2002

Interspecific interactions between mayflies (Hexagenia) and midges (Chironomus).

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38

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INTERSPECIFIC INTERACTIONS BETWEEN MAYFLIES

\textit{(Hexagenia)} AND MIDGES \textit{(Chironomus)}

by

Wes Plant

A Thesis
Submitted to the Faculty of Graduate Studies and Research
through the Department of Biological Sciences
in Partial Fulfillment of the Requirements for
the Degree of Master of Science at the
University of Windsor

Windsor, Ontario, Canada

2002

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ABSTRACT

Both Hexagenia (mayfly) nymphs and Chironomus (midge) larvae live in the soft sediments of Lake Erie, showing a non-overlapping mosaic distribution. The objective of this study was to quantify the importance of interactions between Hexagenia nymphs, and larval Chironomus.

The field distributions of Hexagenia nymphs and chironomid larvae were analysed to examine the co-occurrence of these two taxa. Little evidence of negative interactions between these taxa were found based on these analyses. Laboratory experiments were conducted that measured survivorship and increase in body length of Hexagenia nymphs and Chironomus larvae reared individually and together to determine the strength of competition for space between these taxa. The results of the experiments did not suggest competition for space. Duration effects were tested by adding Chironomus larvae to containers of Hexagenia nymphs at different stages in the development of Hexagenia. Newly hatched Hexagenia showed the smallest increase in body length after being exposed to Chironomus after 0 and 10 days, but exhibited no significant difference from the control when Chironomus were added on days 20, 40, and 60. These were the only results suggesting the possibility of competition for space between mayflies and midges. Increase in body length was not measured for Chironomus larvae because Chironomus adults emerged before the end of the experiments. The results may have important life history implications for Hexagenia.
If *Hexagenia* nymph growth is slowed in the presence of *Chironomus* larvae, the nymphs would be expected to emerge later, with negative implications for reproductive success.

Chironomid larvae are present in the western Lake Erie sediments when *Hexagenia* are depositing their embryos. Laboratory experiments were conducted to determine if *Chironomus* larvae consume *Hexagenia* embryos. *Chironomus* larvae do consume *Hexagenia* embryos. *Hexagenia* nymphs did not consume *Hexagenia* embryos. The consumption of *Hexagenia* embryos could be an important interaction affecting the distribution of *Hexagenia* nymphs in the presence of large numbers of *Chironomus* larvae.
ACKNOWLEDGEMENTS

I would like to thank my supervisor Dr. Lynda Corkum for her guidance and support throughout the thesis process. Thanks to Dr. Jan Ciborowski for being on my committee, assisting with the experimental design, and letting me use his western Lake Erie data sets. Thanks to Dr. Jerry Cohen for being on my committee. I would like to thank Jesse Baillargeon and André Bachtaram for their advice and ideas. Thanks to Teresa Mulcaster and all the others who helped me collect mayflies and midges. Thanks to the biology department staff, faculty, and graduate students. This research was supported by an NSERC grant to Dr. Lynda Corkum. Finally I would like to thank my family for all of their support.
TABLE OF CONTENTS

ABSTRACT iii
ACKNOWLEDGEMENTS iv
LIST OF TABLES vi
LIST OF FIGURES vii
GENERAL INTRODUCTION 1

CHAPTER

1. DO COMPETITIVE INTERACTIONS EXPLAIN THE OVERLAPPING MOSAIC DISTRIBUTION IN WESTERN LAKE ERIE SHOWN BY Hexagenia AND Chironomus? 14

INTRODUCTION 14

MATERIALS AND METHODS 20
Field Study – Analysis of previous data sets 20
Laboratory Experiment #1: Competitive Interactions 22
Laboratory Experiment 2: Priority Effects 29

RESULTS 34
Field Study – Analysis of previous data sets 34
Laboratory Experiment #1: Competitive Interactions 34
Laboratory Experiment 2: Duration Effects 43

DISCUSSION 51
Field Study – Analysis of previous data sets 51
Laboratory Experiment #1: Competitive Interactions 53
Laboratory Experiment 2: Duration Effects 54

2. DO Chironomus LARVAE CONSUME Hexagenia EMBRYOS? 59
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Experimental design of the competitive interactions laboratory showing the treatments of <em>Hexagenia</em> nymphs and <em>Chironomus</em> larvae used in containers and the equivalent field densities.</td>
<td>27</td>
</tr>
<tr>
<td>2.</td>
<td>Containers inoculated with 20 <em>Chironomus</em> larvae at different points in the development of <em>Hexagenia</em> nymphs during the 61 day duration effects experiment. Small and large <em>Hexagenia</em> nymphs were tested separately. N = number of replicates.</td>
<td>30</td>
</tr>
<tr>
<td>3.</td>
<td>Containers inoculated with 8 large <em>Hexagenia</em> nymphs at different points in the development of <em>Chironomus</em> larvae during the 31 day duration effects experiment. N = number of replicates.</td>
<td>33</td>
</tr>
<tr>
<td>5.</td>
<td>Summary of the one-way ANOVA and planned comparisons for the effect of <em>Chironomus</em> larvae on the survivorship of large <em>Hexagenia</em> nymphs in the competitive interactions laboratory experiment after 60 days.</td>
<td>36</td>
</tr>
<tr>
<td>6.</td>
<td>Summary of the one-way ANOVA and planned comparisons for the effect of <em>Chironomus</em> larvae on the increase in body length of large <em>Hexagenia</em> nymphs in the competitive interactions laboratory experiment.</td>
<td>36</td>
</tr>
<tr>
<td>7.</td>
<td>Summary of the one-way ANOVA and planned comparisons for the effect of <em>Chironomus</em> larvae on the survivorship of newly hatched <em>Hexagenia</em> nymphs in the competitive interactions laboratory experiment.</td>
<td>39</td>
</tr>
<tr>
<td>8.</td>
<td>Summary of the one-way ANOVA and planned comparisons for the effect of <em>Chironomus</em> larvae on the increase in body length of newly hatched <em>Hexagenia</em> nymphs in the competitive interactions laboratory experiment.</td>
<td>39</td>
</tr>
</tbody>
</table>
9. Summary of the one-way ANOVA and planned comparisons for the effect of large *Hexagenia* nymphs on the survivorship of 2nd instar *Chironomus* in the competitive interactions laboratory experiment.

10. Summary of the one-way ANOVA and planned comparisons for the effect of *Chironomus* larvae on the survivorship of large *Hexagenia* nymphs in the duration effects laboratory experiment.

11. Summary of the one-way ANOVA and planned comparisons for the effect of *Chironomus* larvae on the increase in body length of large *Hexagenia* nymphs in the duration effects laboratory experiment.

12. Summary of the one-way ANOVA and planned comparisons for the effect of *Chironomus* larvae on the survivorship of newly hatched *Hexagenia* nymphs in the duration effects laboratory experiment.

13. Summary of the one-way ANOVA and planned comparisons for the effect of *Chironomus* larvae on the increase in body length of newly hatched *Hexagenia* nymphs in the duration effects laboratory experiment.

14. Summary of the one-way ANOVA and planned comparisons for the effect of large *Hexagenia* nymphs on the survivorship of *Chironomus* larvae in the duration effects laboratory experiment.
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Number of <em>Hexagenia</em> nymphs and <em>Chironomus</em> larvae over two years.</td>
<td>11</td>
</tr>
<tr>
<td>2.</td>
<td>Size of <em>Hexagenia</em> nymphs and <em>Chironomus</em> larvae over two years.</td>
<td>12</td>
</tr>
<tr>
<td>3.</td>
<td>Densities of <em>Hexagenia</em> nymphs and chironomid larvae collected in spring 1998.</td>
<td>16</td>
</tr>
<tr>
<td>4.</td>
<td>Lake Erie stations sampled in 1998 and 1999 in the western basin.</td>
<td>21</td>
</tr>
<tr>
<td>5.</td>
<td>Expected results if competitive interactions were occurring between <em>Hexagenia</em> nymphs and <em>Chironomus</em> larvae.</td>
<td>23</td>
</tr>
<tr>
<td>6.</td>
<td>Expected results if duration effects were important between <em>Hexagenia</em> nymphs and <em>Chironomus</em> larvae.</td>
<td>31</td>
</tr>
<tr>
<td>7.</td>
<td>Treatments showing the effect of <em>Chironomus</em> larvae on the survivorship of large <em>Hexagenia</em> nymphs in the competitive interactions laboratory experiment.</td>
<td>37</td>
</tr>
<tr>
<td>8.</td>
<td>Treatments showing the effect of <em>Chironomus</em> larvae on the survivorship of newly hatched <em>Hexagenia</em> nymphs in the competitive interactions laboratory experiment.</td>
<td>40</td>
</tr>
<tr>
<td>9.</td>
<td>Treatments showing the effect of large <em>Hexagenia</em> nymphs on the survivorship of <em>Chironomus</em> larvae in the competitive interactions laboratory experiment.</td>
<td>42</td>
</tr>
<tr>
<td>10.</td>
<td>Treatments showing the effect of <em>Chironomus</em> larvae added at different times on the survivorship of large <em>Hexagenia</em> nymphs in the duration effects laboratory experiment.</td>
<td>45</td>
</tr>
</tbody>
</table>
11. Treatments showing the effect of *Chironomus* larvae added at different times on the survivorship of newly hatched *Hexagenia* nymphs in the duration effects laboratory experiment. Treatments showing the effect of *Chironomus* larvae added at different times on the increase in body length of newly hatched *Hexagenia* nymphs in the duration effects laboratory experiment.

12. Treatments showing the effect of large *Hexagenia* nymphs added at different times on the survivorship of *Chironomus* larvae in the duration effects laboratory experiment.

13. Location of the 5 sites samples in July 2001 in the western basin of Lake Erie.


15. Number of *Hexagenia* embryos remaining after 48 hours for the 50 embryos/corer experiment. Number of *Hexagenia* embryos remaining after 48 hours for the 30 embryos/corer experiment. Number of *Hexagenia* embryos remaining after 48 hours in the corrected 10 embryos/corer experiment.

16. Number of *Hexagenia* embryos remaining after 48 hours in the 10 embryos/corer experiment.
GENERAL INTRODUCTION

Community structure is the sum of the factors that determine the relative abundance of species in communities and is responsible for the existence of recurring predictable patterns within a community (Seifert 1984). Few studies have examined the community structure of freshwater macroinvertebrates in muddy sediments, and of these most focus on community composition (Dermott and Kerec 1997, Nalepa et al. 1998, Manny and Schloesser 1999). Others have examined the community structure in streams (Peckarsky and Dodson 1980, McAuliffe 1984), and even marine soft-sediments (Peterson 1977, 1979). The lack of community structure studies in freshwater muddy sediments is likely due to the difficulties involved with studying organisms that cannot be viewed easily in the field, or in the laboratory. Understanding key interspecific macroinvertebrate interactions is critical to benthic community structure. By understanding key structural interactions biologists can make predictions about the state of the freshwater benthic community, and the freshwater community in general.

Competitive interactions may be important in the structuring of freshwater, soft-sediment benthic communities. Unfortunately, the number of field studies examining filter feeders and deposit feeders is very small (Gurevitch et al. 1992). Direct competitive interactions are most frequently found between closely related species (Woodin and Jackson 1979). In some cases, invertebrate species
distributions do not overlap because they use different resources, or they experience competitive exclusion (Death 2000). Competitive exclusion can result in increased mortality, decreased growth, or reduced reproductive success of the excluded population. For example, some competitively dominant haustoriid amphipods have caused increased mortality, and reduced reproductive effort in other less competitively dominant amphipod species (Croker and Hatfield 1980). Growth limitation as a result of competition for food has been shown in Lymnaea snails (Cuker 1983).

My research examines the interactions between two of the more dominant freshwater invertebrate species in the western basin of Lake Erie, the nymphs of the burrowing mayfly Hexagenia, and the larvae of the midge Chironomus. This is an interesting time to be studying interactions between these two taxa. Hexagenia are continuing to recolonize the western basin after being absent for approximately forty years (Krieger et al. 1996), while Chironomus have been present continuously, and have increased in numbers during the absence of Hexagenia (Manny and Schloesser 1999). The goal of this study is to determine if interactions occur between these two taxa that could affect community structure.

