. 1997, Mitsch et al. 1998, Wrubleski 1999, Keiper and Walton 2000). These animals are influenced trophically from below, but the top-down force of predation is considered to be the most important force in shaping wetland aquatic animal communities (Batzer and Sharitz 2006). In temporary wetlands where fish are absent, the first invertebrate predators to arrive could have a significant impact on the primary consumer community due to direct effects of prey consumption, particularly if they select one prey type over another.

In the wetlands at the Jackson Lane Preserve (Caroline County, MD), one of the first predators found at the end of winter are larval predaceous diving beetles (Coleoptera: Dytiscidae; Appendix A- Table 1). These beetles are the only invertebrate predators likely to have evolved to take advantage of the abundant prey available early in the spring (Higgins and Merritt 1999). Larvae of dytiscid beetles are also considered to be very effective predators in temporary waters (Larson et al. 2000), and could impact the overall community if they exhibit selective feeding. As these beetles hatch available prey

include microcrustaceans (e.g. ostracods, cladocerans, and copepods), and diptera larvae (e.g. culicids, chironomids), all of which have been suggested as prey for dytiscids in previous studies (James 1969, Friis 2003). Efficient exploitation of available food resources by selection of prey is critical for the success of these larvae because they must complete development before the habitat dries or other larger predators arrive (Emlen 1966). Selection of prey could be driven by factors such as appropriate size ranges and availability, profitability, and ease of capture (Dicke et al. 1989).

Determining if and why prey selection occurs could provide insight into how these predators impact the primary consumer community. This impact may be diminished if antagonistic interactions between the predatory larvae are common. Intraguild predation and cannibalism are common among predaceous aquatic invertebrates (Wissinger and McGrady 1993, Fincke 1994, Wissinger et al. 1996, Ilmonen and Suhonen 2006), have been observed in dytiscid beetle larvae (L. Culler, personal observation), and may also explain the overall patterns of macroinvertebrate community development in wetlands.

The goal of this study was to determine the potential impact of larval dytiscid beetles on the primary consumer community in constructed wetlands. I used larvae of the two beetle predators present in March, *Agabus punctatus* Melsheimer and *Agabus disintegratus* Crotch (Coleoptera: Dytiscidae) (Figures 7A, 7B) and three prey taxa, ostacods (Podocopida: Notodromadidae), copepods (Cyclopoida: Cyclopidae), and mosquito larvae (*Aedes albopictus*; Diptera: Culicidae). A series of laboratory experiments were conducted to address: 1) the ability of *A. punctatus* and *A. disintegratus* to consume the three different prey types, 2) prey selection by these predators, 3) the

performance of *A. disintegratus* larvae when fed exclusively on one prey type, 4) the behavioral interactions between *A. punctatus* and its prey, and 5) the frequency of cannibalism and intraguild predation within and between these species.

I predicted that larvae of both *A. punctatus* and *A. disintegratus* would be able to consume all three prey but that larvae would exhibit prey selection due to availability, profitability, or ease of capture. Since both *A. punctatus* and *A. disintegratus* are found in similar abundance at the same time of year, I hypothesized that levels of cannibalism within species and intraguild predation between species would not differ. Further, I predicted symmetric intraguild predation since larvae of both species are found in similar size ranges.

Methods

General Set-up

Beetle larvae were collected in the field from the Jackson Lane Preserve in March and April, 2008, and returned to the lab at least two days before the start of the experiments. Each larva was placed in a 300 mL plastic cup containing water from the collection site and a variety of prey items so that feeding prior to the start of the experiment would not influence the results. Beetle larvae were kept in a walk-in environmental chamber set to a temperature of 13°C, with alternating 10 hours of light and 14 hours of dark. At least 24 hours prior to the start of each experiment, all beetle larvae were removed from the cups and held in 16 X 100 mm glass culture tubes without prey in order to standardize hunger levels.

Prey types used were ostracods, copepods, and mosquito larvae. All three make up a portion of the primary consumer community in the wetlands where the beetles are

found. Ostracods (Notodromadidae) and copepods (Cyclopidae) were collected in the field, and mosquito larvae (*A. albopictus*) were obtained from a colony at the Insect Transformation Facility, University of Maryland Biotechnology Institute in Rockville, Maryland.

Experimental microcosms for all experiments were prepared by adding 175 mL of filtered wetland water (13°C, pH = 5.6) and a 7 cm plastic aquarium plant (Tetra®-WaterWonders™ Decorative Plants) to a 300 mL plastic cup. Prey were added to the cups and allowed to settle before the predators were introduced. Predators were introduced after a 24 hour starvation period.

Experiment 1 - Prey consumption

The prey consumption of *A. punctatus* and *A. disintegratus* individually and in different predator combinations was assessed in the lab. The experiment was a randomized complete block (6 x 3 factorial) with predator combination (no larvae as control, one *A. punctatus* larva, one *A. disintegratus* larva, two *A. punctatus* larvae, two *A. disintegratus* larvae, or one of each *A. punctatus* and *A. disintegratus*) and prey type (ostracods, copepods, or mosquito larvae) as the factors. Prey densities were 20 in the single predator treatments, and 40 in the double predator treatments. Prey were not replaced. Each treatment combination was replicated four times, and each replicate was blocked by location in the walk-in chamber.

Predators were allowed to interact with the prey for 24 hours, at which point predators were removed and the number of prey consumed was counted. Dytiscid larvae are piercing-sucking predators with falcate mandibles and leave behind partially digested prey items that are easy to count. A two-way ANOVA (Proc Mixed SAS v.9.1) was

conducted to test for effects of prey type and predator combination on the instantaneous prey mortality rate (m) calculated as:

$$m = (\ln N_o - \ln N_f)/t,$$

where N_f represents the final density of prey (adjusted for the number of prey lost due to natural mortality in the controls, and divided by two in the double predator treatments to estimate number of prey taken per predator), N_o represents the initial prey density (20 individuals), and t is the duration in days of the experiment (Dodson 1975, Peckarsky 2006). The units of the parameter m are prey mortality per prey per predator per day, hereafter termed mortality rate (Peckarsky 2006).

Experiment 2 - Prey selection

Feeding trials were set up to compare the consumption of mosquito larvae and microcrustaceans in the presence or absence of alternative prey, to determine which prey larval *A. punctatus* and *A. disintegratus* prefer. The treatments consisted of prey ratios (mosquito larvae: microcrustaceans) of 30:0, 20:10, 10:20, or 0:30. The microcrustaceans consisted of equal numbers of copepods and ostracods. Each beetle species was tested individually and each experiment was replicated 5 times. After 24 hours, predators were removed and the numbers of prey consumed were counted.

Beetle larvae were expected to consume prey in the proportions that were offered if no selection was occurring. For example, in the treatment with 30 mosquito larvae and 0 microcrustaceans, the expected proportion of mosquito larvae consumed was 1. In the treatment with 20 mosquito larvae and 10 microcrustaceans, the expected proportion of mosquito larvae consumed was 0.67. A chi-square analysis was used to test for differences between expected proportions (P_e) and the observed results (P_o) (Proc Freq

SAS v.9.1). Selection was considered to have occurred if the observed numbers of each type of prey consumed differed significantly from the expected proportions.

Experiment 3 - Performance of *A. disintegratus*

The performance of *A. disintegratus* when fed on different prey types was assessed by feeding larvae one type of prey (ostracods, copepods, or mosquito larvae) for 9 days and measuring growth. Initial size of individuals was obtained by photographing each beetle and measuring abdomen length using ImageJ software (Rasband 2007). At the start of the experiment (day 0), each cup was stocked with 40 prey items. At day 3 and day 6, prey were restocked to the original density of 40 prey items, and the number of prey consumed was recorded. A final photograph of each beetle was taken at day 9 to obtain a final measurement of abdomen size, and each beetle was dried and weighed on a microbalance. Each prey type treatment was replicated 5 times. A one-way ANOVA was used to test that initial sizes were equal across treatments (Proc Mixed SAS v.9.1). ANCOVA was used to test for the effect of prey type on the final size of the beetle larvae, with initial size as a covariate (Proc Mixed SAS v.9.1). There was no relationship between final beetle size and total number of prey consumed, so the total number of prey consumed was left out of the analysis. Dry weight and length were strongly related ($R^2 = 0.78$, $p < 0.0001$). I used length as the measurement of final size.

Experiment 4 - Prey capture

Behavioral trials were used to determine which components of the predator-prey interaction may be responsible for the observed patterns of selection (Peckarsky 2006). For each trial, I placed 20 prey items and one predator (*A. punctatus*) in a Petri dish and

observed predation events for 10 minutes. Additional lab personnel helped with the observations. Number of encounters (times a predator encountered prey), number of attacks (times a predator attempted or successfully grasped prey), and number of captures (times a predator successfully captured and consumed prey), were tallied for each predator. Eight trials were run for each prey type, and a new larva was used for each trial. Number of encounters, attacks per encounter, and captures per attack were compared among prey types using one-way ANOVA's (Proc Mixed SAS v. 9.1). Encounter data were log transformed and capture data were log (n+1) transformed prior to analysis to meet the assumptions of normality and homogeneity of variances.

Experiment 5 - Predator interactions

A randomized complete design with three predator levels (two *A. punctatus* larva, two *A. disintegratus* larva, or one of each *A. punctatus* and *A. disintegratus*) was used to measure cannibalism within *A. punctatus* and *A. disintegratus* and intraguild predation (IGP) between these species. Each predator level was replicated eighteen times.

A random assortment of prey was added to each cup. Predators were introduced, and every 24 hours, any occurrence of cannibalism or IGP was recorded. The hypothesis that frequency of cannibalism and IGP did not differ was tested using a chi-squared test at two time periods, day 5 and day 18 (Proc Freq SAS v.9.1). A second chi-squared test was performed to determine if IGP was symmetric (each species exhibited IGP on the other species equally) at these same time periods (Proc Freq SAS v.9.1). Prey were not measured or replaced in this experiment.

Results

Experiment 1 - Prey consumption

A two-way ANOVA showed a non-significant interaction between prey type and predator combination (df = 8, 42; $F = 1.27$; $p = 0.29$), but the main effects of prey type (df = 2, 42; $F = 40.63$; $p < 0.0001$) and predator combination (df = 4, 42; $F = 2.85$; $p = 0.036$) were significant. Mortality rate for mosquito larvae (mean = 1.21) was almost twice the mortality rate for copepods (mean = 0.66), and over four times the mortality rate for ostracods (mean = 0.28; Figure 8A). There were significant differences in mortality rate due to predator type and number, with a trend of lower mortality rate in the double predator treatments (Figure 8B). The combination of one of each *A. disintegratus* and *A. punctatus* resulted in the lowest prey mortality rate (mean = 0.52), and this was significantly different from both of the single predator treatments (mean = 0.85, mean = 0.89 for *A. disintegratus* and *A. punctatus,* respectively).

Experiment 2 - Prey selection

When beetle larvae were offered combinations of prey, the observed numbers of mosquito larvae consumed (P_o) were higher than the expected proportions (P_e) in all treatments (Figure 9). These differences were significant in three out of four treatments. When offered 10 mosquito larvae (33%) and 20 microcrustaceans (66%), the proportions of prey taken that were mosquito larvae were 68% for *A. disintegratus* and 66% for *A. punctatus*. A chi-square test revealed significant differences ($\chi^2 = 30.0$, $p < 0.0001$; and $\chi^2 = 27.0$, $p < 0.0001$ respectively). When offered 20 mosquito larvae (66%) and 10 microcrustaceans (33%), the proportions of prey taken that were mosquito larvae were

91% for *A. disintegratus* and 79% for *A. punctatus*. While both of these proportions are higher than the proportion offered, a chi-square test revealed that the difference was only significant for *A. disintegratus* ($\chi^2 = 11.3$, $p = 0.0008$).

Experiment 3 - Performance of *A. disintegratus*

At the start of the experiment, sizes of beetle larvae did not differ between treatments (ANOVA; df = 2, 12; $F = 0.36$; $p = 0.71$) but after 9 days of feeding, a analysis of covariance (with initial size as the covariate) showed a significant effect of prey type on the final size of beetle larvae (ANCOVA; df = 2; $F = 8.22$; $p = 0.0066$; Figure 10). Beetles fed ostracods grew less than beetles fed copepods or mosquito larvae. For beetles fed copepods and mosquitoes, there was a significant difference in initial size and final size ($p = 0.0001$ and $p = 0.0028$ respectively; Figure 10), but there was no difference in initial and final size of beetles fed ostracods ($p > 0.05$).

