

WHAT DEFINES A REFUGE FOR UNIONIDS FROM DREISSENID MUSSELS  
(*DREISSENA POLYMORPHA* AND *D. ROSTRIFORMIS BUGENSIS*)  
IN GREAT LAKES COASTAL WETLANDS?

Jessica J. Sherman

A thesis submitted in partial fulfillment of  
the requirements for the degree of  
Master of Science

Department of Biology

Central Michigan University  
Mount Pleasant, Michigan  
December 2011

Accepted by the Faculty of the College of Graduate Studies,  
Central Michigan University, in partial fulfillment of  
the requirements for the master's degree

Thesis Committee:

Donald Uzarski, Ph.D.	Committee Chair
Brent Murry, Ph.D.	Faculty Member
Daelyn Woolnough, Ph.D.	Faculty Member
David Zanatta, Ph.D.	Faculty Member
April 20, 2011	Date of Defense
Roger Coles, Ed.D.	Dean College of Graduate Studies
December 12, 2011	Approved by the College of Graduate Studies

This is dedicated to my mother, Dalyce.  
You are my inspiration.  
Thank you for your endless support, love, and devotion.

## ACKNOWLEDGEMENTS

I wish to thank my thesis committee, Dr. Don Uzarski, Dr. Brent Murry, Dr. Daelyn Woolnough, and Dr. Dave Zanatta. Each member provided countless hours of guidance through this project and committed themselves to my success. I am very appreciative to the many faculty and staff in the biology department who counseled me through the process of graduate school, especially: Dr. Tracy Galarowicz, Dr. Donna King, and Dr. Scott McNaught. I would like to express my gratitude to the administrative assistants in the biology office who were wonderful in helping me complete this project: Jan Morey, April Roberson, and Gayla Overton. Ray Clark was an instrumental part of building the artificial substrates for my research. Matt Cooper, Joshua Sherman, and Jerry Droll contributed extensively to the design of the water level gauges. Funding for this project was provided by the CMU Graduate Student Research and Creative Endeavors Grant and the Daniel E. and Mildred G. Wujek Endowed Scholarship. I would also like to greatly thank the volunteers that played an integral part of my research: Thomas Clement, Neil Schock, Nathan Barton, Matt Rowe, Erin Fitzpatrick, Dave Schuberg, Eric Calabro, Dave Dortman, Dave Branson, Hilary Kavanaugh, Chad Blass, Dave Coulter, Patrick Cosgrove, Maggie Humenick, Sasha Bozimowski, Lorrin Ortmann, and Robert Bidner. Jenn Bergner and Traci Griffith provided much needed support and friendship throughout this project. A great amount of appreciation goes to Tom Clement for helping me with every aspect of my research, especially for dedicating many hours to field work and musseling in cold waters. Finally, I would like to thank my family for their perennial encouragement, support, and love.

## ABSTRACT

### WHAT DEFINES A REFUGE FOR UNIONIDS FROM DREISSENIID MUSSELS (*DREISSENA POLYMORPHA* AND *D. ROSTRIFORMIS BUGENSIS*) IN GREAT LAKES COASTAL WETLANDS?

by Jessica J. Sherman

Coastal wetland sites around Michigan were studied to locate refuges for native unionids, whose numbers have declined drastically in the past century, and have exponentially declined since the introduction of invasive dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) into the Laurentian Great Lakes in the mid-1980's. Physical and chemical parameters, water level fluctuations, and dreissenid colonization rates were measured in coastal wetlands in Michigan to determine if relationships exist between refuge populations of native unionids and these factors. Fouling dreissenids were enumerated on all surveyed unionids and dreissenid colonization was evaluated in each wetland using artificial substrates. Live unionids were found in coastal wetlands in the Les Cheneaux Islands in Lake Huron, the Lake St. Clair delta, and North Maumee Bay in Lake Erie with significant differences in fouling noted among these regions. *Dreissena polymorpha* colonization densities were as high as 31,007 m<sup>-2</sup> at one site in North Maumee Bay, and 20,231 m<sup>-2</sup> in Saginaw Bay but no colonization occurred in the wetlands of the Beaver Island archipelago, the Les Cheneaux Islands, or Grand Traverse Bay sites though their presence in the open water of these regions was noted. Examination with principal components analysis and discriminate analysis indicated that some physical and chemical parameters are closely related to dreissenid colonization in coastal wetlands.

TABLE OF CONTENTS

CHAPTER

I. INTRODUCTION .....1  
    *Unionid Life History* .....1  
    *Dreissenid Life History* .....5  
    *Scope of Study* .....7

II. METHODS .....12  
    *Site Selection and Description* .....12  
    *Unionid Surveys* .....14  
    *Dreissenid Mussels Colonization* .....15  
    *Physical and Chemical Habitat Measurements* .....16  
    *Data Analysis* .....18

III. RESULTS .....21  
    *Unionid Surveys* .....21  
    *Dreissenid Colonization* .....25  
    *Physical and Chemical Habitat Measurements* .....30

IV. DISCUSSION .....35  
    *Unionid Presence* .....35  
    *Dreissenid Colonization* .....37  
    *Determination of Unionid Refugia* .....39  
    *Conclusion and Management Implications* .....39

APPENDICES .....42

LITERATURE CITED .....47

## CHAPTER I

### INTRODUCTION

Populations of native freshwater mussels (Bivalvia: Unionidae) have declined sharply since the introduction of dreissenid mussels into the Laurentian Great Lakes and because of this, species conservation programs for native mussels have become increasingly crucial. Zebra mussels (*Dreissena polymorpha*, Bivalvia: Dreissenidae), native to the Black and Caspian Sea region of eastern Europe, were introduced into the Great Lakes region in 1986 from the ballast waters of ships traveling from northeastern Europe (Hebert et al. 1989). They were initially discovered in Lake Erie along the western basin on well markers and natural gas wellheads in 1987 (Carlton 2008). By the early 1990's, a close relative also from the Ponto-Caspian region, the quagga mussel (*Dreissena rostriformis bugensis*) began disrupting North American ecosystems along with zebra mussels (May and Marsden 1992, Mills et al. 1993). Dreissenid mussels, an efficient competitor, can reduce the fitness and survival of unionids by attaching to the exterior of the unionid shell, a process referred to as fouling (Ricciardi et al. 1996, Schloesser and Nalepa 1994, Haag et al. 1993).