Hexagenia are burrowing mayflies of the order Ephemeroptera. Ephemeropterans are among the most primitive insects. They arose in the Carboniferous period 230-350 million years ago (Resh and Solem 1984). Ephemeropterans are characterised by their primitive palaeopterous wings, which cannot be folded over their backs (Needham et al. 1935). Immature Hexagenia
nymphs live in simple, u-shaped open burrows in the mud of well oxygenated, mesotrophic waters at depths of less than 20 metres. They generally remain in their burrows until maturity (Keltner and McCafferty 1986). However, some nymphs may leave their burrows due to high temperatures, low dissolved oxygen concentrations, overcrowding, low food levels, or difficulty in constructing burrows (Wright and Mattice 1981, Keltner and McCafferty 1986). *Hexagenia* nymphs use synchronous, metachronal gill movements to direct water through their burrows. The nymphs feed mostly on algae and detritus (Hunt 1953). *Hexagenia* nymphs go through 12 to 45 instars (Merritt and Cummins 1996). Just prior to the final juvenile moult, the nymph swims to the water’s surface and emerges as a winged subimago (Hunt 1953). The winged subimago stage is unique to ephemeropterans. After one or two days, the subimago moult and becomes a sexually mature, winged imago. This final moult is short-lived (1-2 days). The imago stage is only used for reproduction and dispersal (Hunt 1953). Adults mate in large swarms, dominated by males. Females fly into the swarm, copulate and then oviposit their eggs into the water (Fremling 1967). A single female produces an average of approximately 4000 eggs, but may contain up to 7684 eggs (Hunt 1953).

In western Lake Erie two species of burrowing mayflies co-occur *Hexagenia limbata*, and *Hexagenia rigida*. Although species can be distinguished by examining male imagoes (Burks 1953), or embryos (Koss 1968), it is not possible to reliably distinguish between the two species as nymphs, and so I will refer to
the organisms collectively as *Hexagenia*. *Hexagenia* nymphs were randomly distributed among rearing tanks, so any potential differences between *H. limbata* and *H. rigida* would be similar among all experiments (Corkum and Hanes 1992). *Hexagenia* nymphs found in lakes at similar latitudes to Lake Erie may have either one or two year life-cycles (Riklik and Momot 1982, Heise *et al.* 1987).

The *Chironomus*, family Chironomidae, are midges of the order Diptera. The family Chironomidae can be traced back to the Triassic period 200 million years ago (Ashe *et al.* 1987). *Chironomus* larvae inhabit the soft sediments of western Lake Erie. The larvae construct U-shaped tubes in the mud (Hilsenhoff 1966). *Chironomus* larvae undergo four instars, after which they pupate. When pupation is complete, the pupa rises to the water’s surface and emerges as a winged adult (Hilsenhoff 1966). Adults do not feed, and like *Hexagenia*, are short lived lasting only a few days (Edmunds *et al.* 1976). Like *Hexagenia*, *Chironomus* also mate in swarms. The swarms are made up of mostly males, with females only entering the swarm to mate (Hilsenhoff 1966). Females oviposit their egg mass into water, and then die shortly thereafter.

Lake Erie is geologically the oldest of the Laurentian Great Lakes (Bolsenga and Herdendorf 1993). It is also the shallowest Great Lake (64 m maximum depth), with the shortest retention time (1008 d)(Bolsenga and Herdendorf 1993). Lake Erie is divided into three distinct basins. *Hexagenia* nymphs are found in greatest numbers in the western basin due to the presence of a suitable temperature regime and sediment for burrowing. The western basin of Lake Erie lies west of a
line from the tip of Point Pelee, Ontario to the tip of Cedar Point, Ohio. The western basin contains extensive mud habitat suitable for *Hexagenia* nymphs and *Chironomus* larvae. The basin is shallow (average depth of 8 to 11 m) allowing complete mixing of the water column by wind action, which maintains high dissolved oxygen concentrations at the sediment-water interface (Rasmussen 1988).

Historically, *Hexagenia* have been important in transferring energy from the benthic to the pelagic community (Hunt 1953, Riklik and Momot 1982). *Hexagenia* nymphs are important in secondary production and the trophic transfer of energy in soft-bottomed mesotrophic habitats (Edsall et al. 1991). *Hexagenia* are an indicator of good water quality. They also were an important component of the diet of many fish in western Lake Erie, such as yellow perch (*Perca flavescens*), and walleye (*Stizostedion vitreum*) (Rasmussen 1988). Some of the highest rates of growth for yellow perch, freshwater drum (*Aplodinotus grunniens*), and white crappie (*Pomoxis annularis*) have been associated with the consumption of *Hexagenia* (Rasmussen 1988). Prior to 1953, *Hexagenia* nymphs and *Oecetis* caddisfly larvae, both relatively large species, were the dominant benthic fauna in the western basin of Lake Erie (Krieger et al. 1996, Madenjian et al. 1998). After the 1950s, the benthic community became dominated with smaller organisms, mostly oligochaetes (Schloesser et al. 2000). Densities of *Hexagenia* near the Bass Islands between 1930 and the early 1950s averaged between 300 and 500 nymphs m\(^{-2}\) (Krieger et al. 1996). Yellow perch growth
rates and abundance declined during the absence of *Hexagenia* nymphs from western Lake Erie. These growth and abundance rates have increased in recent years, possibly due to the return of *Hexagenia* (Tyson and Knight 2001).

*Hexagenia* nymphs declined in numbers, and quickly disappeared in 1953 after anoxic conditions were reported in the bottom waters of western Lake Erie (Britt 1955, Carr and Hiltunen 1965). *Hexagenia* were absent from the basin from the late 1950s (Carr and Hiltunen 1965) to the early 1990s (Krieger et al. 1996). During this interval organic pollution, high in phosphorus content enhanced phytoplankton and zooplankton production, impaired water quality, and reduced water-column transparency and dissolved oxygen levels (Ludsin et al. 2001). The establishment of late-summer stratification combined with the effects of eutrophication caused the benthic anoxic conditions which ultimately led to the disappearance of *Hexagenia* nymphs (Britt 1955). Anoxic conditions resulting in prolonged dissolved oxygen concentrations of less than 7 mg/L significantly reduce *Hexagenia* nymphal survivorship and growth in the laboratory (Winter et al. 1996).

Unlike *Hexagenia*, some chironomids such as *Chironomus* species are much better suited to low oxygen conditions and consequently were able to survive continuously in the western basin (Carr and Hiltunen 1965). Some *Chironomus* larvae have haemoglobin in their body fluid that can temporarily store oxygen (Cantrell and McLachlan 1977, Ashe et al. 1987). Chironomidae are often the
only insects found in profundal sediments where hypoxic (<3 mg/L) or anoxic conditions prevail (Piude 1995).

During the early 1970s, extensive effort was put into the initiation of programs designed to reduce the amount of pollution, mostly phosphorus, entering the western Lake Erie basin (Dolan 1993). Lake Erie has a short hydraulic residence time of 2.7 years (Quinn 1992), which has allowed Lake Erie water quality to respond quickly to these pollution abatement programs. As a result, the western basin of Lake Erie has gradually undergone oligotrophication, going from a eutrophic to mesotrophic status (Ludsin et al. 2001). *Hexagenia* nymphs did not reappear in the western Lake Erie basin despite the reduced pollution levels and improved oxygen conditions (Carr and Hiltunen 1965, Krieger et al. 1996). Small numbers of *Hexagenia* nymphs were found at low densities (7-41 m$^{-2}$) at nearshore sites in 1982, but none were found in open water sites (Manny and Schloesser 1999).

During the early 1990s, the trophic status of western Lake Erie continued to change resulting in increases in water clarity and reduced phytoplankton abundance, partly as a result of the presence of invasive dreissenids, which appeared in the Great Lakes beginning in 1986 (Griffiths et al. 1991, Holland 1993). Shortly thereafter, *Hexagenia* imagoes were observed along the shores of western Lake Erie, and *Hexagenia* nymphs have been quickly spreading throughout the lake (Schloesser et al. 2000). The first swarm of adult *Hexagenia* since the 1950s was observed in 1992 over the open waters of Western Lake Erie.
(Krieger et al. 1996). The invasion by dreissenids and the resulting ecological changes may have aided *Hexagenia* in recolonizing western Lake Erie (Corkum et al. 1997a).

*Hexagenia* nymphs and chironomid larvae do not typically co-occur spatially or temporally in western Lake Erie (Kolar et al. 1997). When *Hexagenia* nymph densities are high, chironomid larval densities are low, with the reverse being true as well. These taxa show a non-overlapping mosaic distribution. A non-overlapping mosaic distribution such as a checkerboard distribution occurs when two ecologically similar species have mutually exclusive distributions (Diamond 1975). This pattern suggests the potential for competition between these two taxa.

For competition to occur, a shared resource must be limiting. A resource by definition must be consumable, limiting, and have a direct effect on the fitness of the species (Wiens 1984). Food and space are the two most likely limiting resources in this system. Both food and space have been shown to be potentially limiting resources in soft and hard bottomed marine communities (Iribarne et al. 1994, Constable 1999). Competition for space is more likely to occur, since both *Hexagenia* and chironomids burrow in muddy sediments of similar particle sizes (Charbonneau and Hare 1998). These two taxa burrow at overlapping depths (Charbonneau and Hare 1998). Both taxa feed on similar materials, and are generalists. Food material is not likely to be limiting in the western Lake Erie mud (Merritt and Cummins 1996). *Hexagenia* burrow in aquatic muds that are often rich in algae and diatoms (Keltner and McCafferty 1986). One of the major
assumptions I make in this thesis is that western Lake Erie is sufficiently productive such that food is not limiting in the soft sediments.

If competitive interactions occur, they are not likely to be important in the structuring of the community at all times, or else coexistence would be nearly impossible. Competitive interactions are most likely to occur when densities of both taxa are at their highest, or when one taxon is larger than the other. Individuals are largest just prior to an emergence. In some situations the relative size of competing larvae is critical in determining the outcome of competition for space (Cantrell and McLachlan 1977). The peak *Chironomus* emergence times occur in late April and again in early July, whereas peak *Hexagenia* emergence occurs in mid June, but emergence continues until September (Lyman 1944). In western Lake Erie *Chironomus* emerge when the water temperature reaches 12 °C, *Hexagenia* emerge when the water temperature reaches 20 °C (Jan Ciborowski Personal Communication 2002). An emergence of *Hexagenia* can result in a 35 to 90 percent decrease in *Hexagenia* nymph density (Schloesser and Nalepa 2001). Densities prior to an emergence can range between 350 to 2100 *Hexagenia* nymphs m$^{-2}$, while densities after an emergence range between 190 to 925 nymphs m$^{-2}$. Newly hatched *Hexagenia* nymphs are at their highest densities in July (Edsall et al. 2001). The largest *Hexagenia* nymphs (28 – 32 mm body length) are at their highest densities in October and June, and are at their lowest densities in April and July (Edsall et al. 2001). I would therefore expect competitive interactions to be most important in June, and July. In June many large *Hexagenia*
nymphs are present, as are *Chironomus* larvae (Figure 1). In early July
*Chironomus* larvae are large, approaching their second emergence of the year
(Hilsenhoff, 1966), while *Hexagenia* nymphs are small, having just hatched
(Figure 2).

The main objective of my study was to examine the interactions between
*Hexagenia* and *Chironomus* using information collected from the field, and from
experiments conducted in the laboratory. I examined potential competitive
interactions between these two taxa for space in Chapter 1. My first null
hypothesis is that the survivorship, and increase in body length of *Hexagenia*
nymphs is not affected by the presence of *Chironomus* larvae, and *vice versa*. My
second null hypothesis states that there should not be a difference in outcome
when using newly hatched *Hexagenia* nymphs, or larger nymphs. I expected that
*Hexagenia* nymphs would show decreased survivorship and a lower increase in
length relative to the controls when in the presence of *Chironomus* larvae. I
expected this relation due to the apparent absence of coexistence in the field
between the two taxa (Kolar *et al.* 1997). I expected newly hatched *Hexagenia*
nymphs would show decreased survivorship and a lower increase in length than
larger *Hexagenia* nymphs since larger organisms are generally found to be
superior competitors (Cantrell and McLachlan 1977). My third null hypothesis is
that duration effects (differences in competitive ability based on the length of time
exposed) are not important between these two taxa. I expected that duration
Figure 1: Number of Hexagenia nymphs and Chironomus larvae over two years. A two-year life-cycle for Hexagenia nymphs is shown with a two generation per year life-cycle for Chironomus larvae. The vertical arrows indicate emergence from the substratum. Based on data from Hillenmueller et al. 1996, and (Schloesser and Nielson 2001).
Schloesser and Nélida 2001

Arrows indicate emergence from the sub-surface. Based on data from Field collected in 1996, Esqls et al. 2001, and

Hexagenia nymphs is shown with a two-generation per year life-cycle for Chironomus larvae. The vertical

Figure 2: Size of Hexagenia nymphs and Chironomus larvae over two years. A two-year life-cycle for


| Year 1 | Year 2 |

Chironomus

Hexagenia cohort 1

Hexagenia cohort 2

Size of organisms (mm)
effects would be important interactions between these two taxa since each of the taxa have different lengths to their life cycles.