Experiment 4 - Prey capture

Ostracods were encountered more than twice as frequently in ten minutes (mean = 17) than mosquitoes and copepods (7.1 and 6.7 encounters, respectively; ANOVA; df = 2, 16; $F = 10.13$; $p = 0.0014$; Figure 11A). Attacks per encounter did not differ significantly between prey types (ANOVA; df = 2, 16; $F = 0.09$; $p = 0.92$; Figure 11B). Finally, mosquito larvae had the highest captures per attack, with 30.3% of all attacks resulting in a capture, followed by copepods (16.1%) and then ostracods (5.3%), but the overall main effect of prey type on captures per attack was not significant (ANOVA; df = 2, 16; $F = 2.98$; $p = 0.079$; Figure 11C).

Experiment 5 - Predator interactions

After 5 days, cannibalism occurred in 58% of trials with one predator species. Of those, 57% were within *A. punctatus*, and 43% were within *A. disintegratus*. Intraguild predation occurred in 67% of trials with two species. A chi-square test revealed no significant difference in the frequency of cannibalism compared to IGP ($\chi^2 = 1.4$; $p = 0.50$; Figure 12A). By day 18, cannibalism in *A. punctatus* and intraguild predation occurred significantly more times than cannibalism in *A. disintegratus* (Fisher's exact test; $p = 0.0027$; Figure 12A). After 5 days, *A. punctatus* IGP on *A. disintegratus* was observed 5 times, and *A. disintegratus* IGP on *A. punctatus* was observed 7 times (Figure 12B). A chi-square test revealed no significant difference in the number of times each species consumed the other ($\chi^2 = 0.5$; $p = 0.48$). After 18 days, IGP was completely symmetric between the two species ($\chi^2 = 0.0$; $p = 1.0$; Figure 12B).

Discussion

Prey selection, performance, and behavior

Results from these experiments demonstrate that *Agabus* larvae could play a significant role in structuring the primary consumer community through consumption of prey and selection of prey. Both species consumed all three of the prey types offered, but showed selection for mosquito larvae in all of the experiments. Results indicate that both species of *Agabus* consumed more mosquito larvae than microcrustaceans in 24 hours, and that when offered a choice of prey, *Agabus* consumed proportionally more mosquito larvae than were offered. I hypothesized that *Agabus* may exhibit this selection because feeding on mosquito larvae is more profitable (in terms of growth) than feeding on microcrustaceans, or because mosquito larvae are easier to capture, and thus less of an

energy investment. Results from the third experiment showed that *Agabus* larvae reached a larger size when they were fed either mosquito larvae or copepods in comparison to ostracods. The larvae that were fed ostracods did not change in size. These results suggest that mosquito larvae or copepods could be more profitable in terms of nutritional components, or less energy (and thus less body mass) is required to attack and capture these types of prey.

I also predicted differences in the ability to *Agabus* to attack and capture prey. *Agabus* had more encounters with ostracods; this is likely because ostracods made no attempt to avoid the beetle larvae, while the copepods and mosquito larvae seemed to detect the predators and stay on the other side of the Petri dish. Despite the difference in encounter rate, all three prey types were attacked in equal proportions, suggesting that the beetle larvae do not discriminate between prey types prior to attack. However, once attacked, many of the ostracods were rejected, thus leading to a greater capture rate of the mosquito larvae and copepods. Handling time of the prey was not considered in this study, though this could play a role in the number of prey items the predator was able to consume in the 10 minute period, and should be considered in future experiments (Holling 1961).

Cannibalism and intraguild predation

In the first experiment, I set up treatments with two predators to determine if cannibalism and intraguild predation occur, and how this might affect rate of prey consumption. I observed both cannibalism and intraguild predation but did not have the ability to quantify this because the experiment was run for such a short period of time. Overall, treatments with two predators consumed a lower number of prey per predator

than predators in the single predator treatments, regardless of if cannibalism or intraguild predation occurred. To quantify the occurrence of these antagonistic interactions between predators, I ran the fifth experiment to measure the number of times cannibalism and intraguild predation occurred, and to determine if one species was dominant in intraguild predation events. Because the species are of similar size and occur in similar abundances, I predicted equal levels of these interactions across predator combinations. After 5 days, there were no differences in the levels of cannibalism or intraguild predation, but by day 18, cannibalism in *A. punctatus* and intraguild predation occurred significantly more times than cannibalism in *A. disintegratus*. This is consistent with the observation that *A. punctatus* was slightly more aggressive than *A. disintegratus* when in pursuit of prey (L. Culler, personal observation).

Impact on primary consumer community

Both species of beetle larvae were able to consumer up to 20 prey items in 24 hours. This could translate into a significant impact on the overall abundance of primary consumers in the wetlands considering the densities of beetle larvae reached up to 164 individuals per meter^2 on 10 March 2008 (DiPietro and Culler, unpublished data). Because I observed prey selection in my experiments, these beetles may alter primary consumer community structure if they consume a greater proportion of one type of prey than is available in the environment. These beetles do occur in high densities, so antagonistic interactions may dampen the effect on the prey community through cannibalism or intraguild predation, or because behavioral modifications due to the presence of other predators affect foraging behavior and thus indirectly affect prey consumption (Wissinger and McGrady 1993, Finke and Denno 2002, Finke and Denno

2005). Future studies should address: (1) the ability of these predators to consume different prey in the field, (2) if selection of prey occurs within natural prey communities, and, (3) how the density of predators may influence the ability to consume and suppress prey populations.

Conservation Biological Control?

The results of this study are relevant to the field of conservation biological control, which is defined as the manipulation of agricultural habitats to favor the natural enemies of pests, as to conserve biodiversity and reduce pest problems (Barbosa 1998). The habitat studied here is not considered agricultural, though parallels can be drawn because native wetland predators can effectively suppress mosquito populations through predation or by deterring mosquito oviposition (Batzer and Wissinger 1996). Therefore, wetland management strategies aimed at maintaining predator complexes or encouraging colonization by native wetland predators could help to reduce pest problems.

An abundant and diverse prey community may be important in attracting and supporting wetland predators that may be able to later switch to preferred prey. In the system studied here, the high abundance of microcrustaceans as beetle larvae hatch (Chapter 1) could be important in supporting and maintaining *Agabus* populations, even if preferred mosquito prey are not yet present. As mosquitoes become available, *Agabus* beetles may switch to this preferred prey, and thus contribute to suppression of this pest. This is consistent with a previous suggestion that *Agabus* may be effective predators of mosquito larvae, as their activity at low water temperatures corresponded to when mosquito larvae were hatching (James 1964).

Complexity is another factor which may be important to consider when managing, constructing, or restoring wetlands. Studies in terrestrial and agricultural systems show that multiple predator species may be more effective at suppressing prey in complex vegetated habitats because intraguild predation and other antagonistic interactions are diminished (Finke and Denno 2002). In wetlands, habitat management strategies could be developed that would support a predator complex in which antagonistic interactions would be minimized, so that suppression of pest species is maximized. These strategies could include constructing complex habitats consisting of a diverse assemblage of wetland plants, microtopographical features, and coarse woody debris. Including complexity may also attract a greater number of predators by virtue of providing more habitats for a greater number of species that may be able to contribute to suppression of prey populations. Some studies have indicated that vegetation and structural heterogeneity generally increases diversity and abundance of macroinvertebrates, including predators (Shrewsbury and Raupp 2006, Mogi 2007). While I attempted to find such relationships from my analyses in Chapter 1, the lack of any relationship could be due to the fact that all of the wetlands constructed at the Jackson Lane site are relatively complex, compared to other constructed wetlands which are structurally simple.

Future studies should address questions concerning predator complexes in constructed wetlands and how complexity affects the ability of predators to suppress prey. One possible area of important research is how the presence of fish in constructed wetlands may enhance suppression of prey, or lead to antagonistic interactions such as intraguild predation and thus dampen predator effects on prey. Studies have

demonstrated both positive, negative, or no correlation between the presence of predatory fishes and species richness, densities or biomass of macroinvertebrates (Thorp and Bergey 1981, Crowder and Cooper 1982, Bohanan and Johnson 1983, Gillinsky 1984, Morin 1984, Mallory et al. 1994, Hanson and Riggs 1995, Pierce and Hinrichs 1997, Batzer et al. 2000, Baber et al. 2004). If fish preferentially feed on larger aquatic invertebrates, including many predator taxa, prey populations may be able to escape predation pressure and increase in abundance. Alternatively, fish may prefer to feed on smaller prey items and thus contribute to further suppression of prey populations. The trophic importance of fish in wetlands is poorly understood (Batzer 1998), so feeding studies of fish that are commonly found in constructed wetlands may contribute to an understanding of how adding or excluding fish during restoration and construction of wetlands may impact the prey community.

Few studies have addressed the issue of how complexity in constructed wetlands impacts predator abundance and diversity, as well as the interaction between prey and predators. As stated above, complexity is generally thought to increase diversity and dampen negative predator-predator interactions, both of which could be important if the goal of any project is to maintain a predator complex that is capable of suppressing prey pest populations. Studies examining how adding complexity in restored or constructed wetlands affects predator complexes could yield important knowledge that could help to inform future wetland restoration and construction projects.

Summary

The results of this study reveal that larval dytiscid beetles have the potential to exert a strong influence on community structure in constructed wetlands by virtue of prey consumption. These beetles also show selection of mosquito larvae, and, therefore, likely contribute to natural suppression of mosquitoes in constructed wetlands. While macroinvertebrates are not recommended for inundative biological control due to problems with production, storage, and release, continued study of predator ecology may yield clues for development of mosquito control tools using macroinvertebrates (Mogi 2007). For now, wetland management for control of pest species should focus on constructing wetlands with high ecological value that function like natural wetlands.

Figure 7 Pictures of beetle species used: (**A**) *Agabus punctatus*, and (**B**) *Agabus disintegratus.*

