DOES HISTORY MATTER? AN EXPERIMENTAL ASSESSMENT OF WHETHER

DRAGONFLY COLONIZATION HISTORY AFFECTS INSECT BIODIVERSITY WITHIN

EPHEMERAL PONDS

by

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Current interactions among species could have an important role in controlling biodiversity. Some studies, however, have shown that the particular time a species arrives at a site during the process of community assembly could alter the strength of species interactions within ecological communities. Such priority effects should be important in frequently disrupted environments, such as temporary ponds, which provide opportunities for new collections of species to colonize the refilled pond. In temporary ponds, the top predators are often dragonfly naiads. The particular time that dragonflies arrive at a pond is dependent, in part, on dragonfly breeding phenology and pond isolation. I tested the hypothesis that the arrival time of dragonfly naiads to ephemeral ponds influences the biodiversity of aquatic insects present in the pond. To test this hypothesis, I experimentally altered the time dragonflies could oviposit eggs into artificial ponds (modified stock tanks) and quantified insect biodiversity within each pond after four months of community assembly.

I found that early-arriving dragonflies inhibited the successful recruitment of late-arriving dragonflies. The dragonfly colonization history of a pond affected the total

number of insect species in a pond by altering the number of coleopteran and heteropteran species present. Coleopterans were less diverse in ponds where dragonflies colonized at any point in time during the process of community assembly. However, heteropterans were more diverse in ponds that had only early-arriving dragonflies compared to ponds with continuous dragonfly colonization. The presence of dragonflies during any time of colonization decreased the abundance of adult insects. Alternatively, dragonfly arrival time did not influence the species richness, abundance or species evenness of juvenile insects. The results indicate the timing at which key species arrive to a community can substantially alter the biodiversity of an ephemeral pond. Dragonfly colonization history most impacted aquatic obligates, such as coleopterans and heteropterans. Changes in adult species richness and abundance of aquatic insects were likely because of a combination of two factors: *(i)* coleopterans and heteropterans preferentially selecting ponds with low abundances of dragonfly naiads for increased success of offspring; *(ii)* dragonfly predation on juvenile insects which reduced the abundance of individuals able to complete metamorphosis.

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INTRODUCTION

To better conserve our planet's biodiversity, an important challenge to ecologists is to enhance our understanding of spatial and temporal variability in biodiversity and the processes that produce this variation (Pianka 2000). One factor thought to play an influential role in controlling biodiversity is the time at which particular species arrive to a community (Morin 1999). The relative arrival time of species to a community could substantially alter the intensity of species interactions (e.g., predation or competition) known to affect biodiversity (Morin 1999). These priority effects result when early colonizers have (or gain) a trait that causes them to exclude, hinder or facilitate colonists arriving later (Connell and Slatyer 1977). Generally, the first species to arrive at a resource likely would gain an advantage and could be responsible for changing species dominance within a community, although the first species to arrive to a habitat does not always change the community structure (Polis et al. 1989).

At least two processes could influence the relative arrival time of a species to a habitat. First, differences in species-specific breeding phenology could cause different species to arrive to a community at different times in the process of community assembly. Species that breed earlier in the year will arrive to a habitat before species that breed later in the year (Corbet 1954, Corbet and Corbet 1958, Benke and Benke 1975, Benke et al. 1982). Anisoptera (dragonflies) could be grouped into either spring or summer species based on when dragonfly naiads emerge as adults, although intermediate emergence does occur. Spring species of dragonfly will oviposit eggs during late summer and adults will synchronously emerge the next spring. Alternatively, summer breeders oviposit eggs early in the summer with adults emerging asynchronously throughout that summer. It is likely both spring and summer species will be present in a body of water at one time. The spring species oviposit eggs into waters that may have summer dragonfly

naiads present, while the summer adults will oviposit eggs throughout the summer into waters that may have early species already present (Corbet 1954, Corbet and Corbet 1958, Morin 1999).

A second factor affecting the relative arrival time of a species to a habitat is the extent to which the habitat patch is isolated from other patches (Ims and Yoccoz 1997, Conrad et al. 2002, Massot et al. 2002, Dingemanse et al. 2003, Cote and Clobert 2007). For example, variation occurs in the time it takes dragonflies to find and oviposit eggs into a body of water (McCauley 2006, 2007, McCauley et al. 2008, McCauley et al. 2010). Adult dragonflies likely would oviposit in a body of water closer to a source pond, rather than a more isolated body of water. The dispersal distance from a source habitat to an isolated habitat could cause variation in colonization (e.g. oviposition) rates both within and among dragonfly species (McCauley et al. 2010).

Here I examine whether the arrival time of dragonflies to an ephemeral pond undergoing community assembly affects the diversity and abundance of insects in the pond. Previous studies have examined how variation in the time that dragonfly naiads were introduced into an assembling community affected species interactions between early-arriving dragonfly naiads and late-arriving dragonfly naiads (Benke 1978, Morin 1984a). These studies examined how the timing of dragonfly oviposition affected species richness and abundance of dragonfly naiads present in enclosures placed within fish ponds. Benke's (1978) and Morin's (1984a) work demonstrated that the arrival time of dragonflies to a fish pond alters the strength of species interactions among dragonfly naiads. Early-arriving dragonflies inhibited the success of late-arriving dragonflies such that species composition was altered and the abundance of dragonflies later in the season was reduced (Benke 1978, Benke et al. 1982, Morin 1984a). In these studies, dragonfly individuals that arrived early likely gained a competitive advantage because a larger

size allowed them to better deplete resources (exploitative competition) or fight over a limited resource (interference competition) (Benke 1978, Benke et al. 1982, Morin 1984a).

Cannibalism may be another mechanism hindering the success of late-arriving dragonflies, which the larger early-arriving dragonflies likely consume (Benke 1978, Morin 1984a, 1999). Cannibalism is more likely to occur in habitats when a species is present in multiple sizes and different age classes (Polis et al. 1989) that are likely for dragonfly naiads because of phenology and species size differences. In studies by Benke (1978) and Morin (1984a), dragonfly naiads colonized throughout the experiment, allowing both early-arriving (large size class) and late-arriving (small size class) individuals in the enclosures simultaneously, allowing different size classes of a species to coexist in a habitat. This phenomenon was previously recognized in other dragonfly communities (Kormondy and Gower 1965, Benke and Benke 1975, Wissinger 1988a, 1988b). However, not all dragonflies are equally susceptible to cannibalism (Robinson and Wellborn 1987, Johansson 1993b). Visual predators will more easily detect an actively foraging organism (Woodward 1983, Lawler 1989, Werner and Anholt 1993) or that higher prey activity levels increase the encounter rates of a predator (Gerritsen and Strickler 1977). These traits may cause active individuals to be at a greater risk of predation by a visual predator than less-active individuals (Lima and Dill 1990, Werner and Anholt 1993, Skelly 1994). Cannibalistic odonates occur frequently (Warren 1915, Wilson 1920, Benke et al. 1982, Morin 1984a, Johnson et al. 1985, Robinson and Wellborn 1987, Polis et al. 1989, Wissinger 1989, Johansson 1993a, 1993b, Morin 1999) and will consume conspecifics as well as other dragonfly species (Wilson 1920). Within odonate communities, as well as in Benke's (1978) and Morin's (1984a) experiments, populations may be regulated by a combination of

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competition for prey items and predation of the small dragonflies by the larger dragonflies (Morin 1984a, 1999).

Differences in dragonfly arrival time also could influence the abundance of potential dragonfly prey items. Benke (1978) found Chironomidae, Tanypodinae and *Caenis* (all potential dragonfly prey items) were more abundant in enclosures placed in fish ponds where only late-arriving dragonflies were present and less abundant in enclosures with only early-arriving dragonflies. However, Morin (1984a) found no difference in abundance of Chironomidae, *Cloeon* spp. or *Caenis* (Tanypodinae was not measured in his study) when dragonfly arrival time was altered.

Although Benke's (1978) and Morin's (1984a) experiments were conducted in permanent fish ponds, they intended to create a fish-free environment in which to examine dragonfly assemblages by not allowing fishes into enclosures. The influence of dragonflies in such ponds, however, may still be affected by the presence of fishes outside enclosures. Prior studies have shown that prey items behave differently in the presence of chemical cues emitted by a non-lethal predator (Dodson et al. 1994, Peacor and Werner 1997, Peckarsky and McIntosh 1998). Even though fishes were not present in Benke's (1978) and Morin's (1984a) experiments, the chemical cues emitted by fishes would be present within the experimental enclosures. Dragonfly naiads were less active in the presence of lethal or non-lethal fish predators compared to dragonfly naiads in fish-free environments (Dixon and Baker 1988, Blois-Heulin et al. 1990, McPeek 1990, Johansson et al. 2006, McCauley 2008).