In chapter 2, I examine the effect, if any, of *Chironomus* larvae feeding on *Hexagenia* embryos. My null hypothesis stated that *Chironomus* larvae would not consume *Hexagenia* embryos. I expected *Chironomus* larvae would consume a significant number of *Hexagenia* embryos relative to the control since *Chironomus* are generalists, feeding on organic material.
CHAPTER 1: Do Competitive Interactions Explain the Non-Overlapping Mosaic Distribution in Western Lake Erie Shown by *Hexagenia* and *Chironomus*?

Introduction

Competitive interactions between freshwater invertebrates have been poorly studied. In a summary of competition experiments Connell (1983) did not cite any experiments that examined competition between freshwater invertebrates. Death and Winterbourn (1995) noted a lack of research conducted on the effects of productivity on competition in stream benthic communities. Istock (1973) conducted a study of twelve species of water boatmen in enclosures. Interspecific competition at different densities was observed between the two dominant species *Hesperocorixa lobata* and *Sigara macropala*. Mackie et al. (1978) noted interspecific competition between the freshwater clams *Musculian securis* and *Musculium transversum*. Clearly, more research needs to be directed towards the area of freshwater invertebrate competitive interactions, especially in soft sediments. In a review of the literature, I was unable to find competition studies between freshwater benthic invertebrates in soft sediments. A lack of research pertaining to marine soft-sediment invertebrate competition studies has also been noted (Peterson 1977, Constable 1999). Understanding the importance of interactions among resident organisms is crucial to comprehending their distribution and abundance.
There are three main reasons to suspect competitive interactions between *Hexagenia* and *Chironomus*. First, *Hexagenia* nymphs and chironomid larvae show a non-overlapping mosaic distribution in the soft sediments of western Lake Erie (Figure 3), which may be due to competitive interactions for space between these two taxa. Partitioning of suitable habitat can be indicative of competition between organisms (Gilpin and Diamond 1982). If there were no interactions between the two taxa, both should be able to coexist given identical conditions. In other species, interspecific competition can result in a shift in habitat use. For example, the Jamaican lizard, *Anolis opalinus* utilizes higher perch heights when its competitor *Anolis lineatopus* is present (Jenssen 1973). In the soft sediment habitats of Lake Erie, this shift in habitat use is not possible since the habitat appears homogeneous. The result of competition would likely be a non-overlapping mosaic distribution.

The second suggestion of competition comes from the distributional pattern of *Chironomus* larvae over time. While *Hexagenia* were absent from the western basin of Lake Erie from the 1950s to the early 1990s, *Chironomus* larvae densities increased from an average density of 51 m⁻² in 1930 to 326 m⁻² in 1961 (Manny and Schloesser 1999). *Chironomus* larvae increased in density throughout the basin, even in areas previously dominated by *Hexagenia* nymphs (Carr & Hiltunen 1965). These data could be interpreted as showing competitive release. When two species are competing, the removal of the aggressively superior species results in an expansion of habitat use by subordinate (Williams and Batzli 1979). During
Figure 3: Densities of *Hexagenia* nymphs and chironomid larvae collected in spring 1998.
the absence of *Hexagenia* nymphs from western Lake Erie, many fish species such as yellow perch consumed *Chironomus* larvae in place of *Hexagenia* nymphs (Clady and Hutchinson 1976).

The *Hexagenia* nymph population exhibited exponential growth between 1991 and 1997 suggesting that they are competitively dominant to the chironomids present in the western basin of Lake Erie (Madenjian *et al.* 1998). Hanson and Leggett (1985) demonstrated that the introduction of a new species of freshwater fish reduces the growth of original fish species through competition.

The third suggestion of competition comes from the size differences between the two taxa. *Hexagenia* nymphs are considerably larger than *Chironomus* larvae. Size has been shown to be important in determining the outcome of competition for space (Cantrell and McLachlan 1977). Typically when two species compete for a shared limiting resource, the outcome can depend on the size of the two potentially competing species, with larger individuals often being superior (Persson 1985). Schoener (1983) demonstrated that for 27 of 32 competition studies where the outcome was related to size differences, the larger organism was competitively dominant.

Using species density information collected from western Lake Erie I will analyze the observed non-overlapping mosaic distribution. Field data showing this non-overlapping mosaic pattern would support any evidence of competitive interactions found in the laboratory.
If competition for space is occurring, the competitive mechanism is most likely to be interference competition. Interference competition occurs when one species denies access, or use of an essential resource to another species (Folt and Goldman 1981). Both of these taxa depend on establishing burrows for survival. They burrow in identical substrate types, with overlapping burrow depths Charbonneau and Hare 1998). *Hexagenia* nymphs burrow at a mean depth of approximately 6.7 cm, while *Chironomus* larvae burrow at a mean depth of approximately 4.5 cm (Charbonneau and Hare 1998). Space for burrowing has been found to be a limiting factor for chironomid larvae (Wiley 1981). At the maximum possible density, chironomid larvae burrows are continuous and any additional larvae could not establish a new burrow (Wiley 1981). It is conceivable that a competitively dominant taxon could interrupt the other taxon’s burrow, disrupting essential feeding, or aeration currents.

I tested competitive interactions for space in laboratory experiments. Competitive interactions were quantified by measuring survivorship and increase in body length of *Hexagenia* nymphs and *Chironomus* larvae over time. I expected that as *Chironomus* larval densities increase, *Hexagenia* nymphal survivorship would decrease. Large *Hexagenia* nymphs were expected to show higher survivorship and increase in body length than small *Hexagenia* nymphs in the presence of *Chironomus* larvae. As *Hexagenia* nymph densities increase, *Chironomus* survivorship was expected to decrease.
Duration effects may be important in the distribution of these two species in the western Lake Erie basin. In some systems, the outcome of competition may be influenced by the length of time one taxon is present with the other during key times in development. Since *Hexagenia* begin their life cycle in July (Hunt 1953), and *Chironomus* begin their life cycle in May (Hilsenhoff 1966), the presence of one taxon on the other may be important (Figure 1, 2). If initial size differences, or the time available for resource usage determines the strength of duration effects, the success of a given species should decrease as it is introduced increasingly later than its competitor, as noted in larval frogs (Alford 1989). Duration effects could be important following a mass emergence when one of the species loses significant numbers in the muds of western Lake Erie, and space becomes available. Chironomid larvae are slow colonizers in soft sediments after a disturbance such as a mass emergence; only the pelagic first instars colonize new sediment (Hare 1995). *Hexagenia* nymphs rarely leave their burrows and do not colonize new sediment at all (Hare 1995). This could potentially provide a competitive advantage for the more mobile *Chironomus* larvae if duration effects prove to be important in the distribution of *Hexagenia* and *Chironomus*.

I expected duration effects to be important in *Hexagenia* and *Chironomus* interactions since both taxa leave the substrate in large numbers at different times of the year. I expected that the trials in which *Chironomus* larvae are present the longest would show the lowest *Hexagenia* nymph survivorship and vice versa.
Materials and Methods

Field Study – Analysis of previous data sets

I analyzed the non-overlapping mosaic pattern of *Hexagenia* nymphs and chironomid larvae collected from western Lake Erie by Dr. Jan Ciborowski and colleagues at the University of Windsor. I used two data sets from 1998 and 1999 for benthic invertebrate densities. A data set collected from year 2000 was not used in the analysis. The samples for year 2000 were collected later in the season (June 1\(^{st}\) to July 24\(^{th}\)) than the 1998 and 1999 samples and as a result many samples were taken after the mass emergence of *Hexagenia*.

The Ciborowski samples were collected using a petite ponar (225 cm\(^2\) jaw opening), rinsed through a 250 μm sieve bucket, washed into plastic bags and preserved with Kahle’s solution (95% ethanol 30%:100% formalin 10%:water 60%). In the laboratory, each sample was washed through a sieve series of 4 mm, 1 mm, 500 μm, and 250 μm. Benthic invertebrates were sorted from debris using a dissection microscope and numbers of each taxa were recorded for each site. In 1998, 39 locations in Western Lake Erie were sampled from April 28\(^{th}\) to June 4\(^{th}\) (Figure 4). In 1999 data set, the same 39 locations within Western Lake Erie were sampled from May 4\(^{th}\) to June 10\(^{th}\). For each site, 5 replicate ponar samples were taken. In my analysis of the data I used only the information for density (no. m\(^{-2}\)) of *Hexagenia* nymphs, and chironomid larvae.
Figure 4: Lake Erie stations sampled in 1998 and 1999 in the western basin.
Linear regression analysis (GraphPad Software Incorporated 1999) was used to analyse relations between *Hexagenia* nymphs and chironomid larvae in 1998 and 1999.

*Laboratory Experiment #1: Competitive Interactions*

Survivorship of *Hexagenia* nymphs and *Chironomus riparius* larvae, and increase in body length over time of *Hexagenia* nymphs were determined in an experiment with manipulated densities of *Hexagenia* nymphs and *Chironomus* larvae.

In the first trial, the effects of 2nd instar *Chironomus* larvae on large *Hexagenia* nymphs were determined. Large *Hexagenia* nymphs were 20.0 ± 3.1 mm in length excluding the cerci. Second instar *Chironomus riparius* larvae were 9.6 ± 1.5 mm in length.

For the second trial, the effects of second instar *Chironomus* larvae on newly hatched *Hexagenia* nymphs were determined. Newly hatched *Hexagenia* nymphs were 1.0 ± 0.1 mm in length. Finally, the effects of large *Hexagenia* nymphs on second instar larval *Chironomus riparius* were determined. If competition for space was occurring I would expect results to show an increase in survivorship or increase in length of *Hexagenia* in treatments with fewer *Chironomus* larvae (Figure 5).
Figure 5: Expected results if competitive interactions were occurring between *Hexagenia* nymphs and *Chironomus* larvae. Treatment refers to the densities of *Hexagenia*/*Chironomus* per container.
Hexagenia nymphs and Chironomus larvae were required for this experiment. Large Hexagenia nymphs were either collected from the field or grown in the laboratory from embryos previously collected.

The Hexagenia embryos were collected from Lake Erie female imagos at Colchester Harbour, Ontario Canada (41°59'N, 82°56'W). Female imagos were placed in 2 L polyethylene soil bag containing aerated, dechlorinated water. The female imagos oviposit their eggs into the water. The embryos were kept at 20°C for 6 days, then at 14°C for 6 days, and finally stored at 8°C until required (Friesen 1981). Hexagenia embryos can be stored at temperatures below 8°C without hatching (Giberson and Rosenberg 1992a). When the embryos are returned to room temperature, they are still viable, with nymphal vitality decreasing with storage time.

Large Hexagenia nymphs collected in the field were obtained from Lake St. Clair at Walpole Island, near Wallaceburg, Ontario, Canada (42°38'N, 82°28'W). The nymphs were collected using dip nets.

Chironomus riparius larvae were reared in tanks from embryos (Appendix 1).

Natural sediment was obtained from the western basin of Lake Erie collected with petite ponar grabs. The sediment was frozen to kill any organisms. The sediment was then filtered with a sieve of mesh size 125 μm to eliminate organisms from the sediment, and to ensure uniform consistency of the sediment.

For this laboratory experiment, each replicate was conducted in a separate glass container. Each container (surface area 156.25 cm², volume 2 L) was
aerated with capillary tubes, attached to an aerated main line of tygon tubing connected to an air pump. Dechlorinated water was added as required to maintain water levels after evaporation. The photoperiod was constant at 16 h light (5:00 - 21:00 h), 8 h dark to mimic spring field conditions. The containers were maintained at a temperature of 23 °C ± 3. The containers were individually covered with lids to protect against potential contamination among treatments. Sediment (5 cm deep) was added to each container to provide sufficient volume for burrowing (Hanes and Ciborowski 1992).