#### *Unionid Life History*

There are approximately 1000 described species of freshwater mussels (Order: Unionoida) around the world with roughly 300 species (belonging to two families: Unionidae and Margaritiferidae) occurring in North America (Williams et al. 1993, Strayer et al. 2004, Graf and Cummings 2007). The family Unionidae is categorized into two subfamilies: Ambleminae (which represents approximately 250 species in North America and consists of the Tribes Lampsilini, Amblemini, Pleurobemini, Quadrulini,

and Gonideini) and Unioninae (including the Tribes Unionini and Anodontini) (Campbell et al. 2005, Graf and Cummings 2006, 2007).

Unionids, the colloquial term for members of Unionidae, are considered to be the most imperiled group of organisms in North America and are critically jeopardized in other parts of the world (Strayer et al. 2004). Approximately 70% of the freshwater mussels that live in North America are listed as endangered, threatened, or as species of special concern (Williams et al. 1993). There are many factors that have contributed to unionid population declines including overharvesting, habitat loss from dams or channelization, pollution, loss of host fish species, and the introduction of invasive species (i.e., dreissenids) (Hallac and Marsden 2001, Strayer et al. 2004, Lydeard et al. 2004, Watters et al. 2009). Downing et al. (2010) lists the three most frequent and co-occurring causes for unionid decline as degradation of water quality, habitat destruction, and changes in hydrology.

Unionids are typically dioecious (separate male and female individuals), but in some cases have been known to change sexes or become hermaphroditic (containing both male and female reproductive organs) (Mackie 1984, Bauer 1987, Downing et al. 1989, Strayer et al. 2004). Males disperse sperm into the water column as spheres called spermatozeugmata and fertilization of the eggs occurs on the gill marsupia of the female (Cummings and Graf 2010). The fertilized eggs develop into larval glochidia and can be brooded short-term (several weeks) or long-term (several months) depending on the unionid species (Cummings and Graf 2010). Some females are capable of producing up to 2,000,000 glochidia, but mortality rates are exceedingly high with only about 1 in 10,000 glochidia surviving to maturity (Ellis 1978). Jansen et al. (2001) reported

estimated mortality rates for during glochidial stages as a range between 99.9982 – 99.9999% for some unionid species.

Unionids have a unique life history that involves a parasitic larval glochidia that attaches to the gill filaments (and sometimes skin or fins) of a host fish while developing to the juvenile stage (Barnhart et al. 2008). Unionids have evolved elaborate strategies to transfer their glochidia in either a general manner to many species of fish or to specific host fish (Zanatta and Murphy 2006, Barnhart et al. 2008). There are five main host infection strategies identified by Barnhart et al. (2008); broadcasting free larvae, glochidia contained within conglutinates, reflexive release, mantle lures, and host trapping. Unionids that utilize the broadcast method are not adapted to attract host fish, but instead release larvae that are free of an egg membrane (hence the term ‘free larvae’). Glochidia released within conglutinates (aggregates of eggs) are bonded together by the egg membranes and appear attractive to host fish as a possible food source. As the fish attempt to eat the conglutinate, the glochidia are released to attach to the host. This mechanism may target specific fish species or feeding groups. Unionids that release their offspring to an array of hosts will create a mucous web that entangles numerous types of fish and allows glochidia to attach to a host (Strayer et al. 2004). Other unionids will target specific host fish by creating lures of glochidia that resemble small fish (Haag and Warren 2000, Haag et al. 1995) or constructing packages of glochidia that mimic invertebrate larva or fish eggs (Jones and Neves 2002, Haag and Warren 2003). These strategies target particular host fish by mimicking a fish, worm, insect larva, fish egg or other diet source specific to the desired host. Glochidia stay encysted on the host fish for a period of a few days to several weeks depending on the species, water temperature and

water chemistry. Glochidia will drop off once they transform into juveniles (Watters et al. 2009). Specific host attraction mechanisms indicate a close evolutionary development between certain unionid and fish species (Barnhart et al. 2008, Strayer et al. 2004).

Along with their extraordinary adaptations for attracting host fish with a variety of strategies, some unionids have incredible life spans and are among the most long-lived invertebrates (Strayer et al. 2004, Cummings and Graf 2010, Haag and Rypel 2011). Bauer and Wächtler (2000) reported that some freshwater unionids can live for decades and have an average age of 50 years, while Haag and Rypel (2011) reported that longevity can range from 4-190 years depending on the family and Tribe (i.e., family Margaritiferidae, 28-190 years; family Unionidae, Tribe Lampsilini, 4-50 years). Their longevity can be problematic in regards to rebuilding unionid numbers after population declines due to overharvesting, habitat degradation and destruction, or fouling by introduced species.

As infaunal organisms, unionids live either partially buried in the benthos or at the water-substrate interface (Mackie 1991, Cummings and Graf 2010). Unionids feed by collecting food particles from the water column or substrate and assimilate the material into feces or psuedofeces that are then concentrated and deposited in the benthos. Their diet consists of dissolved organic matter, phytoplankton, bacteria, protozoans and detritus (Nichols and Garling 2000, Strayer et al. 2004). Their mechanisms for feeding include suspension feeding (filter feeding) through their incurrent aperture, pedal feeding (using their foot to funnel food to the labial palps), and deposit feeding (siphoning food from the substrate) (Strayer et al. 2004, Cummings and Graf 2010).