There are trade-offs to reducing activity in the presence of a predator. More active species are more likely to encounter prey items, thus growing faster than less-active species. However, active foragers also increase their likelihood of being consumed by a predator (Lima

and Dill 1990, Werner and Anholt 1993). Specifically, it is possible that inactive dragonflies are consuming fewer prey than actively foraging dragonflies, which may be the case in Benke's (1978) and Morin's (1984a) dragonfly colonization works conducted in fish ponds. If dragonfly naiad activity is different in fish-free ponds compared to fish ponds, foraging behavior of the predacious dragonflies may not have the same influence on the biodiversity of ephemeral ponds as permanent fish ponds. Consequently, the results of Benke's (1978) and Morin's (1984a) studies may not pertain to a different habitat where fishes are completely absent.

I studied how the arrival time of dragonflies to an assembling ephemeral (fish-free) pond community influences interactions among dragonfly naiads and the biodiversity of aquatic insects present. I hypothesized that ponds with continuous dragonfly colonization should have low biodiversity because predation pressure from dragonfly naiads would be present from the beginning of community assembly. Ponds with no dragonfly colonization should have high biodiversity because there is no predation pressure from dragonfly naiads. Intermediate levels of biodiversity will occur when dragonflies colonize ponds either early or late in community assembly compared to when dragonflies constantly colonize or never colonize ponds. Ponds with only early-arriving dragonflies may have reduced biodiversity because predacious dragonflies prevent other species from successfully colonizing a pond. However, ponds with only late-arriving dragonflies should have greater biodiversity since there would be a delay in colonization. A delay in dragonfly colonization may allow some insects to grow large enough to escape predation from relatively small dragonflies that have just arrived to the pond, thus allowing some insect populations to persist after dragonfly naiads arrive.

METHODS

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Experimental Design

To test the hypothesis that differences in arrival time of dragonfly naiads will influence the biodiversity of the insect community, I conducted an experiment that simulated fish-free ephemeral ponds. Artificial ponds were created by modifying an 1100 l cattle tank that contained a rotatable L-shape pipe within the tank to control water depth (e.g. Morin 1981). Artificial ponds such as these have been proven to be useful in the past and are an important study venue because (*i*) many factors of interest can be controlled that natural systems may not allow, (*ii*) they offer the opportunity for greater replication that could increase statistical power and (*iii*) each pond is considered an independent experimental unit (Wilbur 1987, Chalcraft et al. 2005). The experiment included four different treatments (*i*) open treatments that allowed dragonflies to colonize a pond throughout the summer, (*ii*) early treatments that allowed dragonfly colonization early in the summer, (*iii*) late treatments that allowed dragonfly colonization later in the summer and (*iv*) a closed treatment that inhibited dragonfly colonization during the entire summer.

Five groups of four artificial ponds spaced approximately 1.5 m apart were placed in an open field at East Carolina University's West Research Campus (WRC) in Greenville, North Carolina (35°37'57"N 77°28'56"W). Each group was identified as a different statistical block. All methodological steps were conducted on a block-by-block basis to minimize within-block variation not attributable to treatment. Such blocking allows for the removal of effects of any spatial gradient (e.g. proximity to roads and ditches) or methodological differences that may influence response variables. Each of the four treatments was randomly assigned to one tank within each of the five blocks.

On May 13, 2008 each artificial pond was filled with approximately 1000 l of well water. To increase the realism of artificial ponds, 0.75 kg of mixed hardwood/pine leaf litter was added as substrate and refugia. At the beginning of the experiment, ponds designated as closed treatments or late summer treatments were covered with a mesh cover. The mesh covers had 3.2 cm by 3.8 cm openings, sufficient to inhibit organisms with wide wing spans (i.e., dragonflies) from colonizing while at the same time allowing all other aquatic invertebrates to colonize and oviposit eggs into the artificial ponds. On June 23, 2008 the late summer treatment was uncovered, and the early summer treatment was covered with mesh covers to prevent dragonfly colonization. This date was chosen because it was the halfway point between the start and end of the experiment (end of summer).

Throughout the experiment, ponds were checked at least three times a week for dragonfly exuvia that were identified to species (Brigham et al. 1982). The number of dragonfly exuvia collected from a pond provides the population density of newly emerged adults (Southwood 1978). The date dragonfly exuvia were collected was used to estimate the average time at which dragonflies completed metamorphosis (Southwood 1978).

The experiment was maintained until August 12, 2008. At the end of the experiment, each artificial pond was subsampled for organisms. Four people took sweeps simultaneously with a fine meshed aquarium net four times for a total of sixteen sweeps per artificial pond. Sampling location and sampling depth were consistent in all ponds. The mesh net opening used for insect collection was large enough to sample the entire water column, including leaf substrate, in one sweep event because the water depth in ponds was lowered because of natural water evaporation. This sweeping method allowed a uniform collection and representative sample of the aquatic insects from an artificial pond (Blaustein 1998). Insects and leaves were

preserved in 70% ethanol and returned to the laboratory for processing. Once in the lab, insects were separated by size classes using three different sieve sizes (>2mm, >1mm and >500μm). I randomly selected 30% of the sieve >500μm to subsample because of time constraints. To select 30% of the sample, the mass of the >500μm subsample was divided equally into 20 sections. I randomly selected 6 of the 20 sections (i.e., 30% of the original subsample) to sample for insects. The insects in 30% of the >500μm sample is sufficient and accurately represents the diversity within the sample (Lamberti et al. 1991). Insects were identified to lowest classification, often to species (Brigham et al. 1982, Merritt et al. 1996, Ciegler 2003). Chironomid spp. larvae and pupae were identified to morphotype because of difficulty distinguishing among species.

Response Variables and Data Analysis

Dragonflies

I measured the following response variables: (*i*) the number of dragonflies that completed metamorphosis on a particular day, (*ii*) the abundance of naiads collected at the end of the experiment, (*iii*) the abundance of dragonfly naiads at the end of the experiment that were greater than 2mm in body length and (*iv*) the total abundance (summed value of exuvia and naiads) of each dragonfly species in a pond. Examining different size classes of dragonfly naiads could reveal how many dragonfly naiads successfully achieved a larger size class without being eliminated from a pond by competition or cannibalism.

To examine whether early-arriving dragonflies caused a greater reduction in the abundance of late-arriving dragonflies in an ephemeral pond environment than in a permanent fish pond, I quantified the strength of priority effects in this study (conducted in an environment designed to simulate an ephemeral, fish free habitat) with the strength of priority effects derived

from Morin's (1984a) study conducted in a permanent fish pond. The strength of a priority effect within an experiment was estimated as:

$$\frac{\text{(dragonfly abundance in all summer treatment} - \text{dragonfly abundance in late summer)}}{\text{dragonfly abundance in late summer}}$$

The equation describes the proportional change in dragonfly abundance that was associated with allowing early breeding dragonflies to access a pond where late breeding dragonflies would be found. Calculated values of the strength of priority effect closer to zero indicate a smaller priority effect while values of -1 indicate that early-arriving dragonflies completely hindered the arrival of the late-arriving dragonflies.

Insect Biodiversity

I calculated species richness (S), total abundance and species evenness ($E = (1/\Sigma p_i^2)/S$ where p_i is the proportional abundance of species *i*) of the insects collected from each artificial pond. Dragonfly naiads were excluded from all measurements since dragonflies were the treatment manipulation. Species richness (S) was estimated in each pond by counting the number of distinct species present in the pond. Individuals identified only to genus were excluded from species richness estimates unless they were the sole representatives of the genus. In this case, the sole representative of the genus would increase species richness by 1 species although the individuals of the genus may actually be multiple species. The few times the sole representative of the genus was used to calculate species richness were dispersed evenly among treatments and should not bias species richness in this study. Species evenness was conducted at the genus level because it was the lowest taxonomic level ascertainable for all insects collected.

Species richness, abundance and species evenness were calculated for the total community, juvenile insects and adult insects. Juvenile insects are composed of larvae, pupae or

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nymphs life history stages of insects. Some insects have distinct juvenile life history stages before completing metamorphosis to adults. Adult is a life history stage of some aquatic insects that are capable of dispersing to other habitats. However, adult insects are primarily aquatic insects. For example, the coleopteran, *Laccophilus proximus,* occurs in aquatic environment developing as larvae then completes metamorphosis. As an adult, *Laccophilus proximus* may remain in natal habitats or disperse to new habitats. Successful oviposition of offspring could be examined by comparing the juvenile insects, whereas a focus on the adult insects allows us to examine colonization by adults. To determine if dragonfly arrival time influenced the total community biodiversity, three individual ANOVAs with block effects were used to determine if treatments differed in species richness, abundance and species evenness. Similar ANOVAs with block effects were conducted for the same three measurements when applied only to the juvenile insects present and when applied only to the adult insects present.