The study organisms were fed based on initial densities per container, and given a suspension of tetramin, baker's yeast, alfalfa, and distilled water (Hanes and Ciborowski 1992, Appendix 2). Food was gently poured into the containers so as to not disturb the sediment. Three mL of food were added to each container one week before the experiment began.

The data were analysed using a one-way ANOVA, and planned comparison tests. Planned comparison tests were conducted since in each case, I expected results to be significant in certain trials (Figure 5). In cases such as these, planned comparison tests are more powerful than more general tests such as Newman-Keuls, or Tukey tests. Significance was determined at the P < 0.05 critical level. Survivorship and increase in length was analysed for Hexagenia nymphs, while only survivorship was analysed for Chironomus larvae. Increase in length was not analysed for Chironomus larvae due to their short life span. In many cases, Chironomus larvae emerged as winged adults before the conclusion of the
experiment. I recorded whenever a chironomid emerged, and hence survived. However, once a larva had emerged to an adult, determining the body length of the larva was not possible.

The effect of *Hexagenia* nymphal and *Chironomus* larvae densities on survivorship and increase in length was studied using manipulated *Hexagenia* nymph densities of 0, 4, 8, 12, and 16 per container, with *Chironomus* larvae densities of 80, 40, 20, 10, and 0 per container, with two controls (Table 1). The *Hexagenia* densities represent 0, 256, 512, 768, and 1024 nymphs m\(^{-2}\). The *Chironomus* densities represent 5120, 2560, 1280, 640, and 0 larvae m\(^{-2}\). These densities were selected to represent the range of densities for these taxa found in western Lake Erie. Mortality of *Hexagenia* larvae is higher at densities less than 7 larvae/container due to Allee effects (Hanes and Ciborowski 1992). The Allee effect acts on a population whose numbers are below a certain threshold necessary to maintain the population over time. *Hexagenia* nymphs living close together may generate stronger currents within their burrows than a single nymph could produce (Hanes and Ciborowski 1992). The treatments run with 0 *Chironomus* larvae, and 16 *Hexagenia* nymphs were to demonstrate if intraspecific competition occurred. If density-dependent effects are found, there would be an intraspecific confounding factor.

Experiments were conducted with large *Hexagenia* nymphs with 2\(^{nd}\) instar *Chironomus* larvae, and repeated with small *Hexagenia* (newly hatched) nymphs and 2\(^{nd}\) instar *Chironomus* larvae. On the first day of the experiments, *Hexagenia*
Table 1: Experimental design of the competitive interactions laboratory experiment showing the treatments of *Hexagenia* nymphs and *Chironomus* larvae used in containers and the equivalent field densities.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Laboratory Density (number of organisms/container)</th>
<th>Field Density (number of organisms m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Hexagenia</em></td>
<td>0  4  8  12  16  8  0</td>
<td><em>Hexagenia</em>  0  256  512  768  1024  512  0</td>
</tr>
<tr>
<td><em>Chironomus</em></td>
<td>80  40  20  10  0  0  20</td>
<td><em>Chironomus</em>  5120  2560  1280  640  0  0  1280</td>
</tr>
</tbody>
</table>
nymphal body length (from the tip of the rostrum to the base of the caudal filaments) was determined for each of the Hexagenia nymphs used in the experiments. Body length was determined using Mocha image analysis software (Jandel Scientific 1993).

The experiments with the large Hexagenia nymphs were conducted for 60 days, from September 28th to November 27th 2001. The experiments with the newly hatched Hexagenia nymphs were run for 90 days, from July 19th to October 15th 2001. Experiments using newly hatched Hexagenia nymphs were allowed to run 90 days since there was less of a danger of emergence than with the larger Hexagenia nymphs. As Chironomus larvae emerged as winged adults, they were removed from the containers.

At the end of the experiments, the sediment was rinsed through a 500 µm sieve with water to locate surviving Hexagenia nymphs in each treatment. The surviving Hexagenia nymphs were measured once again for body length with the Mocha image analysis software, and increase in length over the duration of the experiment was determined.

A similar short-term (30 d) experiment was repeated for Chironomus larvae. Chironomus larvae survivorship was determined at the end of a 30 day experiment with Hexagenia nymphs run from October 31st to November 30th, 2001. The Chironomus larval experiment was only run for 30 days due to the shorter lifespan of Chironomus.
The *Chironomus* larvae were reared in tanks with sand as the substrate. With a sand substrate *Chironomus* larvae emerged after approximately 6 weeks. In mud the *Chironomus* larvae emerged much faster, after only approximately 10 days.

*Laboratory Experiment 2: Duration Effects*

The importance of duration effects in interactions between *Hexagenia* nymphs and *Chironomus* larvae were determined in laboratory experiments. For this experiment 90 (6 treatments and one control x (2 sizes of *Hexagenia* + *Chironomus*) x 5 replicates = 105) 2 L glass containers were used. Containers with either 8 large, or 8 newly hatched *Hexagenia* nymphs (512 m⁻²) were inoculated with 20 larval *Chironomus* (1280 m⁻²) on day 0, 10, 20, 30, 40, or 60. Eight *Hexagenia* nymphs per container were used to ensure the Allee effect would not be a factor (Hanes and Ciborowski 1992). All 6 treatments and the control were replicated 5 times (Table 2). The experiment was run for 61 days. Survivorship and changes in body length were determined as previously described. The experiment was conducted with the large *Hexagenia* nymphs (August 10th to October 10th, 2001) and newly hatched *Hexagenia* nymphs (July 18th to September 18th, 2001). If duration effects were important, I would have expected the results to resemble figure 6.
Table 2: Containers inoculated with 20 *Chironomus* larvae at different points in the development of *Hexagenia* nymphs during the 61 day duration effects experiment. Small and large *Hexagenia* nymphs were tested separately. \( N = \) number of replicates.

<table>
<thead>
<tr>
<th>Day of chironomid inoculation</th>
<th>Time (d) exposed to chironomids</th>
<th><em>Hexagenia</em> N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>Control</td>
<td>5</td>
</tr>
<tr>
<td>0</td>
<td>61</td>
<td>5</td>
</tr>
<tr>
<td>10</td>
<td>51</td>
<td>5</td>
</tr>
<tr>
<td>20</td>
<td>41</td>
<td>5</td>
</tr>
<tr>
<td>30</td>
<td>31</td>
<td>5</td>
</tr>
<tr>
<td>40</td>
<td>21</td>
<td>5</td>
</tr>
<tr>
<td>60</td>
<td>1</td>
<td>5</td>
</tr>
</tbody>
</table>
Figure 6: Expected results if duration effects were important between *Hexagenia* nymphs and *Chironomus* larvae.
The experiment was repeated to show the effect of adding *Hexagenia* nymphs at different times in the life of *Chironomus* larvae (Table 3). Containers with 20 *Chironomus* larvae were inoculated with 8 large *Hexagenia* nymphs on day 0, 5, 10, 15, 20, 30. All 6 treatments were replicated 5 times. The experiment was run for 31 days. The experiment was only run for 31 days and the inoculation days changed due to the shorter life span of *Chironomus*. At the end of 31 days the survivorship of *Chironomus* larvae was determined. The experiment was conducted from November 19th to December 20th, 2001.

The same experimental conditions were used as in the competitive interactions experiment. The data was analysed using a one-way ANOVA, and planned comparison tests. Significance was determined at the $P < 0.05$ critical level. Survivorship and increase in length were analysed for *Hexagenia* nymphs, while only survivorship was analysed for *Chironomus*.
Table 3: Containers inoculated with 8 large *Hexagenia* nymphs at different points in the development of *Chironomus* larvae during the 31 day duration effects experiment. N = number of replicates.

<table>
<thead>
<tr>
<th>Day of <em>Hexagenia</em> inoculation</th>
<th>Time (d) exposed to <em>Hexagenia</em></th>
<th><em>Chironomus</em> N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>Control</td>
<td>5</td>
</tr>
<tr>
<td>0</td>
<td>31</td>
<td>5</td>
</tr>
<tr>
<td>5</td>
<td>26</td>
<td>5</td>
</tr>
<tr>
<td>10</td>
<td>21</td>
<td>5</td>
</tr>
<tr>
<td>15</td>
<td>16</td>
<td>5</td>
</tr>
<tr>
<td>20</td>
<td>11</td>
<td>5</td>
</tr>
<tr>
<td>30</td>
<td>1</td>
<td>5</td>
</tr>
</tbody>
</table>
Results

Field Study – Analysis of previous data sets

No relationships between chironomid larvae and Hexagenia nymphs were found to be significant (Table 4).

Laboratory Experiment 1: Competitive Interactions

Data transformations in all experiments were unnecessary.

Survivorship of large Hexagenia nymphs in the competitive interactions laboratory experiment was not significantly different in the presence of larval Chironomus, based on a one-way ANOVA (Table 5, Figure 11). Four planned comparison tests were performed and none revealed any significant differences (F = 0.127, p = 0.726, F = 0.211, p = 0.651, F = 0.913, p = 0.351, and F = 0.039, p = 0.845).

The increase in body length of large Hexagenia nymphs was not significantly different in the presence of either higher densities of Hexagenia or larval Chironomus (Table 6, Figure 11). Four planned comparisons were performed and none revealed any significant differences (F = 0.370, p = 0.550, F = 0.005, p = 0.943, F = 0.828, p = 0.374, and F = 0.268, p = 0.610).

Survivorship of newly hatched Hexagenia nymphs in the competitive interactions laboratory experiment was significantly different from the mean
Table 4: Summary of the linear regression analysis of the field data for western Lake Erie 1998 and 1999.

<table>
<thead>
<tr>
<th>Sites</th>
<th>1998</th>
<th>1999</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Sites</td>
<td>N.S</td>
<td>N.S</td>
</tr>
</tbody>
</table>
Table 5: Summary of the one-way ANOVA and planned comparisons for the effect of *Chironomus* larvae on the survivorship of large *Hexagenia* nymphs in the competitive interactions laboratory experiment after 60 days.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>S.S.</th>
<th>d.f.</th>
<th>M.S.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>0.051</td>
<td>4</td>
<td>0.013</td>
<td>0.323</td>
<td>0.860</td>
</tr>
<tr>
<td>Residual</td>
<td>0.791</td>
<td>20</td>
<td>0.040</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>0.842</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4H:40C vs. others</td>
<td>0.005</td>
<td>1</td>
<td>0.005</td>
<td>0.127</td>
<td>0.726</td>
</tr>
<tr>
<td>8H:20C vs. others</td>
<td>0.008</td>
<td>1</td>
<td>0.008</td>
<td>0.211</td>
<td>0.651</td>
</tr>
<tr>
<td>12H:10C vs. others</td>
<td>0.036</td>
<td>1</td>
<td>0.036</td>
<td>0.913</td>
<td>0.351</td>
</tr>
<tr>
<td>16H:0C vs. control</td>
<td>0.002</td>
<td>1</td>
<td>0.002</td>
<td>0.039</td>
<td>0.845</td>
</tr>
</tbody>
</table>

Table 6: Summary of the one-way ANOVA and planned comparisons for the effect of *Chironomus* larvae on the increase in body length of large *Hexagenia* nymphs in the competitive interactions laboratory experiment.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>S.S.</th>
<th>d.f.</th>
<th>M.S.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>12.252</td>
<td>4</td>
<td>3.063</td>
<td>0.368</td>
<td>0.829</td>
</tr>
<tr>
<td>Residual</td>
<td>166.595</td>
<td>20</td>
<td>8.330</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>178.847</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4H:40C vs. others</td>
<td>3.078</td>
<td>1</td>
<td>3.078</td>
<td>0.370</td>
<td>0.550</td>
</tr>
<tr>
<td>8H:20C vs. others</td>
<td>0.044</td>
<td>1</td>
<td>0.044</td>
<td>0.005</td>
<td>0.943</td>
</tr>
<tr>
<td>12H:10C vs. others</td>
<td>6.895</td>
<td>1</td>
<td>6.895</td>
<td>0.828</td>
<td>0.374</td>
</tr>
<tr>
<td>16H:0C vs. control</td>
<td>2.235</td>
<td>1</td>
<td>2.235</td>
<td>0.268</td>
<td>0.610</td>
</tr>
</tbody>
</table>
Figure 11 A: Treatments showing the effect of *Chironomus* larvae on the survivorship of large *Hexagenia* nymphs in the competitive interactions laboratory experiment. B: Treatments showing the effect of *Chironomus* larvae on the increase in body length of large *Hexagenia* nymphs in the competitive interactions laboratory experiment. Letter differences above the standard error bars indicate significant differences between treatments.
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38