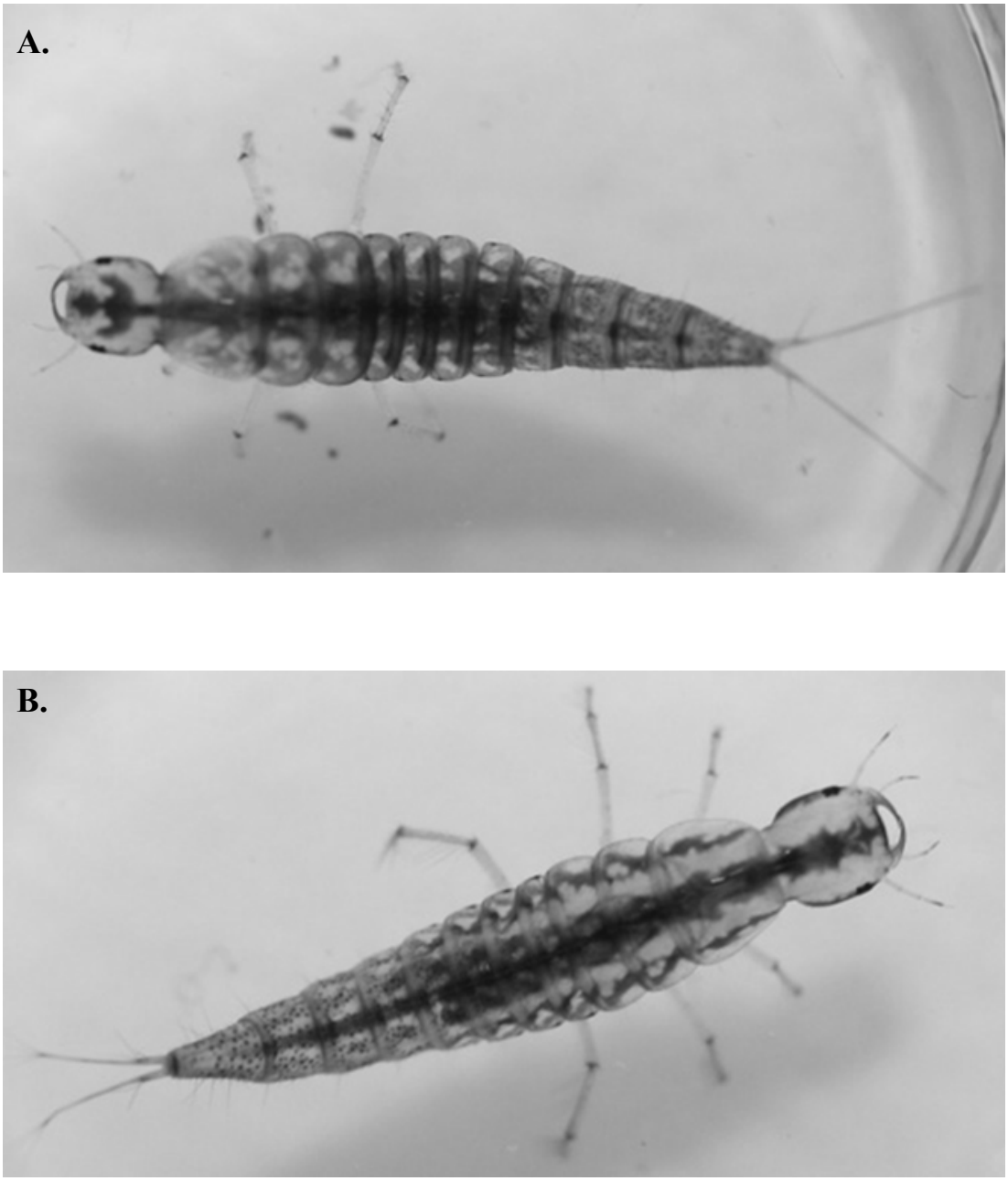


Figure 8 Instantaneous prey mortality rate, *m*, for: (**A**) each prey type (Cop = Copepods; Mos = Mosquito larvae; Ost = Ostracods), and (**B**) each predator combination (D = one *A. disintegratus*; P = one *A. punctatus*; DD = two *A. disintegratus*; PP = two *A. punctatus*; DP= one each of *A. disintegratus* and *A. punctatus*). Bars represent means +/- SE. Comparisons with different letters indicate significant LSD differences at α=0.05.

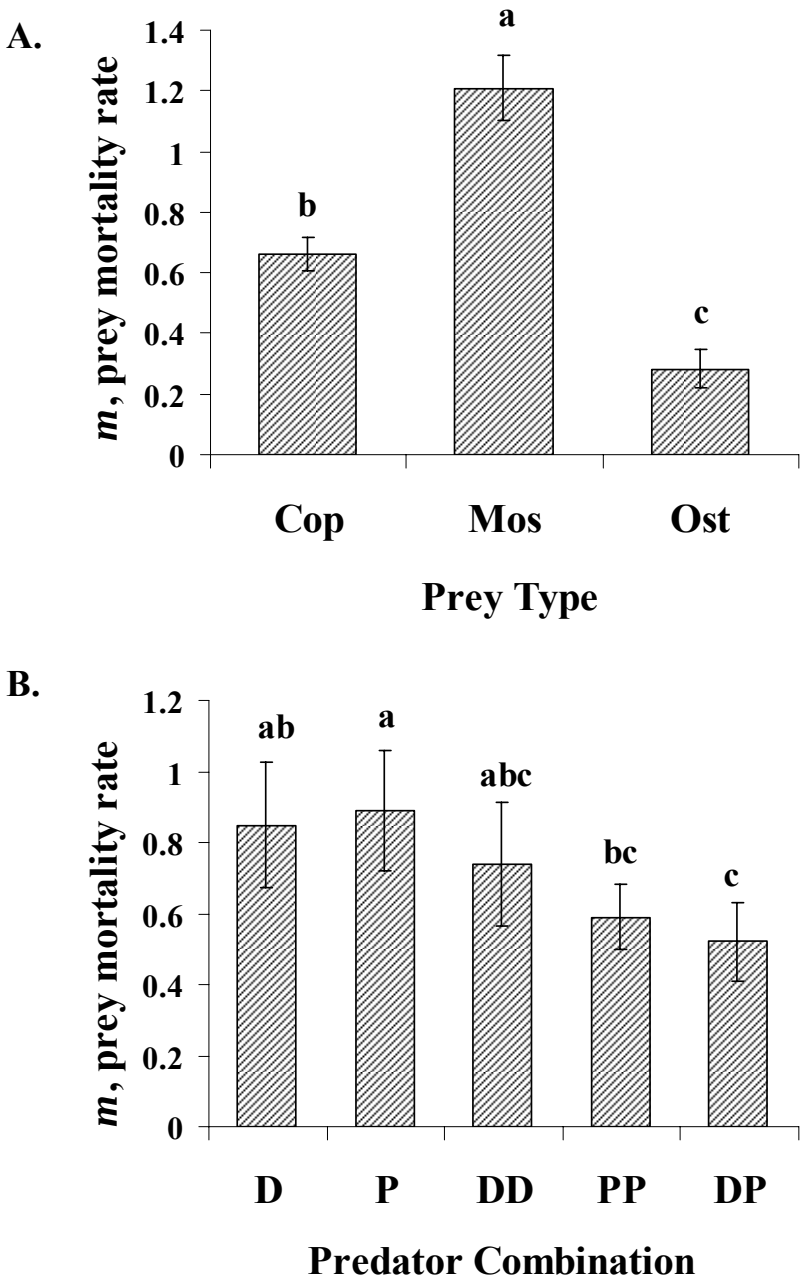


Figure 9 Percentages of prey consumed (observed) that were mosquito larvae compared to percentages that were offered (expected) in: (**a**) *A. disintegratus* and (**b**) *A. punctatus*. Bars represent means of 5 observations.

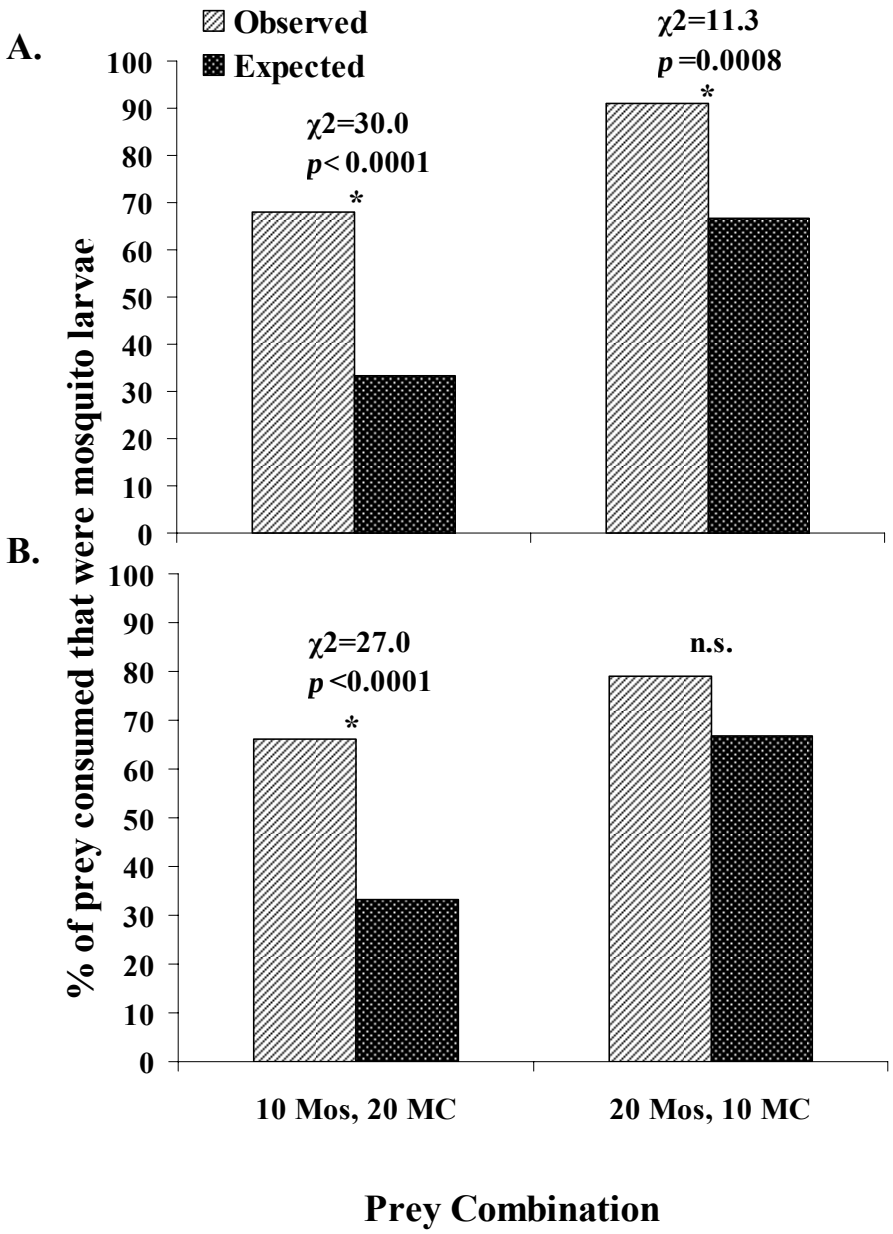


Figure 10 Abdominal length of beetles at day 0 (Initial) and day 9 (Final). Bars represent mean +/- SE.

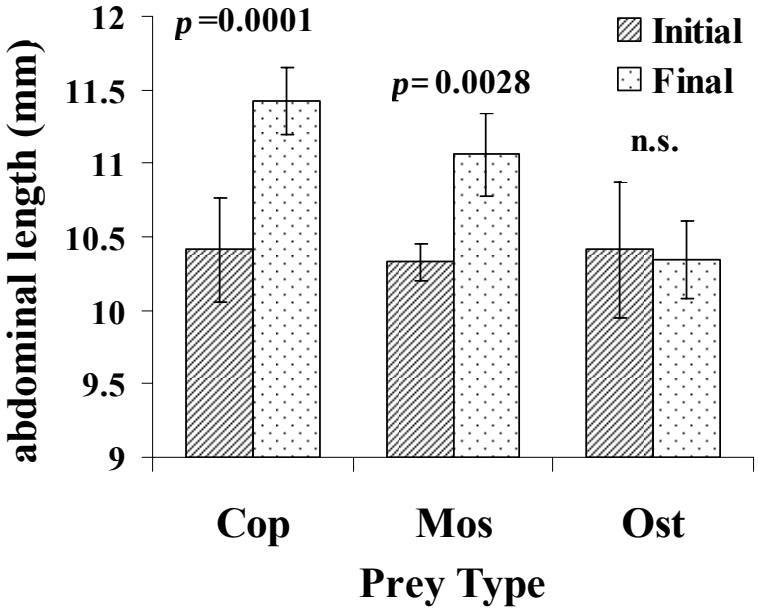


Figure 11 (**A**) Number of encounters with each prey type in 10 minutes, (**B**) number of attacks per encounter of each prey type in 10 minutes, and (**C**) number of captures per attack of each prey type in 10 minutes. Cop = Copepods; Mos = Mosquito larvae; Ost = Ostracods. Bars represent means +/- SE. Different letters indicate significant differences at α=0.05.