The abundance of species in a pond could influence species richness. This phenomenon could be tracked with a rarefaction curve, which I used to make comparisons of species richness of adults among ponds when abundances of adults among ponds differed. (Rarefaction curves were not used to examine total community or juvenile community because some individuals were identified only to genus and could not be identified to species.) Rarefaction curves were based on an equivalent number of individuals collected from a pond to predict the species richness of a pond (Vinson and Hawkins 2003). The number of individuals selected for rarefaction calculations was based on the pond with the lowest abundance. I utilized an individual-based rarefaction curve for each artificial pond using EcoSim (Gotelli 2009). Rarefaction estimation was repeated for 1000 random samplings without replacement, which is considered to be highly accurate (Both et al. 2009). Using this estimate of species richness, I

could compare species richness among ponds to determine if the species richness of a pond differed without species abundance confounding the richness estimate (Gotelli 2009). I examined the correlations between species richness, abundance and evenness to determine how these variables were related to one another. Correlations were conducted at the community, juvenile and adult levels using correlations in SAS.

To determine which orders of insects were most influenced by dragonfly colonization history, I calculated species richness (S) within each of the five insect orders present in a pond. Five separate ANOVAs with block effects were used to examine if treatments differed in the average number of species in each order.

Ten separate ANOVAs with block effects were used to examine if treatments differed significantly in the abundance of the ten most abundant species. Some of the most abundant species included mayflies and dipterans, a major prey source for dragonfly naiads. A Bonferroni adjustment was used in the analysis of the ten most abundant species to account for bias because of employing multiple statistical tests. The random chance of rejecting the null hypothesis by chance when there is no difference among treatment means, increases as the number of similar statistical tests increase. A Bonferroni adjustment decreases the α value so the likelihood of committing a Type 1 error is reduced. The adjusted p-value was α/n, where α is the original α-value, and n is the number of similar statistical tests being conducted (Rice 1989), thus the adjusted p-value was 0.05/10 or 0.005.

Each pond represented an independent experimental unit from which the average values of each response variable across the four different treatments were compared using analysis of variance (ANOVA). Treatment and block were independent variables, and the variable of interest was the dependent variable in the models. Significance value was set as p=0.05.

Pairwise comparisons of means using REGW Multiple Range Test followed ANOVAs with p <0.05 to determine which treatments significantly differ in insect diversity. All analyses were done in SAS (version 9.1 Institute Inc., Chicago, Illinois).

RESULTS

Dragonfly Assemblage

The only dragonfly species identified from the exuvia and naiads collected were *Pantala hymenaea* and *Pantala flavescens*, although there were at least 13 species of adult dragonflies at the WRC (Amoroso, personal observation). No dragonfly exuvia were unidentified. Other dragonfly species may have been collected as naiads. However, early instars were identified only to Libilullidae because species-specific characteristics are not present until later in development. *P. hymenaea* was the most plentiful dragonfly collected in the experiment. *P. hymenaea* was marginally more abundant in all summer and late summer treatments ($F_{3,12}=3.15$, P=0.065; Fig. 1a). *P. hymenaea* was least abundant in artificial ponds where dragonflies colonize only early or never colonize. *P. flavescens* was most abundant in early treatments ($F_{3,12}=3.55$, P=0.048; Fig. 1b).

Experimental manipulations successfully altered total dragonfly abundance. Dragonflies that completed metamorphosis were most abundant in treatments allowing dragonfly colonization at the beginning of the experiment (all summer and early summer) and least abundant in the closed treatment ($F_{3,12}=4.37$, P=0.027; Fig. 2). An intermediate abundance of dragonflies completing metamorphosis was found in the late summer treatment. The abundance of dragonfly naiads collected at the end of the experiment was greater in the all summer and late summer treatments than in the early summer and closed treatments ($F_{3,12}=7.41$, P=0.005; Fig.

1c). The abundance of large dragonflies (greater than 2 mm in body length) was lowest in the closed and early summer treatment ($F_{3,12}$=4.32, P=0.028; Fig. 1d). The abundance of large dragonflies in the all summer treatment was reduced compared to the late summer treatment.

Community Diversity

There were a total of 59 species (excluding dragonflies) from 38 families present in the artificial ponds (Table 1). The most abundant species in all ponds were Chronomid spp. (Dipteran), *Dasyhelea* sp. (Dipteran) and *Berosus* sp. larvae (Hydrophilid beetle). Other species present in most ponds but not necessarily in high abundance were *Tropisternus lateralis nimbatus* (Hydrophilid beetle), *Laccophilus* spp. larvae (Dytiscid beetle), *Berosus ordinatus* and *Cloeon rubropictum* (mayfly).

Species richness of all insects was the only diversity measurement that differed among treatments at the community level. Species richness of all insects was greatest in early summer and closed treatments and lowest in the treatment where dragonflies colonized ponds all summer ($F_{3,12}$=4.79, P=0.020, Fig. 3a). Total abundance and species evenness did not differ significantly among treatments (Abundance: $F_{3,12}$ =0.42, P=0.739; Evenness: $F_{3,12}$=0.48, P=0.701, Figs. 3b-c). The correlations between species richness, abundance and evenness were low at the community level. The correlation between species richness and abundance was 0.015. The correlation between species richness and evenness was 0.008, while the correlation between abundance and evenness was slightly higher at 0.445.

Insects from 5 different orders were collected from the artificial ponds. The species richness of coleopterans (beetles) differed among treatment ($F_{3,12}$ =4.87, P=0.019, Fig. 4a). More coleopteran species were found in closed treatments compared to all other treatments. Some

coleopteran species were found only in ponds with no dragonfly colonization such as *Uvarus lacustris, Hydrochus inaquatus* and *Copelatus chevrolati chevrolati* (table 2). *Hydraena marginicollis* and *Paracynus disperses* were species found only in ponds with early dragonfly colonization. No species were unique to the all summer treatment or late summer treatment. Heteropteran (true bugs) species richness differed significantly among treatment, with more species found in early summer treatments ($F_{3,12}$=5.78, P=0.011, Fig. 4b). The fewest heteropteran species were found in all summer treatments, with intermediate species richness in late summer and closed treatments. *Hebrus sp., Hesperocorixa nitida, Mesovelia amoena* and *Mircovelia austrina* were all species that were found only in the early summer treatment (table 3). *Buenoa marki* and *Limnoporus canaliculatus* were found only in closed treatment and all summer treatment, respectively. Species richness within the diptera (flies), odonata or ephemeroptera (mayflies) did not differ among treatments (Diptera: $F_{3,12}$=0.18, P=0.907; Odonata: $F_{3,12}$=2.36, P=0.122; Ephemeroptera: $F_{3,12}$=1.00, P=0.426 Figs. 4c-e).

Diversity of Juvenile Insects

Treatments did not differ in the species richness, total abundance or species evenness of insects currently in juvenile life history stages (Richness: $F_{3,12}$=1.73, P=0.2143; Abundance $F_{3,12}$=0.37, P=0.773; P=0.310; Evenness $F_{3,12}$=0.49, P=0.693, Figs. 3a-c). The correlations between species richness, abundance and evenness were low at the juvenile level. The correlation between species richness and abundance was 0.157. The correlation between species richness and evenness was slightly higher with a value of 0.585, while the correlation between abundance and evenness was 0.355.

To better understand how dragonfly colonization history influences juvenile populations at a species level, I examined the abundance of the most common species. No differences in abundance were found in Chironomid spp. larvae form A ($F_{3,12}$ =0.39, P=0.761, Fig. 5a), *Dasyhelea* sp. larvae ($F_{3,12}$ =0.38, P=0.767, Fig. 5b), *Berosus* sp. larvae ($F_{3,12}$ =0.18, P=0.905, Fig. 5c), Chironomid sp. pupae form A ($F_{3,12}$ =0.18, P=0.909, Fig. 5d), Chironomid sp. larvae form B ($F_{3,12}$ =1.50, P=0.264, Fig. 5e), Cyclorrhaphous-Brachycera sp. pupae form A ($F_{3,12}$ =0.600, P=0.629, Fig. 5f) or *Notonecta* spp. nymphs ($F_{3,12}$ =0.43, P=0.744, Fig. 5g). *Laccophilus* spp. larvae were most abundant in closed treatments ($F_{3,12}$ =6.26, P=0.008, Fig. 5h). I found *Cloeon rubropictum* (mayfly) were most abundant in early treatments ($F_{3,12}$ =9.81, P=0.002, Fig. 5i) compared to all other treatments.

Diversity of Adult Insects

Species richness of adult insects did not differ significantly among treatments ($F_{3,12}$ =2.75, P=0.089, Fig. 3a). However, more species where present in ponds that hindered dragonfly colonization through the entire summer. Adult insects were most abundant in ponds where dragonfly colonization was hindered throughout the summer ($F_{3,12}$ =8.06, P=0.003, Fig. 3b). The correlations between species richness, abundance and evenness were highest within the adult insects. The correlation between species richness and abundance was 0.784. The correlation between species richness and evenness was 0.362, and the correlation between abundance and evenness was 0.489.

Using a rarefaction estimate of species richness using species abundance, I compared species richness among ponds to determine if the species richness of a pond differed without species abundance confounding the richness estimate. I subsequently found richness did not

differ among treatments when estimated with the same abundance ($F_{3,12}=0.16$, P=0.921).