Unionids are ecologically significant for filtering water, recycling and redistributing nutrients, and increasing productivity in some systems. Unionids have the ability to increase organic and inorganic nutrients in the substrate through biodeposits of feces and pseudofeces (Howard and Cuffey 2006, Vaughn and Hakenkamp 2001). By concentrating nutrients from the water column and depositing them at the sediment-water interface of the system, unionids can increase food availability and productivity in some systems (Howard and Cuffey 2006, Vaughn and Hakenkamp 2001). Burrowing unionids can also release nutrients from the substrate into the system by their movements through the sediments. This process, known as bioturbation, releases oxygen and nutrients to help support epiphytic and epizoic organisms (Vaughn and Hakenkamp 2001). The burrowing of unionids also oxygenates hypoxic substrates (Levinton 1995) and catalyzes the metabolism of microbes (Dame 1996).

#### *Dreissenid Life History*

Dreissenid mussels are dioecious and a mature female can produce as many as 30,000-40,000 larvae, called veligers, per year (Mackie 1991). Dreissenids reach sexual maturity between six months and two years and typically have one reproductive period per year (McMahon and Bogan 2001). In North America, dreissenid spawning can take place at a minimum temperature of 12°C, but occurs more frequently at temperatures greater than 17°C (McMahon 1996). Unlike unionids, dreissenid larvae do not require a host to complete their development and are pelagic in the water column for about four weeks (Mackie 1991). Lack of a parasitic stage and high fecundity are two factors that allow dreissenids to successfully compete with unionid mussels (Barnhart et al. 2008).

Dreissenids, when mature, are epifaunal organisms that attach to hard surfaces with byssal threads and filter feed from the water column (Mackie 1991). Their diet is comprised of phytoplankton, bacteria, and inorganic materials (Mackie and Schloesser 1996, Ram and McMahon 1996). The highly efficient filter feeding ability and the fouling nature of dreissenids generally leads to high competition, starvation, and subsequent death for native mussels.

As epifaunal organisms, dreissenid mussels live attached to objects and use strong, proteinaceous byssal threads to append to firm substrates, a behavior referred to as fouling (Mackie 1991, Haag et al. 1993). When dreissenid mussels attach to unionid shells, they inhibit feeding, respiration, reproduction, and burrowing, all of which can ultimately lead to death (Schloesser and Nalepa 1994). Attached dreissenid mussels can also prevent unionids from closing their shell, which can then subject the unionid to predation, parasitism, and pathogens (Ricciardi et al. 1996). While high densities of dreissenids affixed on unionid shells is a frequent cause of death, dreissenids can also cause reduced unionid body condition (represented by decreased body mass, reduced fecundity, or malformation of shell) and cause death indirectly by limiting their food supply (Strayer 1999, Strayer and Smith 1996, Haag et al. 1993).

Unionid shells provide a suitable attachment site for dreissenid mussels (Burlakova et al. 2000) and are often preferentially colonized over other hard substrates (Mackie 1990, Ricciardi et al. 1996). In a study conducted by Burlakova et al. (2000) 100% of the native unionids sampled in Lake Narochny, Belarus had *D. polymorpha* attached to the shells with an average of  $135 \pm 35$  *D. polymorpha* per unionid. Similar observations have been recorded in the Laurentian Great Lakes (Herbert et al. 1989,

Griffiths 1993, Gillis and Mackie 1994, Mastellar and Schloesser 1992, Haag et al. 1993). During the initial introduction of dreissenids to Lake St. Clair, Hebert et al. (1989) recorded between 47-90% of the unionids sampled at various sites were colonized by dreissenids. A few years later, Griffiths (1993) and Gillis and Mackie (1994) noted that colonization of unionids had increased to 100% of the individuals in their studies. The native mussels of Lake Erie also demonstrated similar dreissenid fouling when surveyed two – three years post invasion (Mastellar and Schloesser 1992, Haag et al. 1993).

Ricciardi et al. (1995) reported that unionids are fouled at an increasing rate when dreissenid densities reach 200 m<sup>-2</sup> or more and high unionid mortality rates are strongly correlated with densities greater than 1000 dreissenids/m<sup>2</sup>. In the same study, the authors estimate the lethal threshold for unionids to be 100 attached dreissenids per shell (as a predictive model). A follow up study found that unionid mortality occurred at mean colonization rates as low as ten dreissenids per unionid, with the negative impact directly related to the size of the dreissenids (Ricciardi et al. 1996).

### *Scope of Study*

Coastal wetlands are shoreline areas containing emergent, and often submergent, vegetation and form an important transition between terrestrial and aquatic environments. Coastal wetlands often contain a wide variety of microhabitats ranging from high-energy wave swept outer (lake-side) zones to calm or even stagnant and shallow inner (nearshore) zones. Because of the wetland vegetation, many wetlands have soft and highly organic substrates supporting much primary and secondary production. Great Lakes coastal wetlands are classified as having a hydrological connection to the Great

Lakes and water levels influenced by Great Lake water level fluctuations, nearshore currents, seiche events, and ice scour (Albert et al. 2003).

Coastal wetlands are critically important to the biology of the Great Lakes basin and offer numerous physical functions. These areas are utilized as nursery and feeding habitats by fish, invertebrates, amphibians, reptiles, waterfowl, and mammals (Herdendorf 1987, Jude and Pappas 1992, Prince et al. 1992, Gathman et al. 1999, Weeber and Vallianatos 2000). It has been found that coastal wetlands provide the greatest amount of food and shelter among all habitats in the Great Lakes (Bookout 1989, Herdendorf, 1987). Nearly all of the fish found in the Great Lakes utilize coastal wetlands for some part of their life cycle (Whillans 1979). In addition to their benefits to wildlife, coastal wetlands are also important for physical processes including flood water storage, shoreline stabilization, groundwater recharge, and improving water quality (Herdendorf 1987).