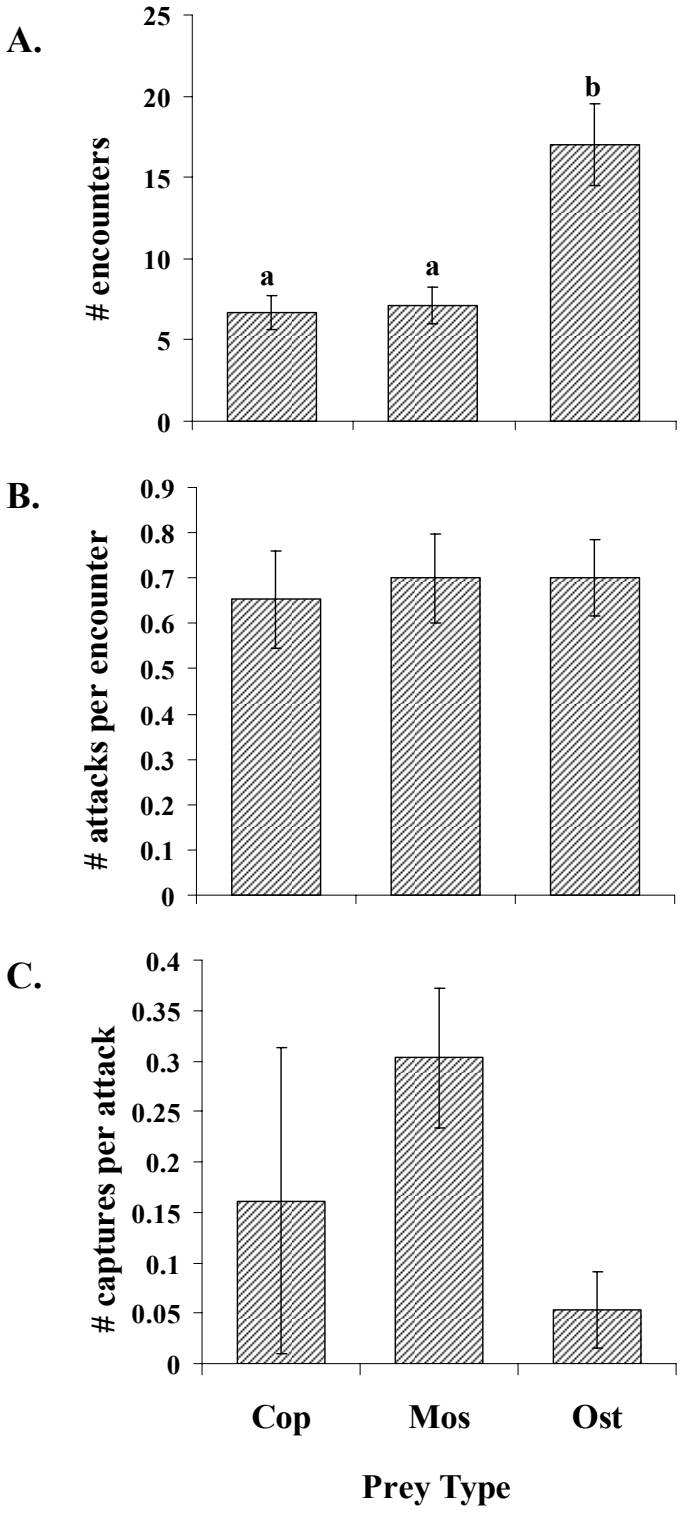
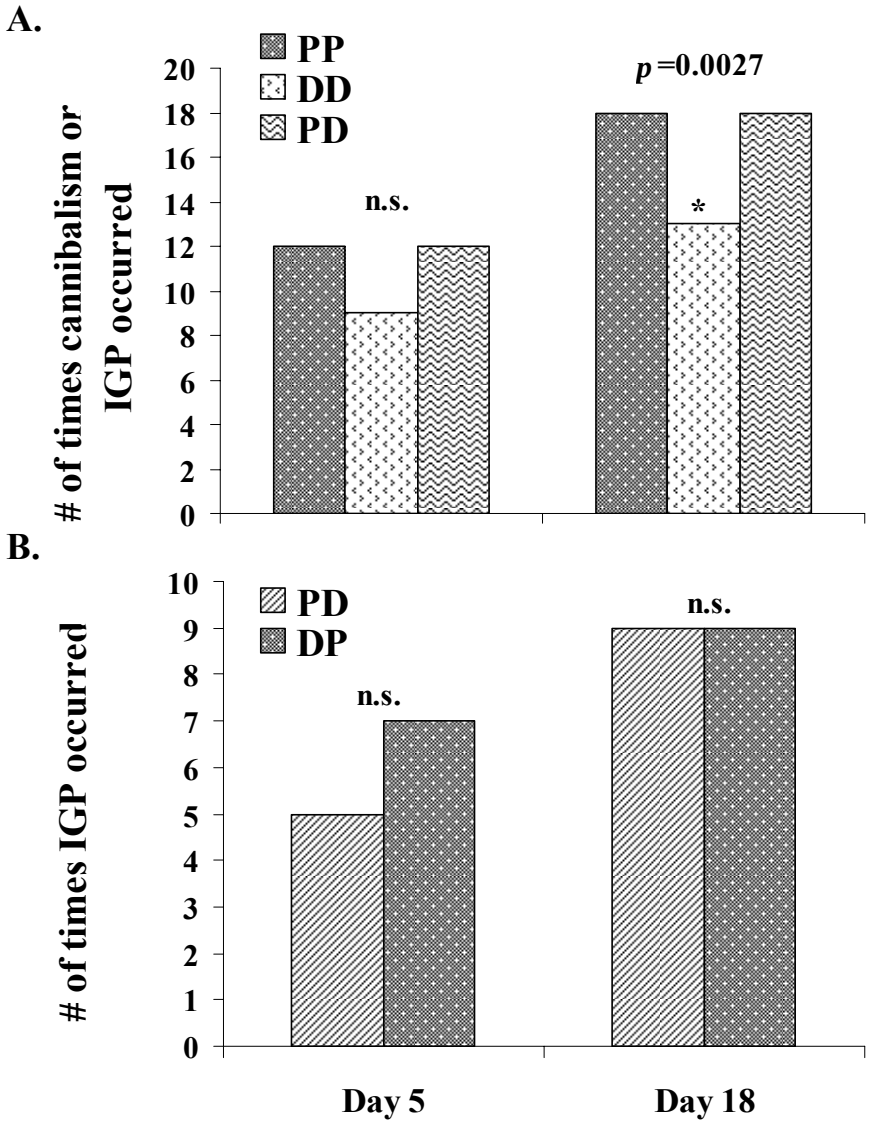


Figure 12 Occurrences of cannibalism or IGP after 5 and 18 days: (**A**) for different predator combinations (PP = two *A. punctatus*; DD = two *A. disintegratus*; DP= one each of *A. disintegratus* and *A. punctatus*), and (**B**) by predator species (PD = *A. punctatus* IGP on *A. disintegratus*; DP = *A. disintegratus* IGP on *A. punctatus*). Bars represent means and significant differences are indicated with an asterisk (α=0.05).



Appendix A

Raw Macroinvertebrate Data

Table 1 The following table contains the count data used for analysis of the macroinvertebrate communities. FG stands for the functional group that each taxon was classified as. PR = predator, PC = primary consumer, P* = predator as larvae, primary consumer as adult (considered separate in analysis), and UN=unknown (not used in analysis). The numbers across the top refer to the wetland, and the numbers in the table are counts from each subsample.

(Table 1)

MARCH 2005

Taxa	FG	2	3	6	7	10	11	15	17	19
Ephemeroptera										
Baetidae										
Callibaetis sp.	PC								4	
Odonata										
Coenagrionidae										
NIF	PR								1	1
Libellulidae										
Libellula sp.	PR			1					1	
Plathemis sp.	PR								1	
Hemiptera										
Corixidae										
Hesperocorixa	PC	2		6	2			1	2	
Sigara sp.	PC			1						
Notonectidae										
Buenoa sp.	PR								3	
Notonecta sp.	PR				1					
Coleoptera										
Dytiscidae										
Agabus sp.	PR	9	140	31	17	4	9	19	102	67
Dytiscus sp.	PR								1	1
Hydroporinae	PR	1			13	1	9		5	5
Hydroporus sp.	PR						1			1
Laccophilus sp.	PR		1							
Uvarus sp.	PR				1					
Hydrophilidae										
Berosus sp.	P*	1				2				
Enochrus sp.	P*				1					1
Paracymus sp.	P*			1						
Tropisternus sp.	P*		1							
Noteridae										
Hydrocanthus	PR	2								
Trichoptera										
Limnephilidae										
Limnephilus sp.	PC		3	1	7	11	4	20		1
Lepidoptera										
Pyralidae										
NIF	PC				1	1	1		1	1
Diptera										
Ceratopogonidae										
Bezzia sp.	PR	3		6						1
Culicoides sp.	PR	3	1	16	1				1	
Chironomidae										
Chironomini	PC	1		2						3
Orthocladinae	PC	34	34	38	117	20	8	14	18	127

(Table 1 Continued)

MARCH 2005

Taxa	FG	2	3	6	7	10	11	15	17	19
Tanypodinae	PR	2		17						
Tanytarsini	PC	3		2						
Culicidae										
Aedes sp.	PC									1
Sciaridae										
NIF	UN						1		3	2
Sciomyzidae										
NIF	PR	4								
Stratiomyidae										
NIF	PC				1					3
Tabanidae										
NIF	PR				1					
Tabanus sp.	PR					1				2
Tipulidae										
Tipula sp.	PC					8		3		1
Gastropoda										
Physidae										
NIF	PC	16	1	37	1	58		23	24	16
Planorbidae										
NIF	PC	1								
Ancylidae										
NIF	PC	1		1				1		
Annelida/Nematoda										
NIF	UN	14	1	16	65	20		1		64
Copepoda										
NIF	PC	47	16	14	39	1	5	11	15	2
Ostracoda										
NIF	PC				4			1		
Cladocera										
NIF	PC		12	5	103	6	33	61	45	

(Table 1 Continued)

APRIL 2005										
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Ephemeroptera										
Baetidae										
Callibaetis sp.	PC								3	
Odonata										
Aeshnidae										
NIF	PR			1						
Coenagrionidae										
NIF	PR	1		1	4				8	
Lestidae										
Lestes sp.	PR			5			1	1		2
Libellulidae										
Libellula sp.	PR	1								
Plathemis sp.	PR								1	
NIF	PR			1						
Hemiptera										
Corixidae										
NIF	UN	112	64	59	9	15	2	16	103	13
Coleoptera										
Dytiscidae										
Acilius sp.	PR					1				
Agabus sp.	PR	7	92	27	21	87	22	48	43	43
Dytiscus sp.	PR							2	3	
Hydroporinae	PR	3	7	1	10	15	21	11	3	9
Hydrovatus sp.	PR						1		1	
Laccophilus sp.	PR			1						1
Uvarus sp.	PR									1
Hydrophilidae										
Berosus sp.	P*						1	1	1	
Enochrus sp.	P*			1	2	41	2		3	9
Hydrochara sp.	P*		1						1	
Tropisternus sp.	P*	3	2	8	1	3			10	16
Noteridae										
Hydrocanthus	PR	1							1	
Lepidoptera										
Pyralidae										
NIF	PC				1				1	1
Diptera										
Ceratopogonidae										
Bezzia sp.	PR	7	6		1				1	5
Culicoides sp.	PR		7	6						
Chironomidae										
Chironomini	PC	98	16	2	44	21	14	14	11	8
Orthocladinae	PC	7	72	62	50	72	22	128	49	118
Tanypodinae	PR	3	2	1					1	10
Tanytarsini	PC			1						

(Table 1 Continued)

APRIL 2005

Taxa	FG	2	3	6	7	10	11	15	17	19
Culicidae										
Aedes sp.	PC									3
Ephydridae										
NIF	PC					3				
Sciomyzidae										
NIF	PR		3	3						
Tabanidae										
Crysops sp.	PR	2								
Tabanus sp.	PR			1		2		1		
Tipulidae										
Tipula sp.	PC					2	1			1
Gastropoda										
Physidae										
NIF	PC	15	1	30	6	42		72	50	12
Planorbidae										
NIF	PC	32								
Ancylidae										
NIF	PC			2						
Viviparidae										
NIF	PC	1								
Annelida/Nematoda										
NIF	UN	17	29	131	150					42
Copepoda										
NIF	PC	65	19	26	15	16	6	6	14	77
Ostracoda										
NIF	PC				23	8		1		
Cladocera										
NIF	PC	127	159	48	167	438	51	128	45	283

(Table 1 Continued)