Species evenness of adult insect species did not differ among treatments (Evenness: $F_{3,12}=1.94$, P=0.177, Fig. 3c).

Of the ten most abundant species examined, the only species in the adult life stage was the coleopteran, *Berosus ordinates*. Differences were found in the abundance of adult *B. ordinates* across treatments ($F_{3,12}=8.06$, P=0.003, Fig. 5j). *B. ordinates* were most abundant in the closed treatment.

DISCUSSION

Colonization history was important in creating priority effects within the dragonfly assemblage and influencing the insect biodiversity in ephemeral, fish free ponds. The prediction that ponds with dragonflies colonizing through out the summer would be the least diverse and that ponds experiencing no dragonfly colonization would be the most diverse was confirmed. As expected, intermediate levels of diversity was observed in ponds with dragonflies colonizing only early summer or only late summer. Contrary to what was hypothesized, ponds with a delay in dragonfly colonization (late summer) had lower biodiversity than ponds with dragonfly colonization only in the beginning of the summer (early summer) because of the influence of dragonfly colonization history on the coleopteran and heteropteran adults.

Dragonfly colonization history influenced coleopteran and heteropteran species richness, which influenced total community species richness. However, dragonfly colonization history influenced coleopterans and heteropterans species richness differently. Coleopteran species richness was lowest in ponds with dragonfly colonization during any time during community development, causing increased total community richness in ponds without dragonfly

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colonization. One coleopteran species, *Uvarus lacustris,* was consistently in ponds with no

dragonfly colonization. However, the other additional coleopteran species that are more likely

found in ponds without dragonfly colonization were random additions with random species being

lost when dragonflies could colonize during any time period.

Dragonfly colonization increased species richness of heteropterans when there were only

early or only late arriving dragonfly naiads, but constant colonization of dragonfly predators

negatively impacted species richness of heteropterans. Many of the unique heteropteran species

that were found in a pond were because of the random addition or loss of a species since no

species seem to be consistently found in most replicates of a treatment. Heteropertan species

richness was negatively associated with the abundance of dragonfly naiads present but positively

associated with the abundance of heteropteran prey items (*C. rubropictum* and *Laccophilus* spp.

larvae) (table 4). When there was a high abundance of dragonflies in the all summer treatment,

the abundance of *C. rubropictum* and *Laccophilus* spp. larvae was low and so was the species

richness of heteropteran adults. However, when the abundance of dragonfly naiads is low in the

early summer treatment, the abundance of *C. rubropictum* was high, allowing a higher species

richness of heteropteran adults. In treatments where dragonflies do not colonize, the abundance

of *Laccophilus* spp. larvae was high allowing for intermediate levels of heteropteran species. In

the late summer treatment there was a high abundance of dragonflies that resulted in low

abundances of *C. rubropictum* and *Laccophilus* spp. larvae that were similar to the all summer

treatments, yet there was an intermediate level of heteropteran species richness in the late

summer treatment instead of low species richness. In treatments that have later dragonfly

colonization, intermediate levels of heteropterans may be found because the abundance of

dragonflies was increasing over time. As dragonflies increase in abundance over time, the prey

resource of *Laccophilus* spp. larvae, was being depleted by dragonfly predation. The adult heteropterans may choose to stay in ponds with only late-arriving dragonflies because small dragonfly naiads are a prey resource for heteropterans (Wilson, 1920), or the heteropteran adults may not be able to leave a pond after colonization. Once aquatic insects disperse to a pond, flying muscles are converted to either swimming or reproductive muscles, making dispersal to other environments difficult (Dingle 1972). The adult heteropterans may not be able to reconvert swimming or reproductive muscle into flying muscle to find a more suitable habitat once the dragonflies reduce the *C. rubropictum* and *Laccophilus* spp. larvae populations.

Species richness of the adult insects differed when there were differences in abundances, but once the species richness was estimated for a given number of sampled individuals using a rarefaction curve, species richness was statistically similar across treatments. The increase in the abundance of adult insects in a pond influenced species richness of adult. Ponds that had the greatest abundance of adult insects should have the greatest species richness because adult insect abundance and species richness of adults were strongly correlated. Since the total abundance of adult insects was reduced when dragonflies colonized at any time period the species richness should also be reduced when dragonflies colonized at any time period. The pattern of high species richness and high abundance when there is no dragonfly colonization was similar to the pattern in coleopterans. Coleopterans adults were more abundant and species rich compared to heteropterans adults.

Dragonfly colonization history could influence adult species richness and abundance through at least three processes. First, competition between the adult insect species and the dragonfly naiads could prevent adult aquatic insects from successfully colonizing ponds with high abundances of dragonfly naiads. There is little experimental evidence of competition

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among dragonfly naiads and coleopteran adults or heteropteran adults (Nilsson 1986). However, carnivorous coleopteran (Dytiscids) and heteropteran adults consume the same types of prey items, mainly chironomids (Nilsson 1986, Bosi 2001, Bay 2003, Mogi 2009). It was possible the adult species experienced a competitive release when larval dragonfly abundance was low, allowing higher species richness of adult insects. This scenario was unlikely, however, as the prey items of the adult species and dragonfly naiads were abundant in all pond treatments and were therefore not likely limiting the species richness of the adult insects. While competition does not seem to influence the species richness of the adult insects, the adult species may still be avoiding ponds with high abundances of dragonfly naiads.

The second way dragonfly colonization could influence adult species richness and abundance of adult insects was through habitat selection for oviposition by adult coleopterans and heteropterans. During colonization, adult insects tend to avoid a habitat or grouping of habitats if a predator is present (Resetarits 2001, Resetarits and Binckley 2009, Vonesh and Kraus 2009). Adult insects could be preferentially colonizing ponds with low abundances of dragonfly naiads in order to oviposit eggs. Adults avoid colonizing and ovipositing juveniles into areas with predators since the predator may consume the juvenile insects before they complete metamorphosis (Blaustein and Kotler 1993). In pond environments, coleopteran abundance generally is inversely proportional to dragonfly naiads abundance (Larson 1990). Similarly, I found *Laccophilus* spp. larvae and *Berosus ordinatus* adult were less abundant when dragonflies were present during any time period. The lower abundance of coleopterans and heteropterans in ponds with dragonfly naiads could be because of a combination of habitat selection and dragonfly predation.

Thirdly, the dragonfly naiads consumed the juvenile stages of coleopteran and heteropteran species, preventing coleopteran and heteropteran species from completing metamorphosis to adults, thus reducing abundance and species richness of adult insects. Dragonfly naiad predation on juvenile coleopterans and heteropterans would reduce the abundance of these juvenile species (Larson 1990, Bosi 2001). A reduction in the abundance of juvenile coleopterans and heteropterans completing metamorphosis would result in a lower adult insect abundance. Dragonfly naiads are generalist predators and consume prey species in the proportion they are found present in a pond (Pritchard 1964, Thompson 1978). It was unlikely rare species were eliminated from the community by dragonfly predation because a rare species would have a low likelihood of being eaten. Common species also should not have been consumed to extinction because once the abundance of a prey item begins to decrease the likelihood of being eaten would have been reduced. It was unlikely that dragonfly predation of juveniles alters species richness of adult insects. However, predation could be influencing the abundance of juvenile insects.

It was likely predation of juvenile insects would be greatest in treatments with high abundances of dragonflies (all summer and late summer treatments) and high abundances of adult community (closed treatment). In early summer treatments the juvenile insects should experience a predatory release at the end of the summer because most of the dragonfly naiads have emerged from these ponds, and the abundance of adult insects was low. The only species detected to have a higher abundance in the early summer treatment was the mayfly, *Cloeon rubropictum*. *C. rubropictum* breeds mid to late summer (Lyman 1955). A large breeding event later in the summer after many of the early-arriving dragonfly predators were removed from the

pond allowed populations of *C. rubropictum* to have greater abundances in ponds with low predation pressure compared to ponds with high predation pressure.

Dragonfly colonization history influenced species that have a longer aquatic life history stage, such as adult aquatic insects and juveniles that require a longer time period to metamorphosis more strongly than species with fast development. Abundance of dipteran species such as chironomid spp. larvae, chironomid spp. pupae, *Dasyhelea* sp. larvae were not influenced by the abundance of dragonfly naiads or the time at which dragonflies arrived at a pond. Adult dipterans' reproduction rates in ephemeral ponds by adult insects were sufficiently rapid to overwhelm the effect of predators. Chironomid spp. and *Dasyhelea* spp. have high turnover rates because development from larvae to adult is approximately seven days (Benke 1976). High amounts of variability in the abundance of dipterans and other insects, may have affected the statistical power's ability to detect differences in species abundances among treatments.

Colonization history of dragonfly naiads did not influence the species evenness for juvenile, adult insects or the entire insect community. No treatment differences were detected in species evenness because there were similar total community abundance values across treatments and high amounts of variability of insect abundance within a treatment. Although there were differences among adult insect abundance and a strong trend for species richness of adults, these differences were not strong enough to cause differences in species evenness.