Previous research has suggested that coastal wetlands contain several factors that may allow them to serve as refuges for unionids from dreissenids. Soft benthic sediments allow unionids to burrow into the substrate, which may remove or suffocate attached dreissenid mussels (Nichols and Wilcox 1997, Schloesser et al. 1997, Bowers and de Szalay 2004, Bowers et al. 2005). Dreissenids cannot tolerate hypoxia to the extent that unionids can, therefore, a burrowed unionid will be able to survive much longer in the sediments than the attached dreissenids (McMahon 1991). Although the ability to burrow in soft sediments may benefit unionids populations, Jokela and Ricciardi (2008) found that fouling intensities on unionids can be greater in soft sediments because the

unionids are the only available colonizing substrate for the dreissenids in these conditions.

Fluctuating water levels and shallow water depth in coastal wetlands are also important factors that may enhance unionid survival in the presence of high dreissenid densities. Bowers and de Szalay (2005) found that the frequency and duration of low water levels greatly impacted the survival of adult dreissenids and the colonization of veligers (the free swimming larval form of dreissenids) and decreased their presence in wetlands. In an experiment conducted by Bowers and de Szalay (2004), the authors implanted artificial substrates consisting of three tiers of PVC plates on posts in a Lake Erie coastal wetland. The tiers were placed 1 cm, 18 cm and 35 cm above the substrate and measured periodically for dreissenid colonization. The authors discovered that as little as 1% exposure to open air during water fluctuations greatly decreased the colonization rates on the 35 cm plate compared to the colonization of the 28 cm and 1 cm plates. Unionids can endure longer periods of aerial exposure than dreissenids therefore, unionid populations found in shallow waters or areas that have frequent water level fluctuations are less likely to be impacted by dreissenids (Bowers and de Szalay 2004).

Low levels of dissolved calcium and low pH can inhibit dreissenid populations and could also be used to determine if an area is a refuge for unionids. Jokela and Ricciardi (2008) studied calcium concentrations in lakes and concluded that areas with very low dissolved calcium ( $<8 \text{ mg}\cdot\text{L}^{-1}$ ) could sustain native mussels while preventing the colonization of dreissenids. This is also supported in a study conducted by Hincks and Mackie (1997) in which the authors correlated a decrease in veliger growth with low calcium levels (less than  $8.5 \text{ mg}\cdot\text{L}^{-1}$ ). The authors also reported that zebra mussels do not

grow efficiently in areas with pH less than 8.3, while McMahon (1996) reported that adult dreissenids require a minimum pH of 6.5 and juvenile dreissenids require a minimum pH of 7.4.

In several Great Lakes studies, researchers have attributed remnant unionid populations and refugia sites in part to the presence of soft or fine sand sediments that allow unionid burrowing, high water level fluctuations, wave action, shallow water depths, and offshore currents (Nichols and Wilcox 1997, Schloesser et al. 1997, Schloesser and Masteller 1999, Zanatta et al. 2002, Bowers and de Szalay 2004, 2005, McGoldrick et al. 2009). Aside from surveys in Lake St. Clair (Zanatta et al. 2002, McGoldrick et al. 2009), little research has been conducted in Michigan's coastal wetlands to determine which sites could be possible refugia for unionid populations. Using information and strategies from past experiments, the goal of this project is to determine what constitutes a refuge for unionids from dreissenid mussels and locate if, and where, these sites exist in Great Lakes coastal wetlands in Michigan.

The word refuge can be interpreted in different contexts. For this study, the term refuge will be applied to wetlands that support relatively diverse (regionally dependent) populations of unionids of >2-3 species. Sites with sustainable unionid populations could be used as natural nurseries to transplant unionids from sites where they are less likely to survive (due to either fouling by dreissenids or other factors). Bowers and de Szalay (2004) suggested that identifying the characteristics that enable unionids to exist among dreissenids will be crucial for protecting unionid populations. If dreissenid populations ever decrease, as suggested by Hunter and Simons (2004), refuge sites can also be used for propagating unionids to replace devastated populations throughout the Great Lakes. It

is also important to identify wetland habitats with healthy, diverse populations of unionids that could be of use as future research sites or candidate sites for protection and conservation programs.

This project also aimed to identify habitats that contained heavily fouled unionids whose populations need protection. If these areas are identified during this study, future projects can be designed to conserve the unionids in these wetlands by *in situ* removal of dreissenids, as suggested by Hallac and Marsden (2001).

The objectives of this study were to 1) evaluate coastal wetlands for unionid populations and determine what factors could contribute to their survival in these areas, 2) measure dreissenid colonization in wetlands and identify which physical and chemical factors could support or restrict dreissenid presence, and 3) determine which coastal wetlands are potential refuges for unionids in Michigan.

## CHAPTER II

### METHODS

#### *Site Selection and Description*

Coastal wetland sites were evaluated during the summers of 2009 and 2010. During the first field season, three regions were sampled including Saginaw Bay (SGB) and the Les Cheneaux Islands (LCX) in Lake Huron and Beaver Island (BVI) in Lake Michigan. In 2010, wetland sites in the Lake St. Clair delta (SCL), North Maumee Bay of Lake Erie (ERI), the Les Cheneaux Islands in Lake Huron and Grand Traverse Bay (GTB) and Garden Island (GDI) sites in Lake Michigan were sampled. For this study, the term region applies to sampling areas not directly connected to one another and consisting of multiple sites (i.e., region = Les Cheneaux Islands, Garden Island, Grand Traverse Bay). Refer to Figure 1 for an outline of all sampling regions and Appendix 1 for a description of each site.