MAY 2005										
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Ephemeroptera										
Baetidae										
Callibaetis sp.	PC								1	
Odonata										
Lestidae										
Lestes sp.	PR			5	5		5	1	2	1
Libellulidae										
Libellula sp.	PR			1						
NIF	PR								1	
Hemiptera										
Belostomatidae										
Belostoma sp.	PR			2						
Corixidae										
NIF	UN	16	116	20	80	19	58	13	45	17
Gerridae										
Trepobates sp.	PR								1	
Mesovelidae										
Mesovelia sp.	PR	1							2	
Notonectidae										
Notonecta sp.	PR				11	3	30	2		4
Coleoptera										
Dytiscidae										
Agabus sp.	PR		1	1			7	1		
Coptotomus sp.	PR		10	1	1		22	1		
Dytiscus sp.	PR		1		2		1			
Hydroporinae	PR		2				22			1
Hydrovatus sp.	PR						2			
Laccophilus sp.	PR		9						1	3
Thermonectus	PR						2			
Haliplidae										
Peltodytes sp.	PC			2						
Hydrophilidae										
Berosus sp.	P*	3	9	1	4		3	3	5	3
Enochrus sp.	P*				3		3		4	4
Hydrochara sp.	P*		3		2	2	1			1
Hydrophilius sp.	P*				1					1
Tropisternus sp.	P*	1	7		5		10		2	2
Noteridae										
Hydrocanthus	PR	3								
Trichoptera										
Hydroptilidae										
Oxyethira sp.	PC		1							
Diptera										
Ceratopogonidae										
Bezzia sp.	PR	1								
Culicoides sp.	PR	5								3

(Table 1 Continued)

		MAY 2005								
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Chironomidae										
Chironomini	PC	101	45	21	5	1	51	3	3	4
Orthocladinae	PC	51	18	14	23	6	40	6	5	8
Tanypodinae	PR	10	1	5	6	1	27	3	1	3
Sciomyzidae										
NIF	PR				1					
Tabanidae										
Tabanus sp.	PR	2					1			
Gastropoda										
Physidae										
NIF	PC	115	85	242	155	346	14	265	185	243
Planorbidae										
NIF	PC	15								
Annelida/Nematoda										
NIF	UN	1	27	11					40	2
Copepoda										
NIF	PC	8	10	80	39	100	32	47	23	107
Ostracoda										
NIF	PC				21	8				
Cladocera										
NIF	PC	50	10	212	81	149	182	181	34	63

(Table 1 Continued)

JUNE 2005										
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Ephemeroptera										
Baetidae										
Callibaetis sp.	PC		4	1	2					
Caenidae										
Caenis sp.	PC		2						2	
Odonata										
Aeshnidae										
Anax junius	PR				6					
NIF	PR			1						6
Coenagrionidae										
NIF	PR	1	7	5	16	3	8	2	6	19
Libellulidae										
NIF	PR	2	4	3		2	7		4	
Hemiptera										
Belostomatidae										
Belostoma sp.	PR	1								
Corixidae										
Hesperocorixa	PC		3	1				1	6	
Sigara sp.	PC								1	
NIF	UN				4		5			2
Mesovelidae										
Mesovelia sp.	PR				1					
Nepidae										
Ranatra sp.	PR			1						
Notonectidae										
Notonecta sp.	PR		2	1	1			1	3	1
Veliidae										
Microvelia sp.	PR				1					
Coleoptera										
Dytiscidae										
Agabus sp.	PR							1		
Coptotomus sp.	PR						1		1	
Cybister sp.	PR				1					
Hydroporinae	PR				1	1	1		1	
Haliplidae										
Peltodytes sp.	PC								1	
Hydrophilidae										
Berosus sp.	P*	1	1		1	1	5	1		1
Enochrus sp.	P*					1			1	
Tropisternus sp.	P*		1		7		4			3
Noteridae										
Hydrocanthus	PR				1					
Trichoptera										
Hydroptilidae										
Oxyethira sp.	PC								1	

(Table 1 Continued)

JUNE 2005										
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Diptera										
Ceratopogonidae										
Bezzia sp.	PR	16	14	9	29	9	26	11	16	18
Culicoides sp.	PR				4	4	2	5	2	4
Chaoboridae										
Chaoborus sp.	PR						1	1		
Chironomidae										
Chironomini	PC	116	14	38	45	5	207	12	5	
Orthocladinae	PC	21	17	14	5	107	1	38	30	40
Tanypodinae	PR	12	10	31	6	11	11	30	44	11
Tanytarsini	PC		1							
Stratiomyidae										
NIF	PC		1		3				1	1
Tabanidae										
Tabanus sp.	PR								1	
Gastropoda										
Physidae										
NIF	PC	75	241	175	185	170		164	175	228
Planorbidae										
NIF	PC	16		8				5		
Ancylidae										
NIF	PC			3				17	1	
Viviparidae										
NIF	PC	1								
Annelida/Nematoda										
NIF	UN	45			12	0	31	1		
Copepoda										
NIF	PC		20	50	25	54	50	50	101	19
Ostracoda										
NIF	PC								8	
Cladocera										
NIF	PC	2	161	34	133	75	93	170	226	100

(Table 1 Continued)

		JULY 2005								
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Ephemeroptera										
Baetidae										
Callibaetis sp.	PC	1	3	1			1	1		7
Caenidae										
Caenis sp.	PC	9	1					1	2	
Odonata										
Aeshnidae										
Anax junius	PR	1						1		
Boyeria vinosa	PR								1	
NIF	PR				3					4
Coenagrionidae										
Enallagma sp.	PR									
NIF	PR	6	9	5	12	2	2	6	19	5
Libellulidae										
Erythemis sp.	PR		1					3	11	4
Sympetrum sp.	PR							12		
Tramea sp.	PR							3		
NIF	PR	11		6	2	7				
Hemiptera										
Belostomatidae										
Belostoma sp.	PR	1	1		3			2	1	3
Corixidae										
Hesperocorixa	PC	7		1			2		1	
Hydrometridae										
Hydrometra sp.	PR		1							
Mesovelidae										
Mesovelia sp.	PR		8		2	3	2	1	6	8
Naucoridae										
NIF	PR						1			
Nepidae										
Ranatra sp.	PR	1					1			
Notonectidae										
Buenoa sp.	PR		12	6						
Notonecta sp.	PR						1	3	4	1
Veliidae										
Microvelia sp.	PR								2	
Coleoptera										
Dytiscidae										
Acilius sp.	PR						5			
Coptotomus sp.	PR			1			1			
Cybister sp.	PR									1
Hydroporinae	PR				5	5		14	10	1
Hydrovatus sp.	PR						1			
Laccophilus sp.	PR				4		97		2	16
Thermonectus	PR									3

(Table 1 Continued)

		JULY 2005								
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Uvarus sp.	PR						14			2
Haliplidae										
Peltodytes sp.	PC	2								
Hydrophilidae										
Anacaena sp.	P*						1			
Berosus sp.	P*						7			3
Enochrus sp.	P*		1				10	1	2	
Hydrochara sp.	P*				1			1		
Paracymus sp.	P*						1			
Tropisternus sp.	P*		5	1	1		30		1	20
Noteridae										
Hydrocanthus	PR	2	1	4	10	9		6	6	5
Trichoptera										
Hydroptilidae										
Oxyethira sp.	PC	2		1					1	
Lepidoptera										
Pyralidae										
NIF	PC	4			1	1			2	2
Diptera										
Ceratopogonidae										
Bezzia sp.	PR	47	39	39	12	40		51	29	26
Culicoides sp.	PR		3		8	26		6		9
Chironomidae										
Chironomini	PC	92	21	12	2	19	4	36	26	5
Orthocladinae	PC		20	31	25	13	13	62		43
Tanypodinae	PR	30	8	44	7	117	1	105	90	4
Tanytarsini	PC	1								
Culicidae										
Aedes sp.	PC						7	3	2	8
Anopheles sp.	PC	1					4		3	
Culex sp.	PC								6	
Dolichopodidae										
NIF	PR									1
Ephydridae										
NIF	PC		1							
Sciomyzidae										
NIF	PR				1					
Stratiomyidae										
NIF	PC		2		1					
Tabanidae										
Tabanus sp.	PR				2	1	2	1		2
Gastropoda										
Physidae										
NIF	PC	35	149	42	63	16	1	11	72	94
Planorbidae										

(Table 1 Continued)

JULY 2005										
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
NIF	PC	2		1			1	2		
Ancylidae										
NIF	PC	3		1	3			6		
Viviparidae										
NIF	PC									
Annelida/Nematoda										
NIF	UN	34	8	110	140	56	11	8		26
Copepoda										
NIF	PC	1		6	1		1		9	
Ostracoda										
NIF	PC					61				
Cladocera										
NIF	PC	8		38	11		3	24	57	4

(Table 1 Continued)

AUGUST 2005										
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Ephemeroptera										
Baetidae										
Callibaetis sp.	PC	6	19	1				1	1	
Caenidae										
Caenis sp.	PC	16	3	1				11		
Odonata										
Aeshnidae										
Anax junius	PR			3	2				2	
NIF	PR	8	4					7		
Coenagrionidae										
Enallagma sp.	PR			7						
NIF	PR	29	18		6			34	29	
Libellulidae										
Erythemis sp.	PR							1		
Libellula sp.	PR		6	10	24			30		7
Tramea sp.	PR			3						
NIF	PR	15							15	
Hemiptera										
Belostomatidae										
Belostoma sp.	PR	4	1	1	1			2	1	2
Corixidae										
Hesperocorixa	PC	2	9					1	5	
Sigara sp.	PC	2								
NIF	UN			2						
Mesovelidae										
Mesovelia sp.	PR	20	3	2	17			6	31	12
Notonectidae										
Buenoa sp.	PR	4	11							7
Notonecta sp.	PR	2		25	3			3	4	2
Veliidae										
Microvelia sp.	PR	2	1	1	19					
Coleoptera										
Dytiscidae										
Coptotomus sp.	PR				1					2
Dytiscus sp.	PR	1								
Graphoderus sp.	PR								1	
Hydroporinae	PR								1	
Uvarus sp.	PR								1	
Gyrinidae										
Dineutus sp.	PR			1						
Haliplidae										
Peltodytes sp.	PC				1					1
Hydrophilidae										
Berosus sp.	P*							1		
Hydrobius sp.	P*			1						

(Table 1 Continued)

AUGUST 2005

Taxa	FG	2	3	6	7	10	11	15	17	19
Tropisternus sp.	P*	3			1			2	6	4
Noteridae										
Hydrocanthus	PR	14		1	36				13	2
Trichoptera										
Hydroptilidae										
Oxyethira sp.	PC				2					
Lepidoptera										
Pyralidae										
NIF	PC	6			7				1	1
Diptera										
Ceratopogonidae										
Bezzia sp.	PR	55	2	40	54			13	10	66
Chironomidae										
Chironomini	PC	47	12	68	56			67	20	12
Orthocladinae	PC	49	50							51
Tanypodinae	PR	22	21	56	87			85	61	86
Culicidae										
Aedes sp.	PC	3	5		3				13	1
Anopheles sp.	PC	1								
Culex sp.	PC									9
Stratiomyidae										
NIF	PC							1	2	
Tabanidae										
Crysops sp.	PR			1						
Tabanus sp.	PR		1							1
Gastropoda										
Physidae										
NIF	PC	10	64	54	16			38	14	35
Planorbidae										
NIF	PC	3		2						
Ancylidae										
NIF	PC		1							
Annelida/Nematoda										
NIF	UN			14	46			0	78	
Copepoda										
NIF	PC			5	18				6	
Cladocera										
NIF	PC	3	5	12	30			9	12	

(Table 1 Continued)

MARCH 2006										
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Ephemeroptera										
Baetidae										
Callibaetis sp.	PC				1			1		
Caenidae										
Caenis sp.	PC	2								
Odonata										
Coenagrionidae										
NIF	PR	1					2			
Libellulidae										
Libellula sp.	PR							1		
Sympetrum sp.	PR					1				
NIF	PR						4			
Hemiptera										
Corixidae										
Hesperocorixa	PC	1	4		3		3	3		
NIF	UN					1				
Coleoptera										
Dytiscidae										
Agabus sp.	PR				2	17	60	42		
Copelatus sp.	PR						1			
Coptotomus sp.	PR		1							
Hydroporinae	PR				6	9	23	9		
Hydroporus sp.	PR						2			
Laccornis sp.	PR					1				
Liodessus sp.	PR							2		
Neoporus sp.	PR						1			
Rhantus sp.	PR					1				
Uvarus sp.	PR						1	1		
Hydrophilidae										
Berosus sp.	P*		2			1	2	2		
Enochrus sp.	P*					1				2
Paracymus sp.	P*					2				
Tropisternus sp.	P*		1			3				
Noteridae										
Hydrocanthus	PR	1								
Suphisellus sp.	PR	1				2				
Trichoptera										
Phryganeidae										
Agrypnia sp.	PC	1								
Lepidoptera										
Pyralidae										
NIF	PC	1	2					1		
Diptera										
Ceratopogonidae										
Atrichopogon sp.	PC				3					