I was successful in manipulating the arrival times of dragonfly naiads to a pond based on differences across treatments in the average number of dragonfly naiads completing metamorphosis. The reduction in the abundance of dragonfly naiads at the end of the experiment when both early and late-arriving dragonfly naiads were present compared to when only late-

arriving dragonflies were present indicates that the timing at which dragonfly naiads arrive into a community created priority effects within the dragonfly assemblage. Changes in the abundance of late-arriving dragonflies species by early-arriving dragonflies species were also observed within permanent pond communities (Benke 1978, Morin 1984a). It was more likely the late-arriving dragonflies were out-competed (Benke 1978, Benke et al. 1982, Morin 1984a) and cannibalized by larger, early-arriving dragonflies (Warren 1915, Wilson 1920, Kormondy and Gower 1965, Johnson et al. 1985, Robinson and Wellborn 1987, Wissinger 1988a, 1988b, 1989, Johansson 1993a).

The extent to which early-arriving dragonflies decrease the abundance of late-arriving dragonflies may vary among ephemeral and permanent ponds. Comparisons of the strength of priority effects can be made between ephemeral ponds and permanent fish ponds by determining how strongly the early-arriving dragonflies suppress the abundance of the late-arriving dragonflies. Although priority effects occurred in both ephemeral and permanent ponds, there was a trend for a stronger priority effect in permanent fish ponds compared to ephemeral fish free ponds (results in table 5). Differences in the strength of priority effect may differ because of experimental habitat (ephemeral pond versus permanent ponds) or because of differences in the species of dragonflies that colonized the experiments.

I hypothesized that the strength of priority effects associated with dragonfly colonization would be different in a fish free ephemeral pond than in a permanent fish pond because dragonflies behave differently in the presence of fish than when fish are absent. I found that there were differences between fish free ephemeral ponds and permanent fish ponds by comparing results of this study with Morin's study in 1984 (results in table 6). Although neither study found that the timing of dragonfly colonization affected the abundance of chironomid spp.

larvae, a main food resource for dragonfly naiads, other prey items (such as *Cloeon* spp.) were affected by the timing of dragonfly arrival in ephemeral ponds but not in permanent fish ponds. Early arriving dragonflies had a stronger priority effect in permanent ponds than in ephemeral ponds as early arriving dragonflies caused a greater reduction in the abundance of late arriving dragonflies in a permanent pond than in ephemeral ponds. The reduction in the abundance of late-arriving dragonflies by early-arriving dragonflies may be a general assembly rule across all environments where dragonflies are top predators. The timing at which dragonfly naiads arrive to the pond was important in regulating population sizes of dragonfly naiads in a habitat because early-arriving dragonflies decreased the abundance of late-arriving dragonflies in both ephemeral ponds and permanent ponds.

Although priority effects were observed in both permanent fish ponds and ephemeral ponds, priority effects may not persist when there are seasonal shifts in dominant species because of metamorphosis to adult. The early-arriving dragonflies decrease in abundance as they complete metamorphosis, allowing late-arriving dragonflies to colonize a habitat. The early-arriving dragonfly naiads are the dominant dragonflies after a pond fills with water because they were the first to arrive to the habitat. However, once the early-arriving dragonflies leave the ponds as adults, later-arriving dragonflies can become established. Seasonal periods of low abundance such as when insects are completing metamorphosis can allow other species to colonize a habitat (Morin 1984a). The transition from the decreasing abundance of the early-arriving dragonflies and new input of late-arriving dragonflies may be the reason why there were similar abundances of dragonfly naiads in all summer and late summer treatments in ephemeral ponds. The priority effect begins to decrease in the all summer ponds because the early-arriving

dragonflies have left the pond and are no longer hindering the colonization of the late-arriving dragonfly naiads.

Conclusion

Many ecologists are interested in studying the factors that influence the biodiversity and species competition of ecological communities (Diamond 1975). In the development of a community, it is clear that contemporary interactions among species have an important role in controlling the biodiversity of a system (Morin, 1999). However factors such as competition and predation may not be the only factor influencing the biodiversity of a community. Differences in colonization rate or which species arrive to the habitat first are just a few of the reason why biodiversity differs among similar habitat types (Drake 1990; Drake 1991; Robinson and Edgemon 1988).

There may be noticeable differences among species richness that can be observed among habitats even when species assemble from the same source pool (Diamond 1975; McCune and Allen 1985; Wilbur and Alford 1985). Discovering the mechanism of an assembly rule could explain what is driving communities to have different assemblages of species (Samuels and Drake 1997). Contemporary interactions may not always be the factor shaping community biodiversity. Priority effects caused by differences in colonization history are important in developing communities where an area is disturbed and community structure begins again from scratch: storms flipping boulders in the rocky intertidal zone, exposing the bottom of rocks now available for new recruitment (Sousa 1980); plant communities removed after tornado disturbance freeing space for new plants (Peterson and Pickett 1995); or ephemeral ponds in which community structure begins after a dry wetland refills with water (Chase 2007). When

historically contingent factors are important to community assembly, generally the first species

to arrive at a habitat gains a competitive advantage compared to species that arrive later. The

early-arriving species can consume resources and gain a larger size, which may allow these

species to out-compete and prevent late-arriving species from successfully colonizing (Polis et

al. 1989).

More empirical studies need to incorporate how communities assemble in nature to fully

understand colonization assembly with organisms that naturally colonize habitat at different

times. Some species are more likely to arrive first to a developing community (e.g. Corbet

1958). One model organism that has variation in arrival time to an aquatic habitat is dragonfly

naiads. The relative arrival time of dragonfly naiads can be influenced by at least two processes.

First, temporal differences between species arriving into a community due to species-specific

breeding phenology (Corbet 1954; Corbet and

Corbet 1958) or how soon breeding adult dragonflies oviposit eggs into a pond (short or long

after pond filling). Variation from pond location may be influenced by habitat isolation (Ims and

Yaccoz 1997; Cote and Clobert 2007; Dingemanse et al. 2003; Massot et al. 2002; Conrad et al.

2002).

How differences in arrival time influence the dragonfly assemblage of an ephemeral pond

was previously unknown. I found that the timing of colonization into ephemeral ponds by

dragonfly naiads can have important effects on how successful a pond will be in terms of how

many adult dragonflies are produced and in the biodiversity of insects present in the pond.

While this experiment does not directly measure the influence of pond isolation on aquatic insect

assembly, there are implications of pond isolation on how distances of habitats can influence

pond assembly history. Ponds that have dragonfly colonizing either all summer or just early

summer would represent ponds that would be located near source ponds. Ponds that have dragonflies colonizing only late summer would represent isolated ponds and ponds without dragonfly colonization would represent the most isolated environment.

In this experiment we found that in pond isolation can influence insect biodiversity. Ponds that are very isolated and never have dragonflies colonize have higher species richness and higher abundance of adult coleopterans and heteropterans. However, if ponds were only moderately isolated such as ponds that have a delay in dragonfly colonization, dragonfly naiads would begin to decrease species richness and would decrease the abundance adult insects compared to isolated ponds.

Predator species richness decreases more rapidly than prey species richness as pond isolation increases (Shulman and Chase 2007) indicating that there should a greater proportion of predators closer to the source pond. Prey organisms should disperse as far from source ponds as possible to avoid ponds with a greater proportion of predators (Shulman and Chase 2007). Some predator species such as *Notonecta irrorata* will bypass "quality" habitat in close proximity to a source pond in favor of a more isolated pond (McCauley et al. 2009). So colonization site selection not only influences which species are found in a pond, but also the abundance (McCauley et al. 2009).

The timing of dragonfly arrival seems to play an important role in influencing the diversity of some taxa (e.g., coleopterans and heteropterans) but did not affect the abundance or biodiversity within other taxa (e.g., some dipteran species). Aquatic insect biodiversity was greatest when adult aquatic insects colonize and oviposit in ponds with a low abundance of dragonfly naiads or when there is a delay in dragonflies colonizing a pond. Since dragonflies take longer to oviposit eggs into more isolated ponds and there could be a delay in dragonfly colonization (McCauley et

al. 2010), adult insect species may want disperse a further distance to a more isolated pond to avoid dragonfly predators that will prey on insect larvae, thus reducing species richness and abundance of adult species. However, insects such as adult chironomids may not need to put energy into colonizing more isolated ponds with fewer dragonflies since dragonfly colonization history does not decrease their abundance.

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Table 1: Summary of genera collected across all artificial ponds.