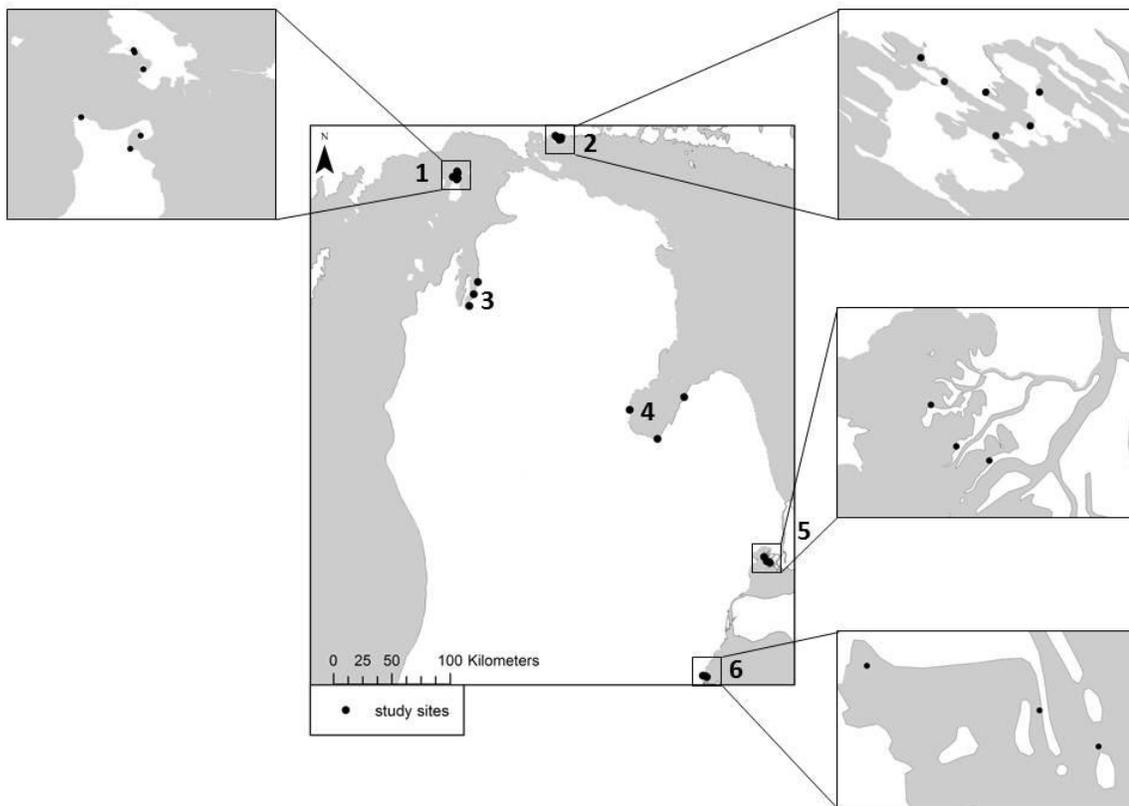


Figure 1. Coastal wetland study sites: region 1, Beaver Island Archipelago (BVI); 2, Les Cheneaux Islands (LCX); 3, Grand Traverse Bay (GTB); 4, Saginaw Bay (SGB); 5, Lake St. Clair Delta (SCL); and 6, North Maumee Bay (NMB).

Sites were randomly selected for the 2009 field season by first identifying wetlands using aerial photographs of study regions and assigning numbers to each potential site. The sites for the 2010 field season were selected based on personal communication and recommendations from other researchers (Grand Traverse Bay, Lake St. Clair, Garden Island in the Beaver Island Archipelago, and North Maumee Bay) or to further investigate possible refugia based on evidence from the prior field season (the Les Cheneaux Islands).

An inner and an outer wetland were determined at each site by the stem density of emergent vegetation. Vegetation zones in coastal wetlands are commonly divided into

two stem density categories; a sparse (outer) bulrush zone that is subjected to heavier wave action, and a protected (inner) bulrush zone that receives less wave actions and contains more vegetation stems per square meter than the outer zone (Burton et al. 1999, Uzarski et al. 2004). The substrate compilation at each site was visually assessed and designated as a percentage of one or more of the following types: cobble, gravel, sand, silt, clay, and detritus. Substrate type was determined from the Wentworth Grain Size Scale (Allan and Castillo 2008) and by assessing texture. GPS waypoints were marked at the outer vegetation zone water gauge of each wetland site using a Garmin® GPS 76™.

### *Unionid Surveys*

Unionid searches were based on the technique used by Zanatta et al. (2002). A minimum 1-person hour search for live unionids was conducted at each site between mid-July and early August. Searches were performed using snorkeling gear and underwater viewers in clear water and a clam rake or tactile senses in turbid waters. When a live unionid was found, a 0.9 meter rebar was staked in its spot with a 4.55 m line attached to it. Using the line as a guide, concentric inward circles around the re-bar were searched to cover an area of 65 m<sup>2</sup>. This area could then be used to calculate the average density of unionids at each site. Any live mussel found during this time was identified to species, measured for length, photographed, and placed back in correct orientation into the substrate in the approximate location it was found. Any attached dreissenids on the unionids were removed, enumerated, and recorded. After the initial circle plot was completed, subsequent circle plots were searched until unionids were no longer located. Each unionid search was conducted for a minimum of 30 minutes.

Due to water clarity limitations from high turbidity, snorkeling surveys could not be performed in North Maumee Bay, Lake Erie, and an alternative surveying technique was implemented to survey unionids in this region. A clam rake, manufactured by the Clam Out™ Equipment Co. (Mohnton, PA), was utilized to survey this region. The clam rake was constructed with a basket width of 27.9 cm and eight 0.6 cm pressed tines spaced 2.5 cm apart. To maintain a standard for surveying area, 10 m trawls were conducted 24 times to encompass an area of 67 m<sup>2</sup>. Due to the low visibility in some areas, the initial visual search to locate unionids could not be conducted. Instead, the clam rake was haphazardly used to search each site. This method was validated in the Lake St. Clair region, where unionid densities were known from earlier surveys for this project to be 0.056 unionids per m<sup>2</sup>. The clam rake method produced a density of 0.015 unionids per m<sup>2</sup> near the same location, 26.6% of the density determined from snorkel searches.