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Table 7: Summary of the one-way ANOVA and planned comparisons for the effect of *Chironomus* larvae on the survivorship of newly hatched *Hexagenia* nymphs in the competitive interactions laboratory experiment.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>S.S.</th>
<th>d.f.</th>
<th>M.S.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>5354.829</td>
<td>4</td>
<td>1338.707</td>
<td>3.729</td>
<td>0.020</td>
</tr>
<tr>
<td>Residual</td>
<td>7180.544</td>
<td>20</td>
<td>359.027</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>12535.373</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4H:40C vs. others</td>
<td>2276.149</td>
<td>1</td>
<td>2276.149</td>
<td>6.340</td>
<td>0.020</td>
</tr>
<tr>
<td>8H:20C vs. others</td>
<td>99.048</td>
<td>1</td>
<td>99.048</td>
<td>0.276</td>
<td>0.605</td>
</tr>
<tr>
<td>12H:10C vs. others</td>
<td>538.226</td>
<td>1</td>
<td>538.226</td>
<td>1.499</td>
<td>0.235</td>
</tr>
<tr>
<td>16H:0C vs. control</td>
<td>2441.406</td>
<td>1</td>
<td>2441.406</td>
<td>6.800</td>
<td>0.017</td>
</tr>
</tbody>
</table>

Table 8: Summary of the one-way ANOVA and planned comparisons for the effect of *Chironomus* larvae on the increase in body length of newly hatched *Hexagenia* nymphs in the competitive interactions laboratory experiment.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>S.S.</th>
<th>d.f.</th>
<th>M.S.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>3.539</td>
<td>4</td>
<td>0.885</td>
<td>0.076</td>
<td>0.989</td>
</tr>
<tr>
<td>Residual</td>
<td>232.701</td>
<td>20</td>
<td>11.635</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>236.24</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4H:40C vs. others</td>
<td>0.773</td>
<td>1</td>
<td>0.773</td>
<td>0.066</td>
<td>0.799</td>
</tr>
<tr>
<td>8H:20C vs. others</td>
<td>1.574</td>
<td>1</td>
<td>1.574</td>
<td>0.135</td>
<td>0.717</td>
</tr>
<tr>
<td>12H:10C vs. others</td>
<td>0.828</td>
<td>1</td>
<td>0.828</td>
<td>0.071</td>
<td>0.792</td>
</tr>
<tr>
<td>16H:0C vs. control</td>
<td>0.364</td>
<td>1</td>
<td>0.364</td>
<td>0.031</td>
<td>0.861</td>
</tr>
</tbody>
</table>
Figure 12 A: Treatments showing the effect of *Chironomus* larvae on the survivorship of newly hatched *Hexagenia* nymphs in the competitive interactions laboratory experiment. B: Treatments showing the effect of *Chironomus* larvae on the final body length of newly hatched *Hexagenia* nymphs in the competitive interactions laboratory experiment. Letter differences above the standard error bars indicate significant differences between treatments.
Table 9: Summary of the one-way ANOVA and planned comparisons for the effect of large *Hexagenia* nymphs on the survivorship of 2nd instar *Chironomus* in the competitive interactions laboratory experiment.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>S.S.</th>
<th>d.f.</th>
<th>M.S.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>141.5</td>
<td>4</td>
<td>35.375</td>
<td>0.814</td>
<td>0.531</td>
</tr>
<tr>
<td>Residual</td>
<td>869.375</td>
<td>20</td>
<td>43.469</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1010.875</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>10C:12H vs. others</td>
<td>0.25</td>
<td>1</td>
<td>0.25</td>
<td>0.006</td>
<td>0.940</td>
</tr>
<tr>
<td>20C:8H vs. others</td>
<td>33.75</td>
<td>1</td>
<td>33.75</td>
<td>0.776</td>
<td>0.389</td>
</tr>
<tr>
<td>40C:4H vs. others</td>
<td>91.875</td>
<td>1</td>
<td>91.875</td>
<td>2.114</td>
<td>0.162</td>
</tr>
<tr>
<td>80C:0H vs. control</td>
<td>15.625</td>
<td>1</td>
<td>15.625</td>
<td>0.359</td>
<td>0.556</td>
</tr>
</tbody>
</table>
Figure 13: Treatments showing the effect of large *Hexagenia* nymphs on the survivorship of *Chironomus* larvae in the competitive interactions laboratory experiment. Letter differences above the standard error bars indicate significant differences between treatments.
Laboratory Experiment 2: Duration Effects

Survivorship of large Hexagenia nymphs in the duration effects laboratory experiment was not significantly different with Chironomus larvae added at different times (Table 10, Figure 14). Six planned comparison tests were performed and none revealed any significant difference (F = 0.621, p = 0.437, F = 0.217, p = 0.645, F = 2.155, p = 0.153, F = 0.044, p = 0.835, F = 1.086, p = 0.306, and F = 2.394, p = 0.133).

The increase in body length of large Hexagenia nymphs in the duration effects laboratory experiment was not significantly different with Chironomus larvae added at different times (Table 11, Figure 14). Six planned comparisons were performed. The comparison between inoculations on day 20 with the other treatments revealed a significant difference (F = 4.631, p = 0.04). None of the other comparisons revealed any significant differences (F = 0.365, p = 0.550, F = 0.649, p = 0.427, F = 0.253, p = 0.619, F = 1.111, p = 0.301, and F = 2.209, p = 0.148).

Survivorship of newly hatched Hexagenia nymphs in the duration effects laboratory experiment was not significantly different with Chironomus larvae added at different times (Table 12, Figure 15). Six planned comparison tests were performed and none revealed any significant difference (F = 0.462, p = 0.502, F = 0.342, p = 0.563, F = 0.885, p = 0.355, F = 0.271, p = 0.607, F = 0.241, p = 0.628, and F = 2.006, and p = 0.168).
Table 10: Summary of the one-way ANOVA and planned comparisons for the effect of *Chironomus* larvae on the survivorship of large *Hexagenia* nymphs in the duration effects laboratory experiment.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>S.S.</th>
<th>d.f.</th>
<th>M.S.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>6125</td>
<td>6</td>
<td>1020.83</td>
<td>1.086</td>
<td>0.395</td>
</tr>
<tr>
<td>Residual</td>
<td>26312.5</td>
<td>28</td>
<td>939.732</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>32437.5</td>
<td>34</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 vs. others</td>
<td>583.33</td>
<td>1</td>
<td>583.33</td>
<td>0.621</td>
<td>0.437</td>
</tr>
<tr>
<td>10 vs. others</td>
<td>204.17</td>
<td>1</td>
<td>204.17</td>
<td>0.217</td>
<td>0.645</td>
</tr>
<tr>
<td>20 vs. others</td>
<td>2025</td>
<td>1</td>
<td>2025</td>
<td>2.155</td>
<td>0.153</td>
</tr>
<tr>
<td>30 vs. others</td>
<td>41.67</td>
<td>1</td>
<td>41.67</td>
<td>0.044</td>
<td>0.835</td>
</tr>
<tr>
<td>40 vs. others</td>
<td>1020.83</td>
<td>1</td>
<td>1020.83</td>
<td>1.086</td>
<td>0.306</td>
</tr>
<tr>
<td>60 vs. control</td>
<td>2250</td>
<td>1</td>
<td>2250</td>
<td>2.394</td>
<td>0.133</td>
</tr>
</tbody>
</table>

Table 11: Summary of the one-way ANOVA and planned comparisons for the effect of *Chironomus* larvae on the increase in body length of large *Hexagenia* nymphs in the duration effects laboratory experiment.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>S.S.</th>
<th>d.f.</th>
<th>M.S.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>1090.753</td>
<td>6</td>
<td>181.792</td>
<td>1.536</td>
<td>0.203</td>
</tr>
<tr>
<td>Residual</td>
<td>3313.213</td>
<td>28</td>
<td>118.329</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>4403.966</td>
<td>34</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 vs. others</td>
<td>43.232</td>
<td>1</td>
<td>43.232</td>
<td>0.365</td>
<td>0.550</td>
</tr>
<tr>
<td>10 vs. others</td>
<td>76.792</td>
<td>1</td>
<td>76.792</td>
<td>0.649</td>
<td>0.427</td>
</tr>
<tr>
<td>20 vs. others</td>
<td>548</td>
<td>1</td>
<td>548</td>
<td>4.631</td>
<td>0.040</td>
</tr>
<tr>
<td>30 vs. others</td>
<td>29.965</td>
<td>1</td>
<td>29.965</td>
<td>0.253</td>
<td>0.619</td>
</tr>
<tr>
<td>40 vs. others</td>
<td>131.407</td>
<td>1</td>
<td>131.407</td>
<td>1.111</td>
<td>0.301</td>
</tr>
<tr>
<td>60 vs. control</td>
<td>261.356</td>
<td>1</td>
<td>261.356</td>
<td>2.209</td>
<td>0.148</td>
</tr>
</tbody>
</table>
Figure 14 A: Treatments showing the effect of *Chironomus* larvae added at different times on the survivorship of large *Hexagenia* nymphs in the duration effects laboratory experiment. B: Treatments showing the effect of *Chironomus* larvae added at different times on the increase in body length of large *Hexagenia* nymphs in the duration effects laboratory experiment. Letter differences above the standard error bars indicate significant differences between treatments.
Table 12: Summary of the one-way ANOVA and planned comparisons for the effect of *Chironomus* larvae on the survivorship of newly hatched *Hexagenia* nymphs in the duration effects laboratory experiment.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>S.S.</th>
<th>d.f.</th>
<th>M.S.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>3276.79</td>
<td>6</td>
<td>546.131</td>
<td>0.701</td>
<td>0.651</td>
</tr>
<tr>
<td>Residual</td>
<td>21812.5</td>
<td>28</td>
<td>779.018</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>25089.29</td>
<td>34</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 vs. others</td>
<td>360.12</td>
<td>1</td>
<td>360.12</td>
<td>0.462</td>
<td>0.502</td>
</tr>
<tr>
<td>10 vs. others</td>
<td>266.67</td>
<td>1</td>
<td>266.67</td>
<td>0.342</td>
<td>0.563</td>
</tr>
<tr>
<td>20 vs. others</td>
<td>689.06</td>
<td>1</td>
<td>689.06</td>
<td>0.885</td>
<td>0.355</td>
</tr>
<tr>
<td>30 vs. others</td>
<td>210.94</td>
<td>1</td>
<td>210.94</td>
<td>0.271</td>
<td>0.607</td>
</tr>
<tr>
<td>40 vs. others</td>
<td>187.5</td>
<td>1</td>
<td>187.5</td>
<td>0.241</td>
<td>0.628</td>
</tr>
<tr>
<td>60 vs. control</td>
<td>1562.5</td>
<td>1</td>
<td>1562.5</td>
<td>2.006</td>
<td>0.168</td>
</tr>
</tbody>
</table>

Table 13: Summary of the one-way ANOVA and planned comparisons for the effect of *Chironomus* larvae on the increase in body length of newly hatched *Hexagenia* nymphs in the duration effects laboratory experiment.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>S.S.</th>
<th>d.f.</th>
<th>M.S.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>159.524</td>
<td>6</td>
<td>26.587</td>
<td>5.007</td>
<td>0.001</td>
</tr>
<tr>
<td>Residual</td>
<td>148.694</td>
<td>28</td>
<td>5.310</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>308.218</td>
<td>34</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 vs. others</td>
<td>68.079</td>
<td>1</td>
<td>68.079</td>
<td>12.82</td>
<td>0.001</td>
</tr>
<tr>
<td>10 vs. others</td>
<td>83.307</td>
<td>1</td>
<td>83.307</td>
<td>15.687</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>20 vs. others</td>
<td>3.006</td>
<td>1</td>
<td>3.006</td>
<td>0.566</td>
<td>0.458</td>
</tr>
<tr>
<td>30 vs. others</td>
<td>0.018</td>
<td>1</td>
<td>0.018</td>
<td>0.003</td>
<td>0.954</td>
</tr>
<tr>
<td>40 vs. others</td>
<td>2.136</td>
<td>1</td>
<td>2.136</td>
<td>0.402</td>
<td>0.531</td>
</tr>
<tr>
<td>60 vs. control</td>
<td>2.977</td>
<td>1</td>
<td>2.977</td>
<td>0.561</td>
<td>0.460</td>
</tr>
</tbody>
</table>
Figure 15 A: Treatments showing the effect of *Chironomus* larvae added at different times on the survivorship of newly hatched *Hexagenia* nymphs in the duration effects laboratory experiment. B: Treatments showing the effect of *Chironomus* larvae added at different times on the increase in body length of newly hatched *Hexagenia* nymphs in the duration effects laboratory experiment. Letter differences above the standard error bars indicate significant differences between treatments.
The increase in body length of newly hatched *Hexagenia* nymphs in the duration effects laboratory experiment was significantly different with *Chironomus* larvae added at different times (Table 13, Figure 15). Six planned comparisons were conducted. There was a significant difference between the other treatments and the treatment with *Chironomus* larvae added on day 0 (F = 12.82, p = 0.001), and between the inoculations on day 20, 30, 40, 60, and the control and the treatment with inoculations on day 10 (F = 15.687, p < 0.001). The other four comparisons revealed no significant differences (F = 0.566, p = 0.458, F = 0.003, p = 0.954, F = 0.402, p = 0.531, and F = 0.561, p = 0.460).