Family	Genus	Family	Genus
Coleoptera		Diptera	
Curculionidae	*Lixus*	Certopogonidae	*Dayshelea*
Dytiscidae	*Acilius*		*Palpomya*
	Agabus	Chaoboridae	*Chaoborus*
	Copelatus	Chironomidae	Unknown
	Coptotomus	Culicidae	*Anopheles*
	Hydroporus	Cyclorrhaphous-Brachycera	
	Laccophilus		Unknown
	Matus	Tanyderidae	Unknown
	Thermonectus	Tipulidae	Unknown
	Uvarus		
Elmidae	*Dubiraphia*		
Haliplidae	*Peltodytes*	Odonata	
Hydraenidae	*Hydraena*	Zygopteran	*Enallagma*
Hydrophilidae	*Berosus*		*Ischnura*
	Hydrochus	Ephemeroptera	
	Tropisternus	Baetidae	*Cloeon*
	Paracynus	Caenidae	*Caenis*
Heteroptera			
Belostomatidae	*Belostoma*		
Corixidae	*Hesperocorixia*		
Gerridae	*Gerris*		
	Limnoporus		
Hebridae	*Hebrus*		
Mesoveliidae	*Mesovelia*		
Nepidae	*Ranatra*		
Notonectidae	*Notonecta*		
	Buenoa		
Veliidae	*Microvelia*		

Table 2: Summary of adult coleopteran species collected across all artificial ponds. N=5 Collected from presence/absence (1,0) data. Each value associated with adult coleopteran species and treatment represents the summed presence/absence values of a adult coleopteran species across treatment. When an adult beetle species is present in all replicates of a treatment, the corresponding value is represented by 5. † Indicates which coleopteran species were unique to a particular treatment.

Treatment	All Summer	Early Summer	Late Summer	Closed
Acilius mediatus adult	1	1	1	2
Agabus stagninus adult	4	2	3	3
Berosus ordinatus adult	5	5	4	5
Copelatus caelatipennis princeps adult	0	2	0	3
† *Copelatus chevrolati chevrolati* adult	0	0	0	1
Coptotomus interrogatus adult	0	0	1	1
Dubiraphia bivittata adult	0	1	1	3
† *Hydraena marginicollis* adult	0	1	0	0
Hydrochus excavatus adult	1	2	2	2
† *Hydrochus inaequalis* adult	0	0	0	1
Hydroporus stagnalis adult	1	2	4	5
Hydroporus americanus adult	4	4	4	5
Laccophilus fasciatus rufus adult	3	4	4	5
Laccophilus macubsus machlosus adult	2	2	0	1
Laccophilus proximus adult	0	1	3	4
Lixus spp. adult	1	0	2	0
Matus Bicarinatus adult	1	2	0	0
† *Paracynus dispersus* adult	0	2	0	0
Peltodytes shermani adult	1	3	2	4
Thermonectus basillaris basillaris adult	1	1	0	1
Tropisternus blatchleyi blatchleyi adult	5	4	4	5
Tropisternus collaris striolatus adult	4	2	0	3
Tropisternus lateralis nimbatus adult	5	5	5	5
Tropisternus natator adult	3	1	5	5
† *Uvarus lacustris* adult	0	0	0	4

Table 3: Summary of adult heteropteran species collected across all artificial ponds. N=5
Collected from presence/absence (1,0) data. Each value associated with adult heteropteran
species and treatment represents the summed presence/absence values of a adult heteropteran
species across treatment. When an adult beetle species is present in all replicates of a treatment,
the corresponding value is represented by 5. † Indicates which heteropteran species were unique
to a particular treatment.

Treatment	All Summer	Early Summer	Late Summer	Closed
Belostoma fluminevm adult	1	1	0	0
Belostoma testaceum adult	0	1	1	1
† *Buenoa marki* female	0	0	0	1
Gerris agrenticollis adult	0	1	0	1
† *Hebrus* sp. adult	0	1	0	0
† *Hesperocorixa nitida* adult	0	1	0	0
Hesperocorixa vulgaris adult	1	2	2	2
† *Limnoporus canaliculatus* adult	1	0	0	0
† *Mesovelia amoena* adult	0	1	0	0
† *Microvelia austrina* adult	0	1	0	0
Microvelia mulsanti adult	0	1	0	1
Notonecta indica adult	1	0	2	0
Notonecta irrorata adult	0	4	2	2
Notonecta undulata adult	2	3	2	1
Ranatra australis adult	0	1	1	0

Table 4: Summary of how treatments differ in dragonfly spp. naiad abundance, *Cloeon rubropictum* abundance, *Laccophilus* spp. larvae abundance and heteropteran species richness. Low, intermediate and high categories represent which treatments had the lowest, intermediate or highest values for a particular response variable. Categories are reflective of pairwise comparisons that were conduced. Values calculated for average heteropteran species richness are included for each treatment.

	All Summer	Early Summer	Late Summer	Never
Dragonfly spp. naiad abundance	High	Low	High	Low
Cloeon rubropictum abundance	Low	High	Low	Low
Laccophilus spp. larvae abundance	Low	Low	Low	High
Heteropteran Species richness	Low 1.6	High 3.8	Intermediate 3	Intermediate 2.4

Table 5: Comparison of strength of priority effect between permanent and ephemeral ponds. Permanent pond data modified from Morin 1984a. Strength of priority effect refers to how early-arriving dragonflies affect the abundance of late-arriving dragonflies. Strength of priority effect ranged in value from zero to -1. Strength of priority effect with a value of zero would indicate that the early-arriving dragonflies had no impact on the abundance of the late-arriving dragonflies, while a priority effect value of -1 would indicate that the early-arriving dragonflies completely hindered the arrival of the late-arriving dragonflies.

Permanent Pond	
Dragonfly species	Strength of Priority Effect
Pachydiplax sp.	-0.780131827
Perithemis sp.	-0.895833333
Erythemis sp.	-0.472671286
Libellula sp.	-0.531034483
Epicordulia sp.	-1
Tramea sp.	-1
Ephemeral Pond	
Dragonfly species	Strength of Priority Effect
Pantala spp.	-0.142038217

Table 6: Comparison of permanent ponds versus ephemeral ponds. Data for permanent ponds from Morin 1984a. Strength of priority effect refers to how strongly early-arriving dragonflies affect the abundance of late-arriving dragonflies.