#### *Dreissenid Colonization*

In both the inner and outer wetland of each site, 10 unglazed clay tiles were used as artificial substrates to measure dreissenid mussel colonization. The clay tiles measured 16 cm by 16 cm by 1 cm and were affixed to a piece of conduit by a U-joint. Prior to inserting the tiles at each site, they were soaked for a minimum of 72 hours in well water to obtain a bio-film. Previous studies have shown that dreissenids prefer to colonize substrates containing bio-films (Bowers and de Szalay 2004, 2005). The tiles were removed from the well water the morning of placement in the wetlands and were transported in totes with enough water on the bottom to keep the tiles moist and maintain the bio-films. The clay tiles were placed in a one meter circle around the water gauges to

allow for easier access and locating. The clay tiles were placed 1 cm above the substrate surface to represent the position of unionids in the habitat.

To measure dreissenid colonization, three tiles were randomly selected at six and 12 weeks during the sampling season. When removed from the site, plates were designated as either plate 1, 2, or 3. Plates with attached dreissenids were scraped into a dissecting pan with the contents then being transferred to a Whirl-pak®. All organisms were immediately preserved in denatured ethyl alcohol. To determine the colonization of dreissenids at each site, the samples were rinsed with water and placed in a dissecting pan for review. Dreissenids larger than 7 mm were separated, counted, and identified to the species level (to differentiate *Dreissena polymorpha* and *D. rostriformis bugensis*). All dreissenids measuring smaller than 7 mm were counted, but not identified to species. The 7 mm cutoff was decided during the initial colonization analysis to be the smallest size range to comfortably identify the organisms to species level. All processed samples were transferred to labeled poly-seal vials and stored in ethanol. The unglazed clay tiles represented 0.0576 m<sup>2</sup> in the habitat which allowed for a calculation of colonization/m<sup>2</sup>. The dreissenid count on each tile was divided by this number to establish the colonization of dreissenids per square meter for both the inner and outer wetland at each site.

#### *Physical and Chemical Habitat Measurements*

All water chemistry procedures were conducted in accordance with those recommended in Standard Methods for the Examination of Water and Wastewater (APHA 1992). Chemical parameters of the wetlands were measured using a Multi-parameter Water Quality Sonde (Yellow Springs International, model 6600 V2). Three replicates were documented at both the inner and outer vegetation zone at each site.

Using the Sonde, the following parameters were measured: water temperature ( $^{\circ}\text{C}$ ), conductivity ( $\mu\text{S}/\text{cm}$ ), specific conductance (temperature compensated conductivity), dissolved oxygen (both as a percentage and in  $\text{mg}/\text{L}$ ), turbidity (NTU), total dissolved solids ( $\text{g}/\text{L}$ ), pH, oxidation reduction potential (ORP), and chlorophyll ( $\mu\text{g}/\text{L}$ ). For the inner and outer wetland of each site, a water sample was collected in a 1 L acid washed polyethylene bottle for alkalinity and nutrient (nitrate, ammonium, and soluble reactive phosphorous) analysis. An unfiltered portion of each water sample was reserved to measure alkalinity. Each sample for nutrient analysis was vacuum pumped through a  $0.45\ \mu\text{m}$  Millipore filter within 24 hours of collection and then frozen until it could be processed.

Alkalinity was determined by performing a titration on a 100 mL sample with  $0.02\ \text{N}\ \text{H}_2\text{SO}_4$  to a pH of 4.5. The results of this titration were multiplied by 10 to provide alkalinity in the form of milligrams of  $\text{CaCO}_3/\text{L}$  of water. An auto-analyzer (Bran+Luebbe QuAAtro) was used to measure soluble reactive phosphorous (SRP), ammonium ( $\text{NH}_3$ ), and nitrate ( $\text{NO}_3$ ) levels in the water samples. Each nutrient analysis had an associated detection limit, the lowest level that the machine could accurately read. For any value that was below the detection limit of the machine, the detection limit of that nutrient analysis was divided by half and this value was used for data analysis. The detection limit on the Bran+Luebbe QuAAtro for SRP, nitrate, and ammonium was  $0.3\ \mu\text{g}/\text{L}$ ,  $1.0\ \mu\text{g}/\text{L}$ , and  $0.5\ \mu\text{g}/\text{L}$ , respectively.

Water gauges were constructed to measure the highest and lowest water levels for the inner and outer vegetation zones at each site (Figure 2). A full description of the water gauge design and construction can be found in Appendix 2. At each site, water

depth, organic substrate depth and total depth were measured. A meter stick was placed directly on top of the substrate to measure the depth of the water column. Then, the meter stick was pushed into the sediment until it met resistance and the total depth (sediment depth plus water depth) was recorded. The organic sediment depth was then calculated by subtracting the water depth from the total depth. This was conducted in replicates of three for both the inner and outer wetland at each site and this information was used to assess the feasibility of burrowing behaviors for unionids.