Survivorship of the 2nd instar *Chironomus* larvae in the duration effects laboratory experiment was not significantly different with *Hexagenia* nymphs added at different times (Table 14, Figure 20). Six planned comparison tests were performed and none revealed any significant difference (F = 0.398, p = 0.533, F = 0.011, p = 0.916, F = 0.273, p = 0.605, F = 0, p = 1.0, F = 2.049, p = 0.163, and F = 0.683, p = 0.416).
Table 14: Summary of the one-way ANOVA and planned comparisons for the effect of *Hexagenia* nymphs on the survivorship of 2\textsuperscript{nd} instar *Chironomus* larvae in the duration effects laboratory experiment.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>S.S.</th>
<th>d.f.</th>
<th>M.S.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>50</td>
<td>6</td>
<td>8.333</td>
<td>0.569</td>
<td>0.751</td>
</tr>
<tr>
<td>Residual</td>
<td>410</td>
<td>28</td>
<td>14.643</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>460</td>
<td>34</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0 vs. others</td>
<td>5.833</td>
<td>1</td>
<td>5.833</td>
<td>0.398</td>
<td>0.533</td>
</tr>
<tr>
<td>5 vs. others</td>
<td>0.167</td>
<td>1</td>
<td>0.167</td>
<td>0.011</td>
<td>0.916</td>
</tr>
<tr>
<td>10 vs. others</td>
<td>4.0</td>
<td>1</td>
<td>4.0</td>
<td>0.273</td>
<td>0.605</td>
</tr>
<tr>
<td>15 vs. others</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1.0</td>
</tr>
<tr>
<td>20 vs. others</td>
<td>30.0</td>
<td>1</td>
<td>30.0</td>
<td>2.049</td>
<td>0.163</td>
</tr>
<tr>
<td>30 vs. control</td>
<td>10.0</td>
<td>1</td>
<td>10.0</td>
<td>0.683</td>
<td>0.416</td>
</tr>
</tbody>
</table>
Figure 16: Treatments showing the effect of large Hexagenia nymphs added at different times on the survivorship of Chironomus larvae in the duration effects laboratory experiment. Letter differences above the standard error bars indicate significant differences between treatments.
Discussion

Field Study – Analysis of previous data sets

A closer examination of the non-overlapping mosaic pattern observed between Hexagenia nymphs and chironomid larvae in western Lake Erie for the years 1998 and 1999 was expected to show strong interactions between the two taxa. I expected to find very little overlap in the distribution of these taxa. However, no interactions were found when all sites containing all densities of Hexagenia nymphs and chironomid larvae were examined and overlap in distributions was evident.

The results could be attributed to substrate type. For example, some of the sampling sites may have a higher sand content (Hunt 1953), or are rocky, and others may have large numbers of dreissenids, or dreissenid shells (Freeman 1999). In each of these cases, Hexagenia nymph density would be reduced, while chironomid larvae would remain or increase in density in the case of dreissenids (Kuhns and Berg 1999).

Substrate in highly contaminated areas of the western basin of Lake Erie may be too toxic for Hexagenia nymphs, but may not be too toxic for Chironomus larvae. Corkum et al. (1997b) demonstrated that Hexagenia nymphs are not found in areas of very high contaminant concentrations. Chironomus larvae are able to tolerate higher concentrations of contaminants (Manny and Schloesser 1999) and therefore may be found in areas where Hexagenia nymphs are not found. This is
an alternative explanation for the non-overlapping mosaic distribution in western Lake Erie.

It was surprising to find such little evidence of relationships between these taxa based on my analyses. Hergenrader and Lessig (1980) found that when *Hexagenia* densities are high, chironomid larvae densities are typically low in flood control reservoirs in eastern Nebraska. Cooper and Knight (1985) found that when chironomid larvae densities are high, *Hexagenia* nymph densities are generally low at Ross Barnett Reservoir in Mississippi.

Based on the different life cycles between chironomids and *Hexagenia* early July would have the most potential for competitive interactions with chironomids more likely to dominate. *Hexagenia* nymphs would have just hatched being very small in size, while chironomid larvae would be quite large in size preparing for their second emergence of the season. The data analysed here was taken from late April to early June when *Hexagenia* nymphs would be at their largest and most likely to dominate. It would be interesting to examine data sampled from early July to see if more significant relationships appear. More significant results may be found when data for more years can be analyzed. Since *Hexagenia* numbers have only returned to their historical densities since 1997, only a few years worth of data is available. As more years go by, more reliable trends for taxa distribution in Lake Erie will be available.
Laboratory Experiment 1: Competitive Interactions

I expected the treatments with the lowest number of *Hexagenia* nymphs and the highest number of *Chironomus* larvae to show lower survivorship, and smaller increase in body length compared to the control. Survivorship and increase in length were not different from the control treatment for large *Hexagenia* nymphs, suggesting that competition for space with *Chironomus* larvae is not an important interaction for large *Hexagenia* nymphs.

The survivorship of newly hatched *Hexagenia* nymphs was higher than the control in the containers with the lowest density of *Hexagenia* nymphs and the highest density of *Chironomus* larvae. If competition for space was occurring, the opposite results would have been expected. These results do not suggest competition for space is important at all. The increase in length of newly hatched *Hexagenia* nymphs was not different from the control treatment, suggesting that competition for space with *Chironomus* larvae is not an important interaction.

Likewise, survivorship of *Chironomus* larvae in treatments with large *Hexagenia* nymphs was not found to be significantly different from the control, suggesting that competition interactions for space are not important.

I did expect to see competitive interactions for space; however my results show at these densities that these interactions may not be important in the distribution of these taxa. Previous studies have found that larger mobile grazers, such as non-burrowing mayflies (*Ameletus* sp.) and frog tadpoles (*Ascaphus* sp.), tend to reduce the abundance of smaller sessile invertebrates, such as chironomids of the
subfamily Orthocladiinae (Rosenfeld 1997). My research compares large burrowing *Hexagenia* nymphs, with smaller slightly more mobile *Chironomus* larvae. A reduction in abundance of either of the two taxa was not observed in my experiments.

In my experiments I did not use densities of *Hexagenia* nymphs or *Chironomus* larvae that were unnaturally high. It is possible that competition only occurs at higher densities. In a system such as western Lake Erie if densities of *Hexagenia* nymphs get too high, the more mobile *Chironomus* larvae may move on to unoccupied space, or to a space unsuited for *Hexagenia* nymph colonization such as locations with zebra mussel shells. This may be the cause of the non-overlapping mosaic distribution observed in western Lake Erie.

_Laboratory Experiment 2: Duration Effects_

Interspecific competitors often colonize communities at different times (Lawler and Morin 1993). It was expected that the treatments in which *Chironomus* larvae were added to *Hexagenia* nymphs early on in the experiment would show lower survivorship and a lower increase in body length relative to the control. Fifty percent survivorship of early instar *Enallagma boreale* is shown in the absence of larger conspecifics, but survivorship is only three percent when larger conspecifics are present (Anholt 1994). Large *Hexagenia* nymphs did not show any duration effects in terms of survivorship or increase in body length.
Newly hatched *Hexagenia* nymphs did not show any duration effects in terms of survivorship when exposed to *Chironomus* larvae. However, the newly hatched *Hexagenia* nymphs showed a decreased increase in length when exposed to *Chironomus* larvae. Newly hatched *Hexagenia* nymphs exposed to *Chironomus* larvae at day 0, and day 10 did show a significantly diminished increase in body length relative to the control. These results suggest that duration effects are important.

Limiting resources can often lead to trade-offs between different activities (Avelar 1993). For example, frequent snail interactions with fixed-tube dwelling organisms such as chironomids result in increased maintenance costs (Cuker 1983). While the chironomids are maintaining their burrows, they do not feed and hence show a reduced growth rate. The maintenance of *Hexagenia* burrows following interactions with *Chironomus* larvae may be the cause of the reduction in increase in length I observed. If *Hexagenia* nymphs are spending all of their energy maintaining burrows instead of feeding, a diminished increase in length would be the result. Unfortunately *Hexagenia* nymphs resuspend so much sediment that observing what an individual nymph is doing (feeding, or maintaining burrows) is impossible due to the low visibility.

Priority effects have been observed between different frog larvae species. In the case of frogs, the order of hatching affects the outcome of competition. The results demonstrate the importance of size-specific competition, with the older species being larger, and hence competitively dominant (Alford and Wilbur 1985).
In my experiments, 2nd instar Chironomus larvae caused a reduction in the increase in length of newly hatched Hexagenia nymphs which are smaller than 2nd instar Chironomus, and a reduction in the increase in length of larger Hexagenia nymphs which are larger than 2nd instar Chironomus larvae. Suhling and Lepkojus (2001) demonstrated that survival of early instars of dragonfly larvae, Orthetrum cancellatum was reduced compared to Sympetrum fonscolombii when eggs were laid at same time and place. Blaustein and Margalit (1994) observed later-stage mosquito larvae Culiseta longiareolata opportunistically preying on toad hatchings Bufo viridis demonstrating priority effects (Blaustein and Margalit 1994).

My findings may have important life history implications for Hexagenia. Larger first instar Hexagenia nymphs emerge during the peak of a mass emergence (Corkum et al. 1997a). For mayflies with long emergence periods, early-emerging females are larger and more fecund (Hunt 1953, Brittain 1982). The Hexagenia nymphs whose growth was impeded in the presence of Chironomus larvae would be expected to emerge later, since early growth would be slowed. For Hexagenia all growth occurs during the nymphal stage (Brittain 1982). The size of female Hexagenia imagos present decreases over the length of emergence from mid-June to the end of July, with fecundity likely decreasing as well (Corkum and Hanes 1992, Corkum et al. 1997a). Thus, Hexagenia nymphs exposed to Chironomus larvae may be smaller as adults, emerge later, and may be less fecund if female.
Hexagenia embryos are dispersed passively (Corkum et al. 1997a). For reproduction to be successful female Hexagenia must produce a large quantity of eggs, and both the females and embryos must avoid predation. There are benefits to emerging during peak emergence. Larger embryos would sink more quickly from the water's surface, where the females deposit them, to the sediment where they hatch, faster according to Stokes' Law. Embryos that sink faster may show reduced predation from pelagic predators, such as fish (Corkum et al. 1997a). The annual mayfly emergence period is associated with increased mayfly predation by fish (Hunt 1953). The synchronous release of embryos at night reduces exposure of embryos due to a swamping effect of aquatic nocturnal predators (Corkum et al. 1997a). The synchronous emergence of Hexagenia adults may result in a swamping effect of aerial predators, such as birds (Sweeney and Vannote 1982). Hexagenia nymphs showing a decreased increase in length due to duration effects caused by Chironomus larvae might emerge after peak emergence and would therefore be more susceptible to adult and embryo predation.

Second instar Chironomus larvae did not show any duration effects in terms of survivorship with Hexagenia nymphs added. Increase in length was not measured due to the difficulties of Chironomus larvae emerging before the end of the experiments. Future studies should note that the only evidence of interactions has been shown in decreased increase in Hexagenia body length. The design of future experiments should be modified such that measurements of Chironomus larvae increase in body length can be recorded.
The water temperature was kept constant, in a range ideal for *Hexagenia* nymph, and *Chironomus* larvae growth. Competition resulting in reduced survivorship of *Hexagenia* nymphs may take place at lower temperatures. *Chironomus* larvae are metabolically active above 12°C, while *Hexagenia* nymphs are not. Newly hatched *Hexagenia* nymphs show poor survivorship at low temperatures (Giberson and Rosenberg 1992b). It would be interesting to repeat these experiments at a lower temperature, such as 12°C, to determine if the competitive interactions are magnified. I would suspect the influence of active *Chironomus* larvae, on inactive *Hexagenia* nymphs would be stronger than observed in this experiment.
CHAPTER 2: Do *Chironomus* larvae consume *Hexagenia* embryos?