Effects of dragonfly arrival time on	Permanent Fish Ponds	Ephemeral Fish Free Ponds
Chironomid spp. abundance	no effect	no effect
Cloeon spp. abundance	no effect	inc. when only early dragonfly colonization
Strength of priority effect	stronger	weaker
No. of dragonfly species	8	2
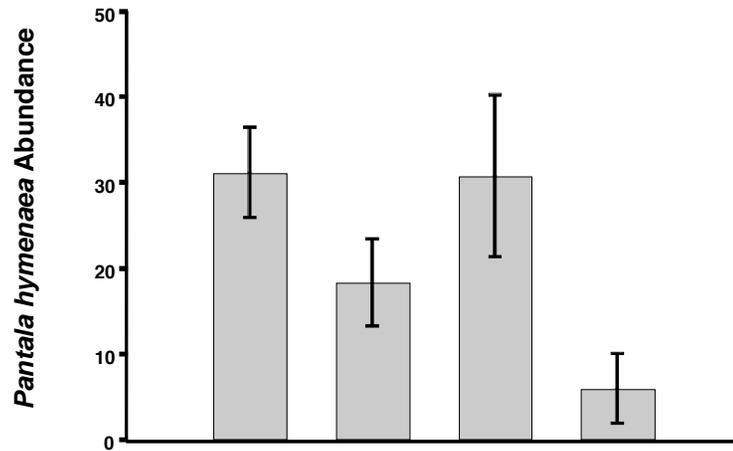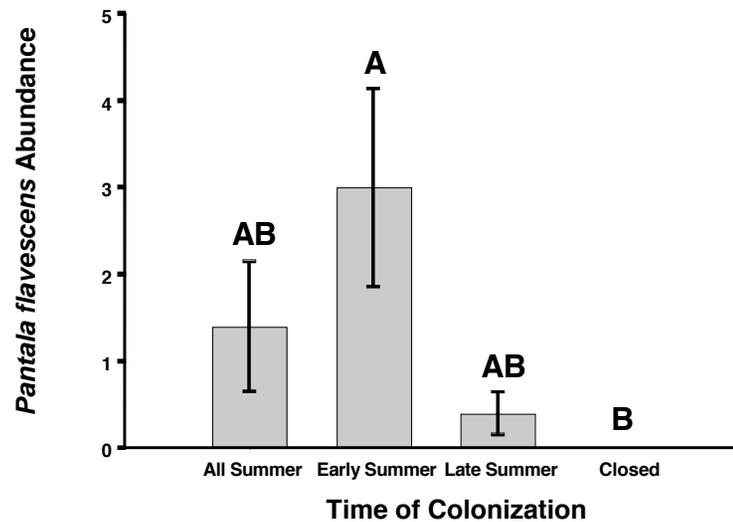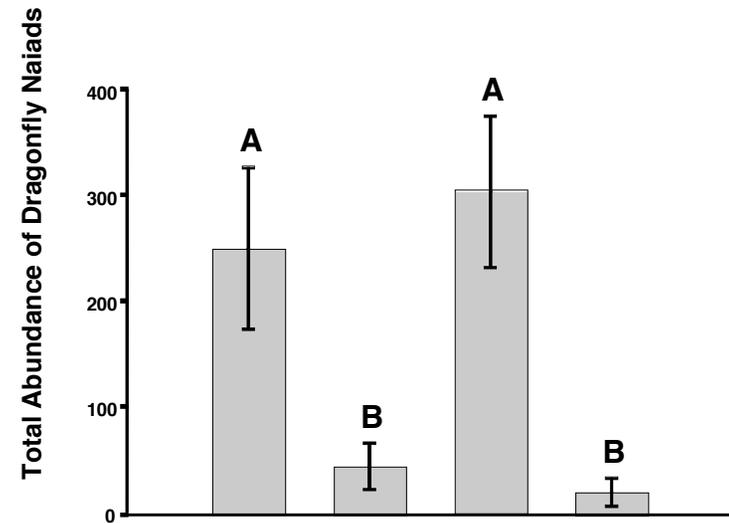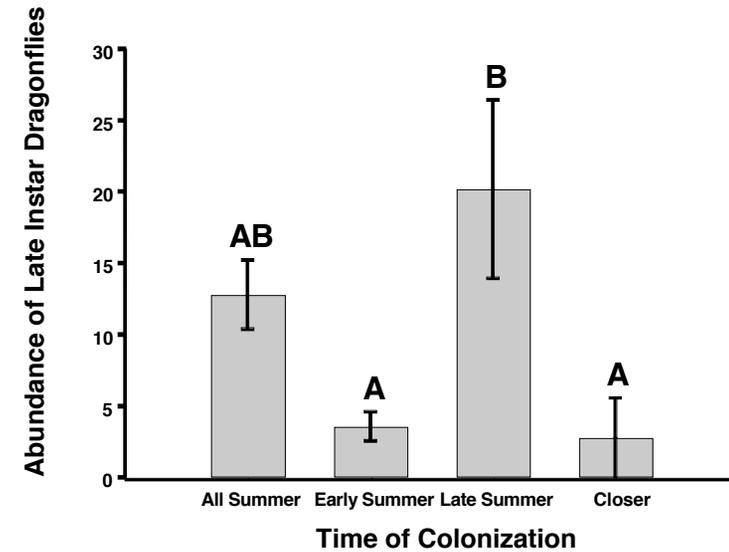
Figure 1: Average abundance (±1SE) of dragonflies. N=5. Different letters above bars indicate significantly different means on the basis of REGW Multiple Range Test. a) *Pantala hymenaea* collected as naiads and exuvia, b) *Pantala flavescens* collected as naiads and exuvia c) all naiads in a pond at the end of the summer, d) average number of dragonfly nymph greater than 2mm.
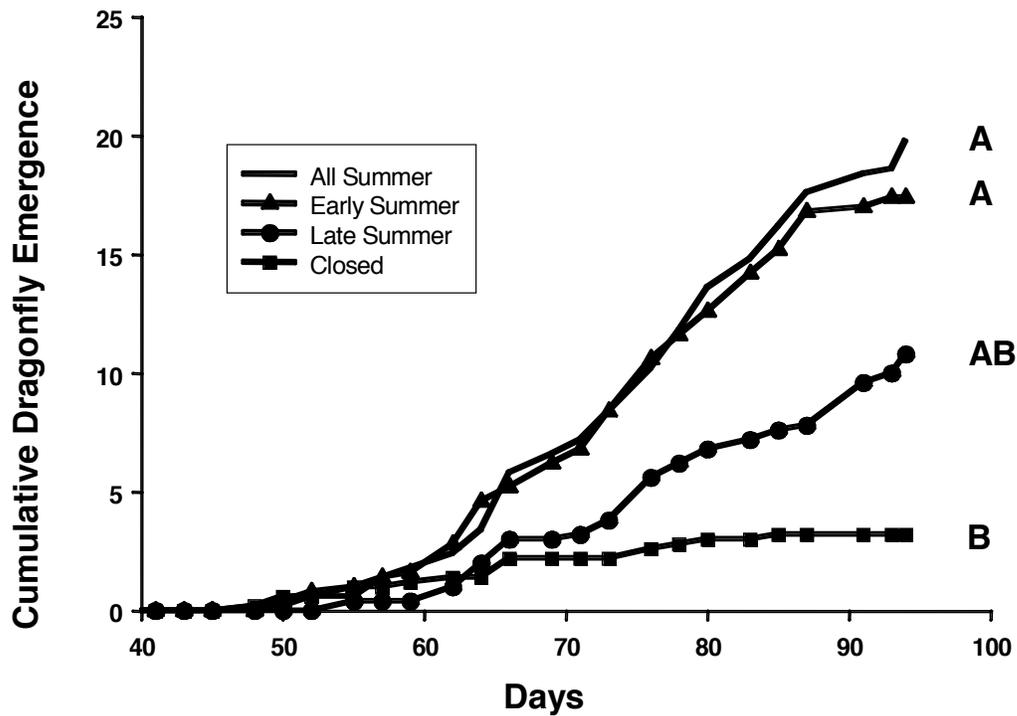
Figure 2. Average cumulative number of dragonflies that metamorphosed throughout experiment.   Statistically significant differences (was determined by REGW Multiple Range test) on only the average total abundance of emerged dragonflies. Treatments sharing the same letter combination during a given time period are not different form each other period are not different from each other.
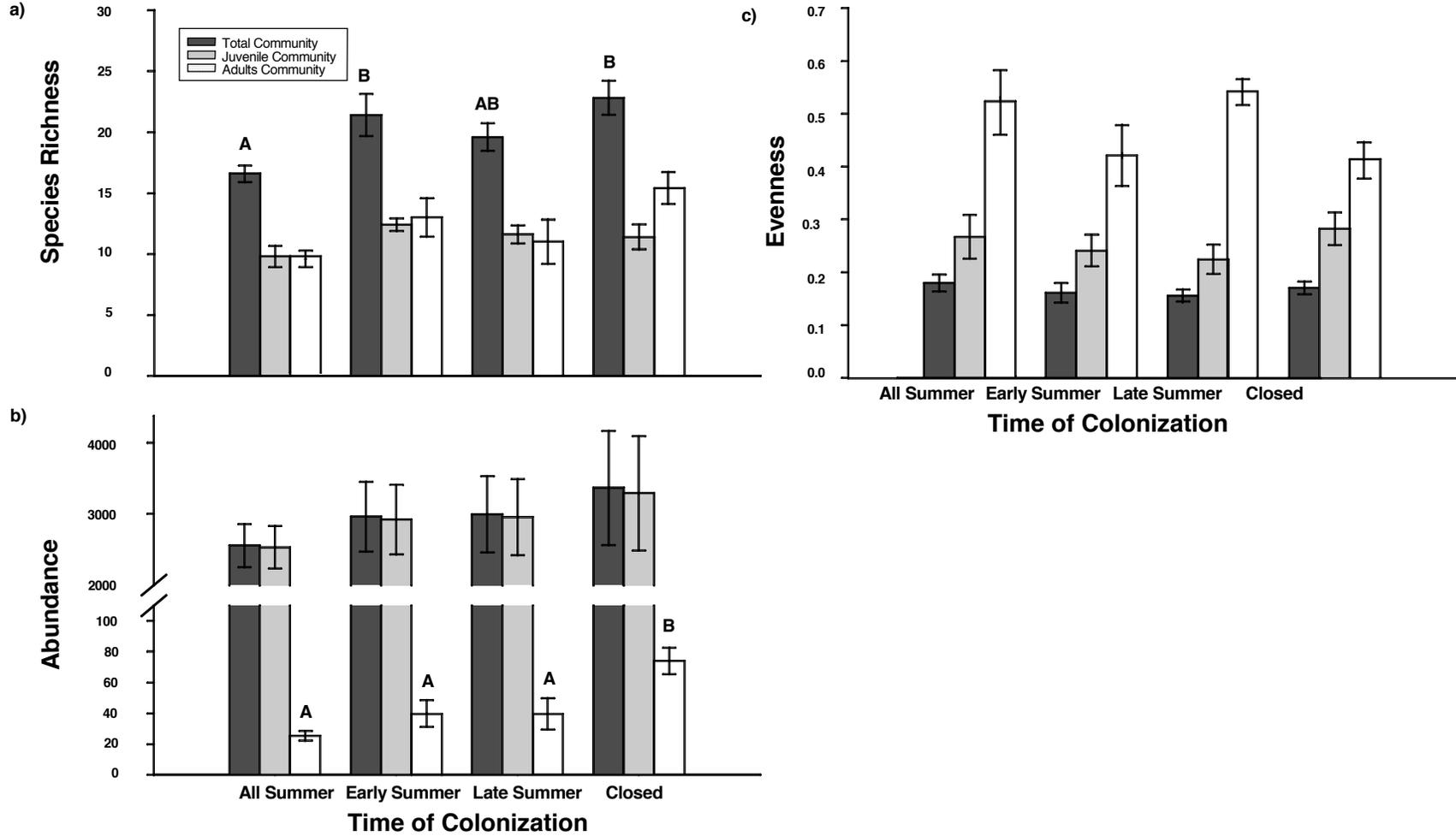