(Table 1 Continued)

MARCH 2006

Taxa	FG	2	3	6	7	10	11	15	17	19
Bezzia sp.	PR	10			1					
Culicoides sp.	PR	9	1		2	1				
Chaoboridae										
Chaoborus sp.	PR						3			
Chironomidae										
Chironomini	PC	8	1				4			
Orthocladinae	PC	9	33		167	74	46	175		3
Tanypodinae	PR	15	1					2		
Tanytarsini	PC	74	3		1					
Dolichopodidae										
NIF	PR					1				
Ephydridae										
NIF	PC				1	1				
Sciaridae										
NIF	UN		1							
Tabanidae										
NIF	PR				1					
Tabanus sp.	PR	1								
Tipulidae										
NIF	PC				5					
Gastropoda										
Physidae										
NIF	PC		1		10	9		4		2
Planorbidae										
NIF	PC							15		
Ancylidae										
NIF	PC					10		1		
Viviparidae										
NIF	PC		5		9					
Annelida/Nematoda										
NIF	UN	172	0		47	183	21	36		295
Copepoda										
NIF	PC	13	18		18	66	16	49		74
Ostracoda										
NIF	PC					4		4		2
Cladocera										
NIF	PC	16				53	7	67		

(Table 1 Continued)

APRIL 2006									
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Ephemeroptera										
Baetidae										
Callibaetis sp.	PC								3	
Caenidae										
Caenis sp.	PC	7								
Odonata										
Aeshnidae										
NIF	PR			1						
Coenagrionidae										
NIF	PR			1					1	
Libellulidae										
Erythemis sp.	PR								3	
Plathemis sp.	PR		1	1				1		
NIF	PR						6			
Hemiptera										
Corixidae										
Hesperocorixa	PC			1						
NIF	UN					3	4	47	5	
Notonectidae										
NIF	PR						3			
Coleoptera										
Dytiscidae										
Agabus sp.	PR						12	35		
Copelatus sp.	PR							1		
Coptotomus sp.	PR							1		
Hydroporinae	PR					3	29	7		
Hydrovatus sp.	PR					2				
Liodessus sp.	PR						18	2		
Neoporus sp.	PR						1			
Uvarus sp.	PR					2	1	1		
Haliplidae										
Haliplus sp.	PC						1	1		
Hydrophilidae										
Enochrus sp.	P*					1		5		
Tropisternus sp.	P*							8		
Noteridae										
Hydrocanthus	PR					2		1		
Trichoptera										
Phryganeidae										
Agrypnia sp.	PC	1								
Ptilostomis sp.	PC								1	
Diptera										
Ceratopogonidae										
Bezzia sp.	PR	14	1	6		2			5	
Culicoides sp.	PR	9	4	19		2	5	6	22	

(Table 1 Continued)

APRIL 2006

Taxa	FG	2	3	6	7	10	11	15	17	19
Chironomidae										
Chironomini	PC	9	5		4	1	37		2	
Orthocladinae	PC	22	25	86	23	18		51	49	
Tanypodinae	PR	23		6			8			
Tanytarsini	PC	223					4	2		
Ephydridae										
NIF	PC							2		
Tabanidae										
Crysops sp.	PR	1				1		1		
Tabanus sp.	PR							1		
Tipulidae										
NIF	PC						2			
Gastropoda										
Physidae										
NIF	PC		13		47			166	6	
Annelida/Nematoda										
NIF	UN	6	280	186	420	307	191	164	242	
Copepoda										
NIF	PC		24	33	81	165	70	94	105	
Ostracoda										
NIF	PC		2		10	14		1	6	
Cladocera										
NIF	PC	1	6	37	165	300	102	67	194	

(Table 1 Continued)

		MAY 2006								
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Ephemeroptera										
Caenidae										
Caenis sp.	PC	3		4						
Odonata										
Coenagrionidae										
NIF	PR	2					2			
Lestidae										
Lestes sp.	PR						8	2	1	
Libellulidae										
Erythemis sp.	PR							3		
Sympetrum sp.	PR						8			
NIF	PR	2		4		1				
Hemiptera										
Corixidae										
NIF	UN			3		2	94	29	4	
Notonectidae										
Notonecta sp.	PR							4		
Coleoptera										
Dytiscidae										
Agabus sp.	PR						2	4		
Coptotomus sp.	PR						2	1		
Hydroporinae	PR			1		2	43	4	2	
Laccophilus sp.	PR						1			
Uvarus sp.	PR						8			
Haliplidae										
Peltodytes sp.	PC						2		1	
Hydrophilidae										
Berosus sp.	P*	2	1	16	1	2	23	8	2	
Enochrus sp.	P*			1			2	14	1	
Tropisternus sp.	P*				1	2	2	3		
Diptera										
Ceratopogonidae										
Bezzia sp.	PR	4			7					
Culicoides sp.	PR	3	3	5	15	3	2	1	1	
Chironomidae										
Chironomini	PC	14	14	3		2	2	1		
Orthocladinae	PC	20	59	34	106	8	54	11	16	
Tanypodinae	PR	10	2	11	3		2	3	2	
Tanytarsini	PC	76	9	2		1			3	
Culicidae										
Aedes sp.	PC						1		2	
Dolichopodidae										
NIF	PR					1				
Sciomyzidae										
NIF	PR		2					1		

(Table 1 Continued)

Taxa	FG	MAY 2006 2	3	6	7	10	11	15	17	19
Tabanidae										
Crysops sp.	PR						1			
NIF	PR			1						
Gastropoda										
Physidae										
NIF	PC		12	45	24	114		115	28	
Planorbidae										
NIF	PC			7				71	3	
Ancylidae										
NIF	PC			1				1	3	
Viviparidae										
NIF	PC	1								
Annelida/Nematoda										
NIF	UN	192	204	176	442	165	59	2	314	
Copepoda										
NIF	PC	11		12	76	68	3	12	271	
Ostracoda										
NIF	PC			2	29	102			137	
Cladocera										
NIF	PC	8		28	79	28	19	47	106	

(Table 1 Continued)

		JUNE 2006								
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Ephemeroptera										
Baetidae										
Callibaetis sp.	PC			1	1				3	
Caenidae										
Caenis sp.	PC	18	1	10						
Odonata										
Coenagrionidae										
Enallagma sp.	PR				7					
NIF	PR	1	1	13				2	9	
Lestidae										
Lestes sp.	PR							1		
Libellulidae										
Miathyria	PR				1					
Sympetrum sp.	PR								1	
Tramea sp.	PR								2	
Plathemis sp.	PR		2							
NIF	PR			13						
Hemiptera										
Belostomatidae										
Belostoma sp.	PR		2						1	
Corixidae										
Hesperocorixa	PC							1		
NIF	UN	1		3						
Nepidae										
Ranatra sp.	PR			1						
Coleoptera										
Dytiscidae										
Copelatus sp.	PR				1					
Hydroporinae	PR			1				1		
Hydroporus sp.	PR							2		
Hydrovatus sp.	PR							4		
Hygrotus sp.	PR				1					
Ilybius sp.	PR		1							
Neoporus sp.	PR							2		
Uvarus sp.	PR				2			1		
Haliplidae										
Haliplus sp.	PC			1						
Hydrophilidae										
Berosus sp.	P*	1	2	4	3				2	
Enochrus sp.	P*			1	5			3		
Hydrochus sp.	P*		2							
Tropisternus sp.	P*		2	2	3			1	4	
Noteridae										
Suphisellus sp.	PR	1						1	16	

(Table 1 Continued)

JUNE 2006										
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Diptera										
Ceratopogonidae										
Bezzia sp.	PR	11	6	33	14			10	54	
Culicoides sp.	PR		27	10	1			1	31	
Chironomidae										
Chironomini	PC	5	24	14	1				5	
Orthocladinae	PC	7	7	40					11	
Tanypodinae	PR	17	12	46	11			16	8	
Tanytarsini	PC	76	46		8			11		
Tabanidae										
Crysops sp.	PR			1					1	
Gastropoda										
Physidae										
NIF	PC	2		22	126			63	62	
Planorbidae										
NIF	PC	14	1	86				118	36	
Ancylidae										
NIF	PC				26					
Viviparidae										
NIF	PC		2							
Annelida/Nematoda										
NIF	UN	152	143	103	282			85	233	
Copepoda										
NIF	PC	24		8	13			56	19	
Ostracoda										
NIF	PC	1		2	12			78	6	
Cladocera										
NIF	PC	40		4	92			36	34	

(Table 1 Continued)

		JULY 2006								
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Ephemeroptera										
Baetidae										
Callibaetis sp.	PC	5		16	14	35		5	16	
Caenidae										
Caenis sp.	PC	40		5						
Odonata										
Aeshnidae										
NIF	PR	1								
Coenagrionidae										
Enallagma sp.	PR								13	
NIF	PR	6		8	5			3		
Lestidae										
Lestes sp.	PR			1		1		2		
Libellulidae										
Libellula sp.	PR	3								
Pachydiplax sp.	PR	1				1				
NIF	PR			2					3	
Hemiptera										
Belostomatidae										
Belostoma sp.	PR			2	2	3	1		1	
Corixidae										
NIF	UN	13			4	4	21	2	2	
Mesovelidae										
Mesovelia sp.	PR	1						1		
Coleoptera										
Dytiscidae										
Agabus sp.	PR			1						
Coptotomus sp.	PR				2	3	8	1		
Hydroporinae	PR	1		1	4	9	11	15	12	
Hydrovatus sp.	PR							2		
Laccophilus sp.	PR	1				4		3		
Liodessus sp.	PR					1	6			
Neoporus sp.	PR					1			1	
Rhantus sp.	PR						1			
Uvarus sp.	PR						1			
Hydrophilidae										
Berosus sp.	P*			1	6	1	46	6		
Enochrus sp.	P*	1				4		8	4	
Paracymus sp.	P*					1				
Tropisternus sp.	P*				10	10	2	3	4	
Noteridae										
Hydrocanthus	PR	1			4	3	3	25	15	
Suphisellus sp.	PR			9	2	3				
Trichoptera										
Leptoceridae										

(Table 1 Continued)

		JULY 2006								
Taxa	**FG**	**2**	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
Oecitis sp.	PR	2								
Diptera										
Ceratopogonidae										
Bezzia sp.	PR	15		21		1		1	28	
Culicoides sp.	PR	10		6	5			7	4	
Chaoboridae										
Chaoborus sp.	PR			3		3	12		1	
Chironomidae										
Chironomini	PC	8			5	1	110	2		
Orthocladinae	PC	13		70	60	15	4	32	47	
Tanypodinae	PR	31		58	1	3			31	
Tanytarsini	PC	148		45	30	5			4	
Culicidae										
Anopheles sp.	PC					1				
Culex sp.	PC				7	3			12	
Uranotaenia sp.	PC				1	3			7	
Tipulidae										
Limonia sp.	PC					1				
Tipula sp.	PC							1		
Gastropoda										
Physidae										
NIF	PC	2		3	93	88		18	36	
Planorbidae										
NIF	PC	5		3		9		65	27	
Ancylidae										
NIF	PC				1				5	
Viviparidae										
NIF	PC				44					
Annelida/Nematoda										
NIF	UN	29		74	7	93	60	98	39	
Copepoda										
NIF	PC	9		13	1	11	9	34	18	
Ostracoda										
NIF	PC			1				5		
Cladocera										
NIF	PC	30		56		45	2	77	164	

(Table 1 Continued)