Introduction

Ecologically similar organisms have a potential to show mutually exclusive distributions in a checkerboard pattern (Diamond 1975). *Hexagenia* nymphs and *Chironomus* larvae both inhabit the muddy soft sediment of western Lake Erie, and appear to show a non-overlapping mosaic pattern as observed in Figures 3. The western Lake Erie basin habitat is for the most part a homogeneous mud substrate suitable for both *Hexagenia* and *Chironomus* colonization. Other studies in more heterogeneous substrates have found that coexistence can be possible. For example coexistence among four species of *Gammarus* is known to occur due to spatial and temporal habitat heterogeneity (MacNeil et al. 2001). Without heterogeneity present in western Lake Erie substrates, coexistence would be unlikely, and a non-overlapping mosaic distribution would be the result of strong taxa interactions. This non-overlapping mosaic pattern suggests that interactions between these taxa may be important.

Competitive release occurs when a species increases its abundance and distribution in the absence of its competitor (Williams and Batzli 1979). There is evidence to suggest competitive release may occur in western Lake Erie during absence of *Hexagenia*. Chironomid larvae densities increased when *Hexagenia* nymphs were absent from the western basin from the late 1950s to the early 1990s (Manny and Schloesser 1999).
The experiments conducted in chapter 1 suggest that competitive interactions may not be as strong as originally suspected. No direct evidence of reduced survivorship was observed between the two taxa in the competitive interactions experiments. Increase in length was reduced in the priority effects experiments. The objective of this chapter was to test an alternative explanation for the checkerboard distribution observed between these two taxa.

Peterson (1979) suggested that adult-larval interactions were important in the structuring of soft-sediment benthic marine communities. Sedimentary marine adults exclude the recruitment of larvae. For example, in 1977, Sutherland demonstrated that recruitment of Schizoporella was strong on empty settlement plates, while little recruitment occurred on adjacent plates covered by an established Schizoporella colony. Hexagenia and Chironomus both have winged adult stages that do not interact with the aquatic larval stages in any way, however the later benthic larval stages of one taxa may interact with the embryos of the other. For example, the egg masses of gypsy moths (Lymantria dispar) are known to be preyed upon by the dermestid, Cryptorhopalum ruficorne (Mason and Ticchurst 1984). Cryptorhopalum ruficorne larvae were found inside, or under 4.0 – 10.3% of gypsy moth egg masses and were therefore thought to be a significant factor affecting the population dynamics of the gypsy moth. A second example of later larval stages affecting embryos involves Hexagenia nymphs. Larger Hexagenia nymphs through their burrowing activities are known to bury Hexagenia embryos causing the embryos to go under anoxic conditions and
retarded development (Gerlofsma 1999). This behaviour is thought to control nymphal numbers in areas of high densities of *Hexagenia* nymphs (Gerlofsma 1999).

*Hexagenia* females in the western Lake Erie region release their embryos into the water in late June. At the same time, *Chironomus* larvae are present in the sediment growing rapidly, preparing for a late July emergence. *Hexagenia* females release an average of 4000 embryos into the water (Hunt 1953). These embryos sink down through the water column to the soft sediments in which *Chironomus* larvae feed. Since, *Chironomus* larvae are generalist feeders, consuming organic material, it is possible that the midge larvae may consume *Hexagenia* embryos.

To determine if *Chironomus* larvae consume *Hexagenia* embryos it must first be established that *Chironomus* larvae are in fact present in the soft sediments at the time of year when *Hexagenia* embryos are added to the system (June and July). This was accomplished by analysing field samples taken from the western basin of Lake Erie in July of 2001, a time when *Hexagenia* embryos are still be in the sediment following peak emergence. Next laboratory experiments will be conducted to demonstrate that *Chironomus* larvae do in fact consume *Hexagenia* embryos.

I expect *Chironomus* larvae to be present in significant numbers in the western Lake Erie soft sediments during the month of July. I expect *Chironomus* larvae
will eat *Hexagenia* embryos because they are generalist feeders who feed on organic material.
Materials and Methods

Field Study

The distribution and abundance of chironomid larvae at five sites along a transect in western Lake Erie was determined for the month of July 2001. The transect was plotted from the southernmost tip of Point Pelee, Ontario, Canada north-west to Kingsville, Ontario, Canada consisting of 5 sampling locations (Figure 13). Each location was sampled once a month from April to September, with five replicate samples taken at each site. Only the July 25th samples were used for this study. The July 25th samples were used since these samples would have the representative chironomid larvae density at the time of year when chironomid larvae may consume Hexagenia embryos. Mayflies swarm and deposit embryos into western Lake Erie in late June, early July. The previous monthly sample was taken June 20th, possibly early for embryo deposition so the chironomid numbers for July were used. The samples were taken from the Canadian Department of Fisheries and Oceans vessel Limnos, using a winch operated petite Ponar with a 225 cm² jaw opening. The samples were rinsed with a hose through a 250 μm sieve bucket. They were then washed into plastic bags and preserved with Kahle’s solution (95% ethanol 30%:100% formalin 10%:water 60%). Each sample was run through a sieve series of 4 mm, 1 mm, 500 μm, and 250 μm. The sieved sample was placed into a petri dish under 6X magnification.
Figure 13: Location of the 5 sites samples in July 2001 in the western basin of Lake Erie.
Hexagenia nymphs and chironomid larvae were sorted from debris and their numbers were recorded for each site.

Laboratory Experiment

The laboratory experiment was conducted to determine whether Chironomus larvae consume Hexagenia embryos. Used in this experiment were 45 sediment corers with a diameter of 66 mm. The corers were capped, and placed in large opaque plastic containers to block out light for the duration of the experiment. The corers contained 4 cm of natural western Lake Erie sediment. Prior to the experiment, the natural sediment was frozen to eliminate foreign organisms, and sieved through a 125 μm sieve. The corers were filled with dechlorinated water, and were aerated using capillary tubing. The Chironomus larvae were obtained from cultures grown in the laboratory from egg masses collected from the western basin of Lake Erie. The Hexagenia embryos were collected from western Lake Erie females using light trapping in spring 2001. The Hexagenia nymphs were obtained from cultures grown in the laboratory from embryos that were collected from adult females in June 2001. For this experiment, three treatments were used: 1 Chironomus larva present, 1 Hexagenia nymph present, and a control with no organisms present. To each of these three treatments 50, 30, or 10 Hexagenia embryos were added. Fifty embryos per corer show a density of 14,615/m². Thirty embryos per corer show a density of 8,769/m². Ten embryos per corer show a density of 2,923/m². There were five replicates per case. The experiment
was run for 48 h. During this time no food was added. At the end of the experiment the sediment was washed through a 90 μm sieve. A dye, lignin pink was added to stain the *Hexagenia* embryos pink to facilitate recovery. The embryos were recovered by hand under a dissection microscope.

The number of *Hexagenia* embryos remaining was analysed using a one-way ANOVA, and planned comparisons.
Results

Field Study

All five sites along the transect had chironomid larvae present in July 2001 (Figure 14).

Laboratory Experiment

The number of Hexagenia embryos remaining in the 50 embryos/corer experiment after 48 hours was significantly different ($F = 12.94, p = 0.001$) in the corers with a Chironomus larva present, from the corers with the Hexagenia nymph present, or the controls (Figure 15). Two planned comparisons were performed. The first comparison between the tubes with the Hexagenia nymph and others showed a significant difference ($F = 6.001, p = 0.031$). The second planned comparison between the tubes with the Chironomus larvae present and the control showed a significant difference ($F = 19.872, p < 0.001$).

The number of Hexagenia embryos remaining in the 30 embryos/corer experiment after 48 hours was significantly different ($F = 24.21, p < 0.001$) in the corers with the Chironomus larva, from the corers with the Hexagenia nymph, or the controls (Figure 15). Two planned comparisons were performed. The first comparison between the tubes with the Hexagenia nymph and others showed a significant difference ($F = 9.481, p = 0.010$). The second planned comparison between the tubes with the Chironomus larvae present and the control showed a significant difference ($F = 38.949, p = < 0.001$).
Figure 14: Average densities of chironomid larvae at 5 sites along a transect in western Lake Erie from July 2001.
Figure 19 A: Number of *Hexagenia* embryos remaining after 48 hours for the 50 embryos/corer experiment. B: Number of *Hexagenia* embryos remaining after 48 hours for the 30 embryos/corer experiment. C: Number of *Hexagenia* embryos remaining after 48 hours in the corrected 10 embryos/corer experiment.
The number of *Hexagenia* embryos remaining in the 10 embryos/corer experiment after 48 hours was not significantly different (F = 2.928, p = 0.092) among treatments (Figure 16). There was a container with one *Chironomus* larva that did not consume any *Hexagenia* embryos. If the replicate in which the *Chironomus* larva that did not consume the *Hexagenia* embryos is removed from the analysis, then the number of *Hexagenia* embryos remaining is significantly different (F = 7.189, p = 0.010, Figure 15). Two planned comparisons were performed. The first comparison between the tubes with the *Hexagenia* nymph and others showed no significant difference (F = 4.693, p = 0.053). The second planned comparison between the tubes with *Chironomus* larvae present and the control tubes showed a significant difference (F = 10.560, p = 0.008).
Figure 16: Number of *Hexagenia* embryos remaining after 48 hours in the 10 embryos/corer experiment.
Discussion

Field Study

It was important to demonstrate that chironomid larvae are present in reasonably large numbers during the month of July otherwise the potential for Hexagenia embryo consumption by Chironomus larvae in western Lake Erie would be small. The field study sampled 5 sites in July of 2001 confirming the presence of chironomid larvae. Hexagenia mass emerge in mid to late June. Large numbers of embryos are deposited on the water’s surface at this time. A July 11, 2000 survey of sediments from Colchester harbour in western Lake Erie showed eggs densities ranging from $25.6 \pm 9.3 \text{ m}^{-2}$ to $66.8 \pm 18.6 \text{ m}^{-2}$, from 0.25 km to 4 km from shore (Corkum unpublished). It is known that in the field the hatching of embryos takes approximately two weeks (Hunt 1953). Therefore, if the consumption of Hexagenia embryos by Chironomus larvae is important in the distribution and abundance of Hexagenia nymphs, Chironomus larvae must be present in significant numbers in July, which they are based upon my field study.

Chironomus plumosus, an important western Lake Erie chironomid, builds up large populations and then suffers high mortality usually related to severe weather (McCall and Soster 1990). This aspect of the Chironomus life cycle could be related to the abundance of potential food available when Hexagenia females oviposit their embryos following a mass emergence. Chironomus larvae are present in very high numbers in July. It may be that they are utilizing Hexagenia embryos for food.
Laboratory Experiment

It was found that *Chironomus* larvae consume significant numbers of *Hexagenia* embryos at all three embryo densities. This could be an important factor affecting the distribution of *Hexagenia* nymphs in the western basin of Lake Erie. Schloesser and Nalepa (2001) suggested that recruitment of *Hexagenia* is dependent on the success of nymph emergence, mating, embryo deposition, and embryo hatching. *Hexagenia* embryos if consumed by predators, will not survive in areas of high predator density. This may be a significant factor affecting the distribution of *Hexagenia* nymphs in western Lake Erie.

Peterson (1979) suggested that the main competitive interaction between adults and larvae was indirect interference competition. The community structure mechanism I observed in my study was predation on embryos. The idea that older, larger organisms can affect the population dynamics of the smaller life stage of a second organism was observed.