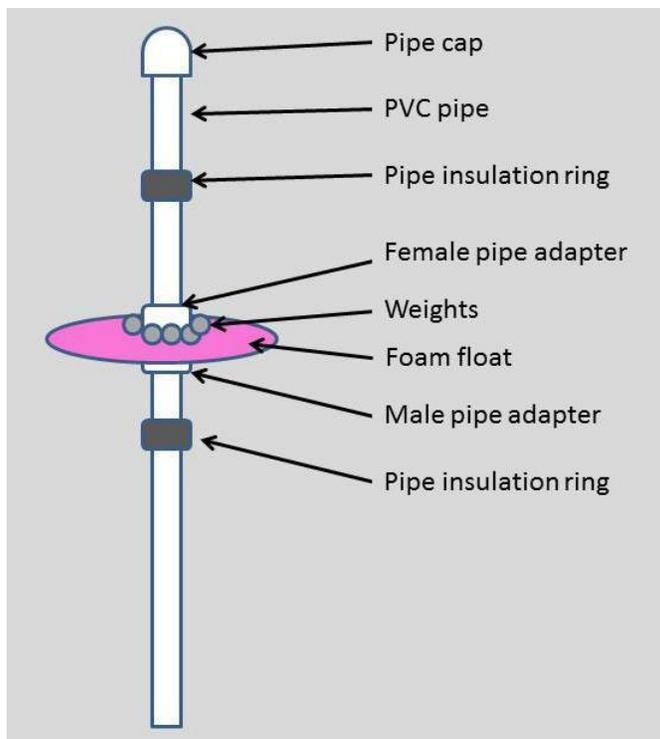


Figure 2. Diagram of the custom made max-min water level gauge.

### *Data Analysis*

Unionid refuges were determined by examining the amount of fouling by dreissenids on the native mussels found in each region. Pearson correlations were performed in Minitab version 16 (Minitab Inc., U.S.A.) to analyze dreissenid fouling by

unionid species and by region. An ANOVA, general linear model (GLM) was conducted in SAS version 9.1 (SAS Institute Inc., Cary, NC, U.S.A.) with a Tukey's pairwise comparison to analyze if fouling was different among unionid species, size classes, or study regions. Pearson correlations were also used to determine if a relationship existed between unionid densities and each of the physical and chemical factors measured at each site.

Dreissenid colonization was measured and compared to all physical and chemical measurements using Pearson correlations. Colonization was compared among regions and the inner and outer wetlands of each site using an ANOVA GLM with a Tukey's pairwise comparison. Dreissenid colonization and unionid densities were compared to each other using a Pearson correlation.

Physical and chemical parameters were analyzed using a Principal Components Analysis (PCA) to determine if any of the measured abiotic and biotic parameters demonstrated differences among each of the sampling regions. Principal Components (PCs) were determined using all physical and chemical data, water level fluctuations, and substrate depth using PC-ORD version 5 (MjM Software, Gleneden Beach, Oregon, U.S.A.). The most powerful PC axes were then correlated with each of the measured variables using a Pearson Correlation to determine which had the highest impact among each wetland. These axes were also correlated with dreissenid colonization and unionid abundance using a Pearson correlation in Minitab to help determine which parameters could have the strongest impact on presence or absence for the biota.

A Discriminate Analysis (DA) was also performed in SAS using all of the chemical and physical data recorded to determine which measurements could be

associated with either dreissenid presence/absence. Seventy-five percent of the data were used to develop the discriminant model and evaluate the physical-chemical factors associated with dreissenid presence/absence, while the remaining 25% of the data was retained for model validation. The model provided an output of measured factors that can predict dreissenid presence and absence.

A Discriminate Analysis could not be conducted with unionid presence/absence data because there were too few sites surveyed that contained unionids. The relatively low number of sites with unionid presence could not be divided up between a developing and verification data set while still providing a robust model.

## CHAPTER III

### RESULTS

#### *Unionid Surveys*

Unionid surveys produced live specimens in three regions; the Les Cheneaux Islands, the Lake St. Clair delta, and North Maumee Bay in Lake Erie. Diversity varied greatly among each of the three sites with the Les Cheneaux Islands having only one species; the Lake St. Clair delta, 10 species; and North Maumee Bay, two species (Appendix 3, Figure 3). Amid these three sites, 100% of the unionids surveyed in the Les Cheneaux Islands ( $n = 6$ ) were fouled by dreissenids, 85% in the Lake St. Clair Delta ( $n = 66$ ) were fouled, and 50% in North Maumee Bay ( $n = 4$ ) had attached dreissenids. None of the unionids observed during this study were state or federally listed.

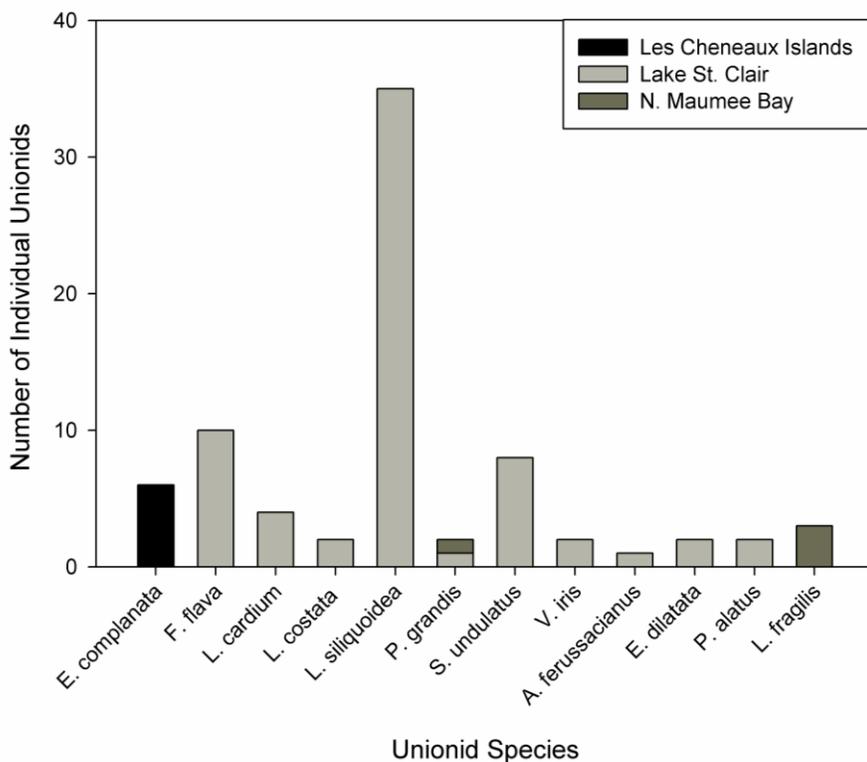


Figure 3. Live unionid abundance by region.