Figure 3. Average values (±1 SE) of a) species richness b) abundance c) evenness. N=5. The different colored bars indicate different groupings of organisms as indicated by the figure legend. Bars with different letters are statistically different from one another using REGW Multiple Range Test. (REGW Multiple Range Test compares same organism groupings across treatments, not to other insect grouping within treatment.)
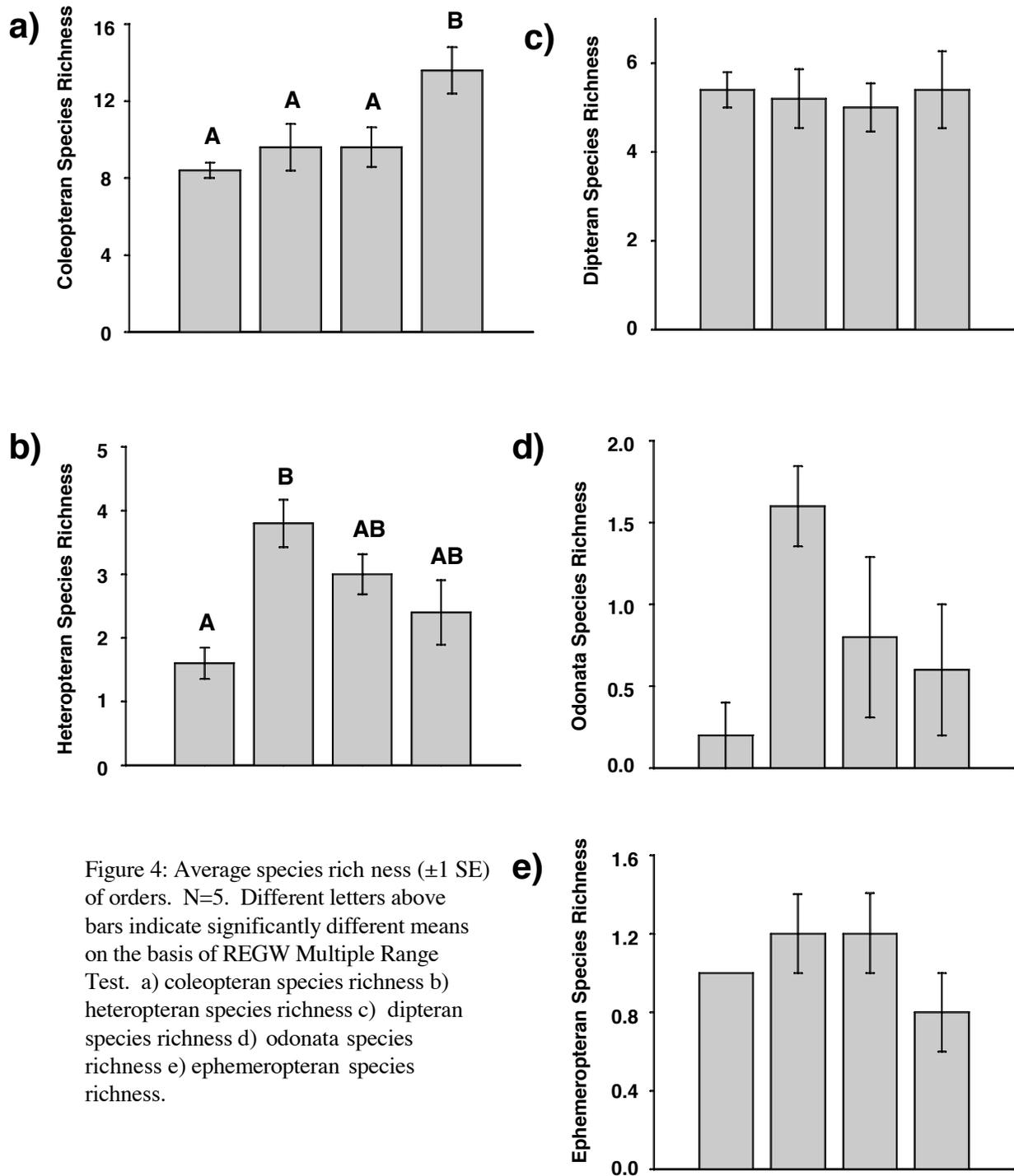
Figure 4: Average species rich ness (±1 SE) of orders. N=5. Different letters above bars indicate significantly different means on the basis of REGW Multiple Range Test. a) coleopteran species richness b) heteropteran species richness c) dipteran species richness d) odonata species richness e) ephemeropteran species richness.
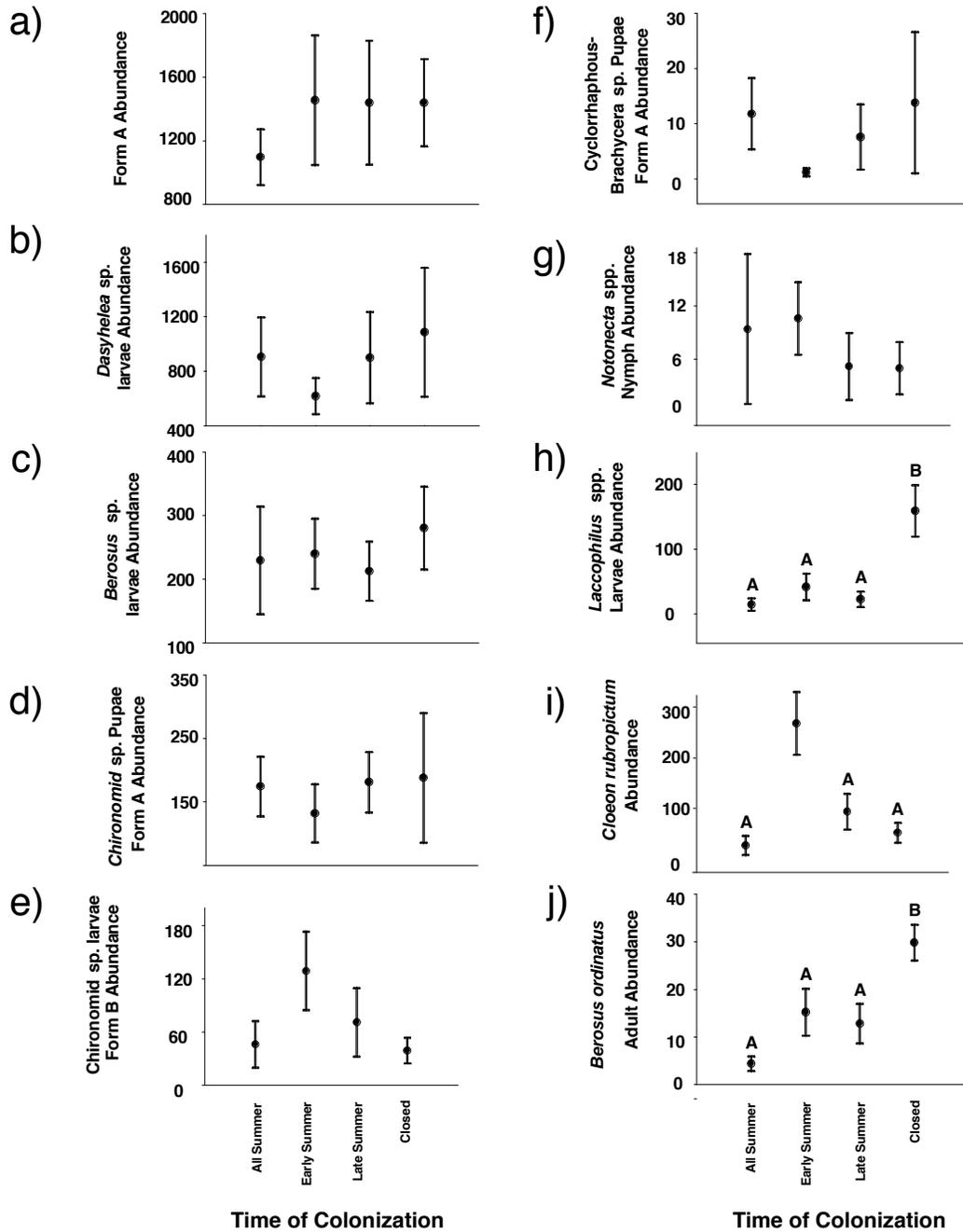
Figure 5.   Total abundance (±1 SE) of colonist of the 10 most abundant species across the 4 treatments. N=5. Different letters above bars indicate significantly different means on the basis of REGW Multiple Range Test. a) Chironomid spp. larvae form A abundance b) *Dasyhelea* sp. larvae abundance c) *Berosus* sp. larvae abundance d) Chironomid sp. pupae form A abundance e) Chironomid sp. larvae form B abundance f) Cyclorrhaphous-Brachycera pupae form A abundance g) *Notonecta* spp. nymph abundance h) *Laccophilus* spp. larvae abundance i) *Cloeon rubropictum* abundance and j) *Berosus ordinatus* adult abundance.