There are examples from previous studies of invertebrate larvae consuming the eggs of fish, salamanders, frogs, and zooplankton. For example, caddisfly larvae of the species *Halesus digitatus*, and *Potamophylax cingulatus* were shown to prey of the eggs of bullhead (*Cottus gobio*) fish in the laboratory (Fox 1978). Previous studies have shown that the copepodites of the cyclopoid *Acanthocyclops robustus* enter the brood pouches of daphniids, where they feed on the eggs (Gliwicz and Lampert 1994). This predation causes a reduction in the daphniid clutch size.
The caddisfly *Banksiola dossuaria* was shown to prey on the egg masses of the spotted salamander *Ambystoma maculatum* in field studies (Stout et al. 1992). *Banksiola dossuaria* were found to be significantly larger when found on salamander egg masses than on the pond bottom. The caddisfly larvae were found to inflict significant mortality on the eggs of the spotted salamander. It would be interesting to compare *Chironomus* larvae growth when fed a diet of only *Hexagenia* embryos, to a controlled food. If *Chironomus* larvae growth is greater when fed a diet of *Hexagenia* embryos this interaction would definitely warrant more attention.

I have established that *Chironomus* larvae do consume *Hexagenia* embryos. The next step would be to determine the importance of this interaction in future studies. Previous studies have shown that some dipterans prey on the eggs masses of the frogs, *Hyperolius lateralis, Hyperolius cinnamomeoventris, Hypperolius platyceps,* and *Hyperolius kivuensis* in the humid tropical forests of Uganda (Vonosh 2000). The dipterans select frog eggs for food during the wet season when frog breeding activity at its highest. In the dryer season they randomly select food. For my study the only food item provided was the *Hexagenia* embryos. In a laboratory experiment, Majecki and Majecka (1998) offered caddisfly larvae (*Oligotricha striata*) a choice among amphibian eggs of *Rana lessonae, R. arvalis, Bufo bufo, Triturus alpestris, T. vulgaris,* and plant material. The caddisfly larvae prey on *R. lessonae, R. arvalis, T.alpestris, T.vulgaris,* but not *B. bufo* eggs. Only in the aquaria with *B. bufo* eggs did the caddisfly larvae eat
the plant material. It would be interesting to determine if *Chironomus* larvae preferentially feed on *Hexagenia* embryos, or if they prefer other food items. If *Chironomus* larvae prefer other food items available in western Lake Erie, then the consumption of *Hexagenia* embryos is probably not a significant factor affecting community structure.

It would be important to conduct an experiment using natural densities of *Hexagenia* embryos and *Chironomus* larvae. If at natural *Hexagenia* embryo densities, *Chironomus* larvae only consume a very small fraction of the available embryos, then the interaction is probably not very important in community structure. However, if *Chironomus* larvae do consume a significant number of the total available *Hexagenia* embryos, areas with high densities of *Chironomus* larvae may be able to exclude *Hexagenia* nymphs by not allowing their embryos to survive. *Hexagenia* nymphs remain in their burrows and only leave when under stress. So if predation by *Chironomus* larvae is an important interaction, areas where embryos are not allowed to hatch would likely not be colonized by the larger *Hexagenia* nymphs. The area would remain exclusive to *Chironomus* larvae.

My research demonstrated that a *Hexagenia* nymph does not consume *Hexagenia* embryos. However, this result may be due to the Allee effect. The feeding currents of only one *Hexagenia* nymph may not be sufficient to move an embryo into a nymph’s burrow. With additional nymphs present, a stronger
combined feeding current could be established, possibly strong enough to move embryos into the nymph’s burrow.

It could also be that the *Hexagenia* nymphs were not feeding during the 48 hour experiment. Charbonneau and Hare (1998) demonstrated that over a three day observation period *Hexagenia* nymphs dig more burrows than any of the other taxa they examined, including *Chironomus* larvae. If the *Hexagenia* nymphs spent the duration of the 48 hour experiment burrowing and not feeding, then the potential impact of *Hexagenia* nymphs consuming *Hexagenia* embryos would not be observed. Perhaps allowing the organisms to establish burrows for a period before the start of the experiment would yield more realistic results.
GENERAL CONCLUSIONS AND RECOMMENDATIONS

Strong competitive interactions between *Hexagenia* nymphs and chironomid larvae were expected to be found in the field data for western Lake Erie to support the observed non-overlapping mosaic pattern, however very few interactions were found. The field data analysed was taken from late April to early June when *Hexagenia* nymphs were at their largest and presumed to be competitively dominant. It would be interesting to examine data sampled from early July when chironomids are at their largest and *Hexagenia* have just hatched to see if alternative relationships appear.

Survivorship and increase in body length were not affected by the presence of *Chironomus* larvae. The survivorship of newly hatched *Hexagenia* nymphs was found to be higher than the control when in treatments with high densities of *Chironomus* larvae. The increase in length of newly hatched *Hexagenia* nymphs was not affected by *Chironomus* larvae. Survivorship of *Chironomus* larvae in treatments with large *Hexagenia* nymphs was not negatively affected. These results suggest that competition interactions for space are not important between *Hexagenia* nymphs and *Chironomus* larvae. Densities of *Hexagenia* nymphs or *Chironomus* larvae used did not exceed values naturally found in western Lake Erie. Competition for space may only occur at densities higher than found naturally. If densities of *Hexagenia* nymphs get too high, the more mobile *Chironomus* larvae may move to unoccupied space, or to a space unsuited for
Hexagenia nymph colonization such as rocky areas, or locations with zebra mussel shells (Kuhns and Berg 1999).

Large and newly hatched Hexagenia nymphs did not show any survivorship duration effects. However, newly hatched nymphs did show a diminished increase in body length when Chironomus larvae were added early in the experiment relative to the control. These results suggest that duration effects may be important in the distribution of these taxa.

Maintenance of Hexagenia nymph burrows following interactions with Chironomus larvae may be the cause of the reduction in increase in length I observed. Hexagenia nymphs may have to maintain their burrows following interactions with Chironomus larvae during which time they would not feed. Hexagenia nymphs resuspend sediment making observations of what an individual nymph is doing impossible due to the low visibility.

There may be important life history implications for Hexagenia based on my duration effects experiments. Larger first instar Hexagenia nymphs emerge during peak emergence. Early-emerging females are larger and more fecund. Smaller Hexagenia nymphs as the result of interactions with Chironomus larvae would be expected to emerge later, since early growth would be slowed. Hexagenia nymphs exposed to Chironomus larvae may be smaller as adults, emerge later, and may be less fecund. For reproduction to be successful female Hexagenia must produce a large quantity of eggs, and both the females and embryos must avoid predation. Larger embryos produced by a female during peak emergence which presumably
had no interactions with *Chironomus* larvae, would be denser than smaller embryos and would therefore sink from the water’s surface to the sediment faster. Embryos that sink faster may show reduced predation from pelagic predators. Smaller *Hexagenia* nymphs, due to duration effects caused by *Chironomus* larvae, might emerge after peak emergence and would therefore be more susceptible to adult and embryo predation. The synchronous release of embryos at night reduces exposure of embryos due to a swamping effect of aquatic nocturnal predators. The synchronous emergence of *Hexagenia* adults may result in a swamping effect of aerial predators.

Second instar *Chironomus* larvae did not show any survivorship duration effects with *Hexagenia* nymphs. Increase in length was not measured due to the difficulties of *Chironomus* larvae emerging before the end of the experiments.

Competition resulting in reduced survivorship of *Hexagenia* nymphs may take place at lower temperatures when *Chironomus* larvae are metabolically active, while *Hexagenia* nymphs are not. Newly hatched *Hexagenia* nymphs show poor survivorship at low temperatures. I would suspect active *Chironomus* larvae, would show stronger competitive interactions with inactive *Hexagenia* nymphs.

The presence of chironomid larvae was confirmed in a field study that sampled 5 sites in July of 2001. *Hexagenia* mass emerge in mid to late June and large numbers of embryos are deposited on the water’s surface. For the consumption of *Hexagenia* embryos by *Chironomus* larvae to be significant, chironomid larvae
must be present in significant numbers in July. It may be that chironomids are utilizing *Hexagenia* embryos for food.

*Chironomus* larvae consume *Hexagenia* embryos at all three embryo densities. This could be an important factor affecting the distribution of *Hexagenia* nymphs in the western basin of Lake Erie. Recruitment of *Hexagenia* is dependent on the success of nymph emergence, mating, embryo deposition, and embryo hatching. If *Hexagenia* embryos are consumed by *Chironomus* larvae, they will not survive in areas of high *Chironomus* larvae density. The only food item provided was the *Hexagenia* embryos, it would be interesting to determine if *Chironomus* larvae preferentially feed on *Hexagenia* embryos, or if they prefer other food items.

It would be important to conduct an experiment using natural densities of *Hexagenia* embryos and *Chironomus* larvae. If at natural *Hexagenia* embryo densities, *Chironomus* larvae only consume a very small fraction of the available embryos, then the interaction is probably not very important in community structure. However, if *Chironomus* larvae do consume a significant number of the total available *Hexagenia* embryos, areas with high densities of *Chironomus* larvae may be able exclude *Hexagenia* nymphs by not allowing their embryos to survive. *Hexagenia* nymphs remain in their burrows and only leave when under stress. So if predation by *Chironomus* larvae is an important interaction, areas where embryos are not allowed to hatch would likely not be colonized by the larger *Hexagenia* nymphs. The area would remain exclusive to *Chironomus* larvae.
Hexagenia nymphs do not consume Hexagenia embryos. This may be due to the Allee effect. The feeding currents of a single Hexagenia nymph may not be enough to move an embryo into a nymph's burrow. Additional nymphs would produce a stronger feeding current that may be able to move embryos into a burrow. Hexagenia nymphs may not have been feeding during the 48 hour experiment. It has been demonstrated that Hexagenia nymphs initially dig more burrows than Chironomus larvae. If Hexagenia nymphs spent the duration of my experiment burrowing and not feeding, then the impact of Hexagenia nymphs consuming Hexagenia embryos would not have been observed.

Future Research Needs

It might be interesting to test survivorship and increase in length of Hexagenia nymphs and Chironomus larvae at unnaturally high densities to examine evidence of competitive interactions.

It should be noted that the only evidence of competitive interactions has been shown in diminished increase in Hexagenia body length. The design of future experiments should be modified such that measurements of Chironomus larvae increase in body length can be recorded.

Future studies should repeat these experiments at a lower temperature, such as 12°C, to determine if the competitive interactions between Hexagenia nymphs and Chironomus larvae are magnified.
Chironomus larvae do consume Hexagenia embryos. Future studies should determine the importance of this interaction. It would be interesting to compare Chironomus larvae growth when fed a diet of only Hexagenia embryos, to a controlled food. If Chironomus larvae growth is greater when fed a diet of Hexagenia embryos this interaction would definitely warrant more attention. If Chironomus larvae prefer other food items available in western Lake Erie, then the consumption of Hexagenia embryos is probably not a significant factor affecting community structure.
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GraphPad Software Incorporated. 1999. GraphPad Prism Version 3.0.


APPENDIX 1 – Rearing of Chironomus

Chironomids were reared in 38 litre glass covered tanks. The tanks were filled halfway (15 cm) with dechlorinated water. Fine silica sand was placed in the bottom of the tanks to a depth of 3 cm for burrowing. It was found that keeping the tanks away from direct sunlight exposure was absolutely essential for rearing success. Initially each tank was seeded with 8 chironomid egg masses. *Chironomus riparius* egg masses were obtained from the Canada Centre for Inland Waters stock, and from chironomids reared at the University of Windsor. The feeding solution consisted of 5 g tetramin fish staple food ground up in a blender with 100 mL of water. New cultures, or cultures with no larvae visible were fed 4 mL of food every other day. Established cultures with visible larvae were fed 8 mL of food every day. If cultures were crowded more food was added. The tank water was replaced and algae was scraped off the sides of the tanks every week. When adults emerged, they were left in the tanks and any egg masses were not removed. New egg masses were added periodically from the existing University of Windsor cultures.
APPENDIX 2 — *Experimental feeding procedure*

The experimental containers were topped up with dechlorinated water to replace water lost due to evaporation at least once a week, or as required. It was found to be essential to the success of newly hatched *Hexagenia* nymphs not to remove any water during the course of the experiments. Scraping algae off the sides of the containers was also found to diminish the survival of newly hatched *Hexagenia* nymphs. The organisms were fed a mixture of 500 mL dechlorinated water, 7 g alfalfa pellets, 7 g yeast and 10 g tetramin staple fish food mixed with a blender. The containers were fed based on density and size of *Hexagenia* nymphs. Food was added to the containers twice weekly. Newly hatched *Hexagenia* nymphs were fed at a rate of 7 mL/organism for the first 75 days of growth. Larger *Hexagenia* nymphs were fed at a rate of 14 mL/organism.
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