AUGUST 2006

Taxa	FG	2	3	6	7	10	11	15	17	19
Ephemeroptera										
Baetidae										
Callibaetis sp.	PC	3	9	25	4		4	3	11	10
Caenidae										
Caenis sp.	PC	88	1	3			1	1	2	4
Odonata										
Aeshnidae										
Anax junius	PR		1	2	1					
Aeshna sp.	PR	1								
NIF	PR						1			
Coenagrionidae										
Enallagma sp.	PR								5	
NIF	PR	4	7	8	1		5	2		13
Libellulidae										
Erythemis sp.	PR			9			3		12	8
Libellula sp.	PR							6		
Sympetrum sp.	PR						18			11
Tramea sp.	PR				1					2
Pachydiplax sp.	PR		10	5	22					
NIF	PR	6								
Hemiptera										
Belostomatidae										
Belostoma sp.	PR		1	2	1				4	
Corixidae										
Hesperocorixa	PC		7							
NIF	UN	7								
Gerridae										
Trepobates sp.	PR				1					
Mesovelidae										
Mesovelia sp.	PR		6	3	6		1		1	6
Notonectidae										
Buenoa sp.	PR	5	5						2	
Notonecta sp.	PR			6	2		8			
Coleoptera										
Dytiscidae										
Copelatus sp.	PR							1		
Coptotomus sp.	PR		1							
Cybister sp.	PR		1				1			
Graphoderus sp.	PR	1								
Hydroporinae	PR			4			2	6	5	1
Neoporus sp.	PR								1	
Uvarus sp.	PR				1					2
Elmidae										
Dubiraphia sp.	PC						1			
Haliplidae										

(Table 1 Continued)

AUGUST 2006

Taxa	FG	2	3	6	7	10	11	15	17	19
Haliplus sp.	PC							1		
Peltodytes sp.	PC								1	
Hydrophilidae										
Berosus sp.	P*				1		4			1
Enochrus sp.	P*							1	3	
Hydrochara sp.	P*				1					
Hydrophilius sp.	P*							1		
Laccobius sp.	P*								1	
Tropisternus sp.	P*		4		2		5	2	5	3
Noteridae										
Hydrocanthus	PR	2	13	9	36		8	3	4	
Trichoptera										
Hydroptilidae										
Oxyethira sp.	PC	2								
Leptoceridae										
Oecitis sp.	PR	10								
Lepidoptera										
Pyralidae										
NIF	PC				3					
Diptera										
Ceratopogonidae										
Atrichopogon sp.	PC							1		
Bezzia sp.	PR	6			10		30	3	6	31
Culicoides sp.	PR	6		3	6		5	3	13	16
Chaoboridae										
Chaoborus sp.	PR			1	1		3		5	
Chironomidae										
Chironomini	PC			5	68		151	1	2	5
Orthocladinae	PC	4		45	66		69	73	41	77
Tanypodinae	PR	46	1	72	31		1	80	59	26
Tanytarsini	PC	103					16	7		3
Culicidae										
Anopheles sp.	PC				1					
Culex sp.	PC		20	6	8					1
Uranotaenia sp.	PC		10	13	2			2	3	
Dolichopodidae										
NIF	PR				1					
Tipulidae										
Tipula sp.	PC									1
Gastropoda										
Physidae										
NIF	PC	3	6	33				30	33	70
Planorbidae										
NIF	PC	20		34				111	117	5
Ancylidae										

(Table 1 Continued)

AUGUST 2006

Taxa	FG	2	3	6	7	10	11	15	17	19
NIF	PC			3					6	
Annelida/Nematoda										
NIF	UN	11	63	19	28		43	3	5	6
Copepoda										
NIF	PC	2	2		2		5			9
Ostracoda										
NIF	PC		2	3	2				2	3
Cladocera										
NIF	PC	32	20	20	23		22	15	5	111

Appendix B

Habitat Characteristics

Table 3A Data collected with handheld YSI probes in 2005 and 2006. Temp. is water temperature in °C. DO is dissolved oxygen. SpC is specific conductivity in µS/cm.

Table 3B Water chemistry data for 2005 and 2006. All values are in parts per million.

Table 3C Habitat characteristics of each wetland. Size was approximated in GIS using GPS boundary data from Towson University, and modified by Doug Samson. Values represent maximum area in acres. CWD added refers to if coarse woody debris was added during the time of construction. CWD amount refers to a subjective assessment by Doug Samson of the amount of coarse woody debris added (L= low, M= medium, and H= high). Straw Type refers to the type of straw added at the time of construction. Hydro is the hydroperiod estimate by the percent of sample dates (Jan. 2005 to Feb. 2007) when the cell water level was at or above half the maximum level. % Alg, % CWD, and % Veg are the percent of wetland containing an algae mat, coarse woody debris or vegetation.

(Table 3A)

2005

		2	3	6	7	10	11	15	17	19
MARCH	Temp.	4.26	4.44	4.34	4.7	5.3	4.42	5.01	5.23	8.95
	pH	7.32	7.31	7.21	7.41	7.30	4.43	7.29	7.52	7.52
	DO (mg/L)	8.79	8.46	8.94	8.1	8.7	7.32	8.18	8.8	9.6
	DO (%)	.	.	.	.	.	.	.	.	.
	SpC	87	75	58	75	88	60	69	100	98
APRIL	Temp.	14	13.6	15.3	13.6	13.9	11.8	13.3	14.1	15.4
	pH	6.82	6.97	6.94	7.01	7.01	4.49	6.85	7.18	6.96
	DO (mg/L)	7.68	7.86	7.22	6.59	7.55	3.97	6.9	9.39	8.26
	DO (%)	74.5	76.1	71.1	62.2	73.1	37.2	66.3	92.3	87.2
	SpC	54.7	59.5	61.1	57.2	57.6	18.9	46.9	31.9	27.2
MAY	Temp.	19	24.35	22.8	17.4	26.15	18.15	20.05	21.75	27.3
	pH	7.13	7.20	7.01	6.86	7.22	5.15	6.98	7.14	6.99
	DO (mg/L)	6.59	5.98	6.76	2.55	10.87	2.64	7.79	5.78	9.1
	DO (%)	73.5	68	78.1	28	129	29.5	84.6	69.1	108.8
	SpC	65.9	76	58.5	71.1	53.6	35.6	59.2	71.8	43.1
JUNE	Temp.	27.6	31.4	30.6	26.4	29.7	26.6	27.5	28.1	30.4
	pH	6.65	6.89	6.90	6.53	6.53	4.84	6.39	6.56	6.52
	DO (mg/L)	3.24	5.43	6.77	2.63	9.21	1.42	3.53	2.82	5.31
	DO (%)	39.2	75.3	90.5	31.5	125.8	18.5	47.1	35.5	73.6
	SpC	60.5	73.2	59.1	58.5	69	40.6	63.9	72	58.2
JULY	Temp.	29.7	35.4	34.8	27.7	32.9	29.6	29.2	29.2	33.3
	pH	7.12	7.18	7.20	6.36	6.86	6.17	6.77	7.20	7.08
	DO (mg/L)	5.11	9.12	7.31	4.3	7.6	2.74	3.74	5.04	6.15
	DO (%)	68.4	133.5	102.2	55.3	104	37.4	50.4	68.2	87.4
	SpC	66.2	46.7	48.5	28.5	57.2	34.3	40.4	66.6	43.7
AUGUST	Temp.	27	27.4	28.2	24.9	.	.	26.1	26.8	26.1
	pH	6.80	6.83	6.87	6.13	.	.	6.50	6.97	6.38
	DO (mg/L)	3.12	5.81	4.69	1.07	.	.	1.46	2.27	1.31
	DO (%)	38.6	72.8	60.2	13.7	.	.	15.3	28	15.4
	SpC	58.8	49.9	64.6	43.9	.	.	58.6	64.4	61.6

(Table 3A Continued)

2006

		2	3	6	7	10	11	15	17	19
MARCH	Temp.	8.7	11.1	11.7	9.8	13.1	9.6	9.7	9.6	12.3
	pH	6.96	7.24	7.28	7.33	7.38	4.90	7.29	8.53	7.74
	DO (mg/L)	12.77	14.54	13.94	11.38	13.37	11.05	13.57	15.87	15.22
	DO (%)	109.2	131.5	126.9	98	134.2	97.3	120.4	138.7	141.5
	SpC	74.4	89.8	72.8	84.6	82.8	42.7	89.1	89.7	104.7
APRIL	Temp.	13.2	14	14.8	12.2	13.6	15.3	14.2	14.4	14.5
	pH	7.12	6.68	7.23	7.36	6.57	5.32	7.42	7.26	7.12
	DO (mg/L)	9.65	11.8	10.65	7.58	10.46	8.33	4.51	11.81	9.77
	DO (%)	93.1	116	106.8	51.6	99.5	83.1	45.4	114.3	99.9
	SpC	94	115	84.6	93	100.2	46.8	45.7	104.4	128.6
MAY	Temp.	15.9	18.7	21.7	14.8	16.3	15.9	15.4	14	18.3
	pH	7.43	7.10	7.32	7.24	6.77	5.05	6.82	7.29	7.39
	DO (mg/L)	7.88	8.24	8.12	6.65	4.36	5.4	11.97	28.2	9.05
	DO (%)	81.4	88.9	100.5	62.8	42.5	58.4	111.5	25.7	96.9
	SpC	95	91.8	83.9	73.2	72.6	47.2	81.1	87.5	82.6
JUNE	Temp.	27.1	26.5	30.4	28.4	.	.	26	25.6	.
	pH	7.08	6.84	6.88	6.74	.	.	6.60	7.03	.
	DO (mg/L)	1.44	0.09	0.007	2.14	.	.	0.92	0.08	.
	DO (%)	17.2	1.1	0.9	27	.	.	7.9	1.9	.
	SpC	110.5	111.6	98.8	75.8	.	.	104.7	100.8	.
JULY	Temp.	27	29.2	27.8	25.5	29.7	25.2	26.5	26.6	27.6
	pH	6.92	6.95	6.85	6.91	6.86	4.54	6.59	6.71	6.82
	DO (mg/L)	3.58	0.86	1.03	1.27	5.49	0.18	0.82	1.27	6.97
	DO (%)	44.7	8.8	13.4	15.6	72.8	3.4	10.4	16	88.8
	SpC	54.8	70.2	70	95.3	78.1	46	58.9	69.3	71.3
AUGUST	Temp.	27.4	31.5	29.2	24.8	.	28.9	24.8	26.6	26.6
	pH	7.01	7.16	6.84	6.40	.	4.90	6.50	6.57	6.03
	DO (mg/L)	6.83	7.42	3.15	2.39	.	6.77	1.25	2.55	2.31
	DO (%)	83.7	96.6	37.1	30.1	.	87.6	16.1	30.5	31
	SpC	53	54.9	64.5		.	27.4	54.6	54.8	33.5

(Table 3B)

2005

		2	3	6	7	10	11	15	17	19
MARCH	NH4-N	0.008	0.007	0.007	0.005	0.008	0.001	0.004	0.004	0.005
	NO3-N	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
	NO2-N	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	PO4-P	0.002	0.011	0.003	0.044	0.007	0.020	0.009	0.028	0.007
	Cl	6.4	4.9	3.9	2.9	5.2	3.8	4.5	5.0	5.7
	SO4	4.0	3.7	2.8	2.3	3.8	4.3	2.6	3.3	5.0
	TN	2.1	1.0	1.2	1.6	1.9	0.9	1.1	1.1	1.4
	TP	0.182	0.073	0.073	0.144	0.180	0.059	0.079	0.097	0.099
	TDN	1.0	0.9	1.1	1.3	1.1	0.8	1.0	0.9	1.1
	TDP	0.029	0.038	0.029	0.092	0.048	0.036	0.045	0.056	0.045
APRIL	NH4-N	0.014	0.010	0.006	0.007	0.014	0.001	0.004	0.006	0.007
	NO3-N	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
	NO2-N	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	PO4-P	0.004	0.008	0.006	0.048	0.016	0.054	0.052	0.029	0.013
	Cl	3.0	2.8	3.2	1.2	2.3	1.9	1.9	2.6	2.7
	SO4	1.5	1.3	1.5	0.7	1.2	0.8	0.9	1.3	0.9
	TN	1.0	0.9	1.0	1.1	0.9	1.3	0.9	0.9	1.0
	TP	0.055	0.057	0.053	0.108	0.061	0.107	0.108	0.075	0.056
	TDN	0.9	1.0	0.9	1.2	0.9	1.3	0.9	0.9	1.0
	TDP	0.038	0.040	0.039	0.095	0.051	0.101	0.094	0.063	0.046
MAY	NH4-N	0.015	0.014	0.012	0.050	0.024	0.126	0.016	0.014	0.009
	NO3-N	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
	NO2-N	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	PO4-P	0.001	0.004	0.003	0.215	0.035	0.149	0.112	0.055	0.041
	Cl	2.9	3.6	3.8	2.4	3.2	2.8	2.4	3.0	5.0
	SO4	1.5	1.4	1.4	0.7	0.6	0.8	0.8	1.1	0.7
	TN	1.8	2.1	2.1	4.4	4.1	2.2	2.4	2.5	4.4
	TP	0.072	0.117	0.108	0.644	0.292	0.246	0.278	0.237	0.364
	TDN	1.6	1.8	1.9	3.6	3.7	2.0	2.2	2.1	3.5
	TDP	0.051	0.076	0.082	0.412	0.219	0.223	0.248	0.178	0.206
JUNE	NH4-N	0.007	0.009	0.006	0.013	0.018	0.001	0.011	0.015	0.007
	NO3-N	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
	NO2-N	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	PO4-P	0.002	0.014	0.002	0.138	0.031	0.125	0.133	0.054	0.034
	Cl	3.0	3.0	2.4	1.7	2.1	2.5	1.6	2.1	1.6
	SO4	1.3	1.5	1.3	0.1	0.9	0.8	0.9	0.9	0.1
	TN	2.4	2.4	2.1	4.0	3.9	2.3	2.3	2.7	3.7
	TP	0.124	0.130	0.092	0.353	0.293	0.195	0.274	0.249	0.235
	TDN	2.8	2.4	2.0	3.8	2.9	2.3	2.2	2.3	3.5
	TDP	0.046	0.095	0.070	0.296	0.129	0.158	0.245	0.150	0.203

(Table 3B Continued)

2005

		2	3	6	7	10	11	15	17	19
JULY	NH4-N	0.013	0.011	0.010	0.005	0.029	0.012	0.011	0.018	0.008
	NO3-N	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
	NO2-N	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	PO4-P	0.004	0.010	0.002	0.018	0.006	0.463	0.011	0.129	0.113
	Cl	1.9	1.8	2.3	0.2	1.6	1.7	1.1	1.3	0.5
	SO4	0.5	1.0	0.7	0.4	0.4	0.9	0.6	0.4	0.4
	TN	2.0	2.1	1.9	2.6	3.6	1.4	2.4	2.1	1.7
	TP	0.105	0.184	0.083	0.349	0.275	0.688	0.219	0.300	0.249
	TDN	1.6	1.5	1.4	1.4	2.1	1.0	1.5	1.4	1.5
	TDP	0.046	0.062	0.040	0.077	0.072	0.548	0.077	0.204	0.202
AUGUST	NH4-N	0.021	0.015	0.034	0.005	.	.	0.012	0.018	0.033
	NO3-N	0.01	0.01	0.01	0.01	.	.	0.01	0.01	0.01
	NO2-N	0.001	0.001	0.001	0.001	.	.	0.001	0.001	0.001
	PO4-P	0.004	0.004	0.005	0.037	.	.	0.006	0.018	0.042
	Cl	1.3	1.1	2.2	0.2	.	.	0.3	0.7	0.4
	SO4	0.5	1.0	0.7	0.1	.	.	0.4	0.4	0.4
	TN	3.0	3.1	3.2	3.5	.	.	2.7	2.6	4.7
	TP	0.196	0.240	0.227	0.308	.	.	0.173	0.310	0.493
	TDN	1.9	1.6	2.1	2.0	.	.	1.7	1.8	2.1
	TDP	0.043	0.056	0.067	0.100	.	.	0.062	0.099	0.117

(Table 3B Continued)

2006

		2	3	6	7	10	11	15	17	19
MARCH	NH4-N	0.011	0.017	0.011	0.007	0.006	0.001	0.010	0.009	0.008
	NO3-N	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
	NO2-N	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	PO4-P	0.001	0.001	0.001	0.003	0.001	0.017	0.004	0.006	0.001
	Cl	5.8	6.8	5.6	3.9	5.9	4.4	7.4	5.7	6.6
	SO4	2.7	4.2	2.5	1.6	2.9	1.6	3.6	3.5	2.1
	TN	1.8	1.3	1.2	1.5	1.5	0.9	1.0	1.0	1.3
	TP	0.124	0.096	0.065	0.097	0.165	0.066	0.044	0.048	0.054
	TDN	1.0	0.9	1.0	1.2	1.1	0.9	0.9	0.9	1.1
	TDP	0.023	0.028	0.023	0.035	0.039	0.061	0.033	0.035	0.033
APRIL	NH4-N	0.013	0.233	0.015	0.015	0.027	0.015	0.009	0.013	0.042
	NO3-N	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
	NO2-N	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	PO4-P	0.004	0.182	0.001	0.003	0.030	0.017	0.074	0.007	0.001
	Cl	9.7	5.6	6.8	5.6	6.3	6.0	6.7	8.6	7.4
	SO4	4.9	1.1	2.6	1.0	2.5	1.2	3.4	1.2	2.9
	TN	2.7	15.8	2.2	2.2	5.3	2.6	2.5	5.2	3.5
	TP	0.302	1.468	0.111	0.063	0.865	0.231	0.319	0.685	0.263
	TDN	1.6	3.5	1.6	2.1	2.1	1.7	1.9	2.0	2.0
	TDP	0.061	0.256	0.030	0.045	0.085	0.077	0.155	0.054	0.031
MAY	NH4-N	0.023	0.018	0.034	0.008	0.009	0.001	0.008	0.007	0.007
	NO3-N	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
	NO2-N	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	PO4-P	0.001	0.010	0.003	0.025	0.012	0.057	0.007	0.107	0.003
	Cl	6.7	5.8	6.3	3.1	3.1	4.5	6.4	4.3	4.3
	SO4	2.3	4.2	2.3	0.7	1.0	0.8	2.3	2.1	0.8
	TN	2.0	2.6	2.9	3.2	10.2	1.9	2.8	2.0	2.7
	TP	0.095	0.244	0.174	0.205	0.899	0.170	0.233	0.280	0.097
	TDN	1.7	1.7	2.4	2.7	3.0	1.5	1.8	1.6	2.4
	TDP	0.040	0.078	0.065	0.104	0.088	0.101	0.072	0.182	0.066
JUNE	NH4-N	0.205	0.028	0.324	3.527	.	.	0.006	0.024	.
	NO3-N	0.01	0.01	0.01	0.01	.	.	0.01	0.01	.
	NO2-N	0.001	0.001	0.001	0.001	.	.	0.001	0.001	.
	PO4-P	0.008	0.006	0.006	0.035	.	.	0.001	0.053	.
	Cl	9.2	9.3	9.3	6.6	.	.	9.9	8.1	.
	SO4	1.8	3.8	1.6	1.1	.	.	2.0	2.0	.
	TN	3.6	12.4	6.3	18.1	.	.	4.8	6.0	.
	TP	0.166	1.247	0.474	1.337	.	.	0.435	0.863	.
	TDN	3.2	3.2	3.3	12.6	.	.	2.8	2.6	.
	TDP	0.085	0.089	0.084	0.309	.	.	0.082	0.171	.

(Table 3B Continued)

		2006								
		2	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
JULY	NH4-N	0.019	0.025	0.019	0.017	0.084	0.041	0.007	0.020	0.015
	NO3-N	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
	NO2-N	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001
	PO4-P	0.020	0.190	0.141	0.266	0.475	0.316	0.238	0.460	0.219
	Cl	2.5	2.7	2.7	1.9	2.8	2.7	2.5	2.2	2.7
	SO4	1.5	0.9	1.0	0.7	0.5	0.6	0.6	0.6	0.7
	TN	1.9	1.5	1.7	2.1	3.3	2.3	1.4	2.0	1.7
	TP	0.181	0.343	0.301	0.701	1.093	0.384	0.397	0.783	0.384
	TDN	1.2	1.2	1.2	1.3	1.7	1.8	1.0	1.3	1.3
	TDP	0.075	0.258	0.209	0.330	0.598	0.321	0.307	0.536	0.283
AUGUST	NH4-N	0.020	0.018	0.012	0.021	.	0.009	0.011	0.125	0.027
	NO3-N	0.01	0.01	0.01	0.01	.	0.01	0.01	0.01	0.01
	NO2-N	0.001	0.001	0.001	0.001	.	0.001	0.001	0.001	0.001
	PO4-P	0.001	0.031	0.081	0.033	.	0.059	0.035	0.144	0.043
	Cl	1.8	1.1	2.1	0.4	.	2.0	2.7	1.4	0.2
	SO4	0.5	0.4	0.6	0.1	.	0.5	0.3	0.3	0.3
	TN	2.7	3.0	2.6	4.2	.	2.8	2.8	3.4	3.3
	TP	0.195	0.300	0.264	0.261	.	0.229	0.237	0.391	0.227
	TDN	1.7	2.5	2.0	3.2	.	1.8	2.0	2.2	2.7
	TDP	0.055	0.134	0.164	0.115	.	0.124	0.114	0.218	0.132

(Table 3C)

		Wetland								
		2	**3**	**6**	**7**	**10**	**11**	**15**	**17**	**19**
ALL MONTHS	Size	9.1	2.1	1.4	2.7	1.4	4.7	2.9	1.9	0.8
	CWD added	Y	Y	Y	N	Y	N	Y	Y	N
	CWD amount	L	H	M	L	L	L	M	L	L
	Straw Type	wheat	barley	barley	barley	wheat	wheat	wheat	none	wheat
	HydroPeriod	94.0	68.8	60.0	65.3	57.1	62.0	78.0	74.0	64.6
		2005								
MARCH	% Alg	0	0	0	0	0	0	0	0	0
	% CWD	5	15	10	0	10	0	10	5	0
	% Veg	25	50	30	95	85	90	55	90	95
APRIL	% Alg	0	0	0	0	0	0	0	0	0
	% CWD	5	15	10	0	10	0	10	5	0
	% Veg	25	30	30	95	100	80	40	60	60
MAY	% Alg	0	20	0	0	60	0	10	0	0
	% CWD	5	30	10	0	10	0	10	5	0
	% Veg	15	40	30	90	100	50	60	50	70
JUNE	% Alg	0	15	0	0	70	0	15	25	0
	% CWD	5	15	10	0	10	0	10	5	0
	% Veg	20	40	50	95	100	60	80	70	90
JULY	% Alg	0	0	0	0	25	0	0	0	0
	% CWD	5	15	10	0	10	0	10	5	0
	% Veg	80	45	40	95	100	50	95	95	90
AUGUST	% Alg	0	0	0	0	.	.	0	0	0
	% CWD	5	15	10	0	.	.	10	5	0
	% Veg	80	60	40	100	.	.	100	95	20
		2006								
MARCH	% Alg	0	0	0	0	0	0	0	10	0
	% CWD	5	30	10	0	10	0	10	5	0
	% Veg	20	60	10	80	75	60	70	20	90
APRIL	% Alg	0	0	0	0	0	0	0	10	0
	% CWD	5	30	10	0	10	0	10	5	0
	% Veg	20	40	30	90	65	60	100	35	30
MAY	% Alg	0	0	0	0	20	0	0	20	0
	% CWD	5	30	10	0	10	0	10	5	0
	% Veg	20	50	30	90	100	60	90	50	30
JUNE	% Alg	0	0	0	0	.	.	0	0	.
	% CWD	5	30	10	0	.	.	10	5	.
	% Veg	30	50	40	100	.	.	100	50	.
JULY	% Alg	0	0	0	0	0	0	0	0	0
	% CWD	5	30	10	0	10	0	10	5	0
	% Veg	20	25	30	90	90	50	90	50	30
AUGUST	% Alg	0	0	0	0	.	0	0	0	0
	% CWD	5	30	10	0	.	0	10	5	0
	% Veg	30	40	40	100	.	50	90	60	90

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