Of the six sites surveyed in the Les Cheneaux Island, Sheppard Bay (site 1) and Government Bay (site 4) contained live unionids; a single species, *Elliptio complanata* (Lightfoot, 1786), at an average density of 0.015 mussels m<sup>-2</sup> at each site (Figure 4). Unionids found at site 1 had an average of 22.8 ±8.3 (S.E.M.) attached dreissenids while the one specimen surveyed at site 4 was fouled by 19 dreissenids, all *D. polymorpha*.

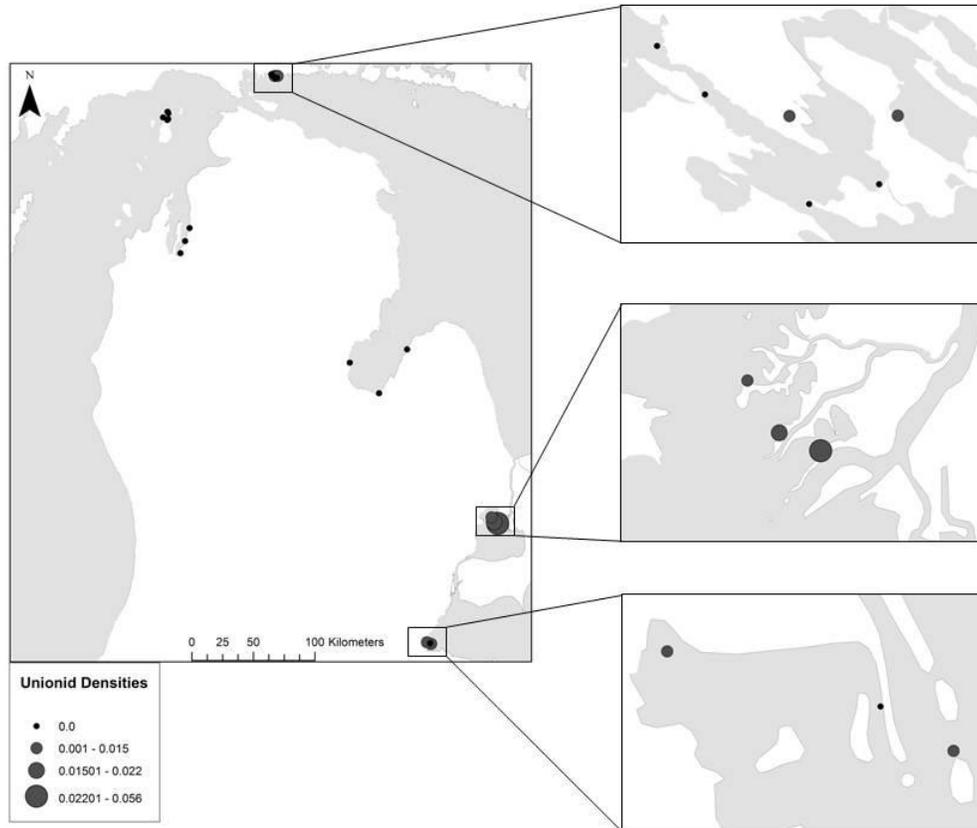


Figure 4. Unionid densities measured at coastal wetland sites.

Unionids were found at all three sites in the Lake St. Clair delta at varying densities and species compositions. Big Muscamoot Bay (site 1) had the highest diversity of unionid species and also had the highest average density of 0.056 m<sup>-2</sup> (Figure 4). Of the ten species surveyed at site one, the average fouling density was 12 dreissenids per unionid with *Lasmigona costata* (Rafinesque, 1820) having the highest average

fouling ( $23 \pm 2$ ) and *Villosa iris* (I. Lea, 1829) with the lowest ( $8 \pm 2$ ). In Goose Bay (site 2), the surveys found six species of unionids with an average density of 0.022 mussels  $m^{-2}$ . The average fouling density on mussels at this site was  $6.2 \pm 2.8$  with the highest fouling rate occurring on *Elliptio dilatata* (Rafinesque, 1820) (17 attached dreissenids) and the lowest on *Anodontooides ferussacianus* (I. Lea, 1834) (0 attached dreissenids), respectively with only one specimen of each observed at this site. At the third site in the Lake St. Clair delta, only one unionid was observed, an *E. dilatata*, harboring one attached dreissenid. The average unionid density for this site was calculated at  $0.015 m^{-2}$ .

In North Maumee Bay, unionids were found at site 1, along the open shoreline, and at site 3, within the embayment. At site 1, *Leptodea fragilis* (Rafinesque, 1820) was the only species documented and they hosted an average of  $1.7 \pm 1.7$  dreissenids per individual and were calculated at an average density of  $0.015 m^{-2}$  (Figure 4). Only one specimen was found at site 3, a *Pyganodon grandis* (Say, 1829) with one attached dreissenid. The approximate density at this location was also calculated to be  $0.015 m^{-2}$ .

In addition to each region having different average fouling rates (Figure 5), the fouling composition was also anecdotally observed to differ on each unionids. Fouling in the Les Cheneaux Islands was predominately by large adult dreissenids ( $> 7$  mm), while fouling in the Lake St. Clair delta was by a mix of small adults and juveniles ( $< 7$  mm). In North Maumee Bay, where fouling was the least, the attached dreissenids were all young of year.

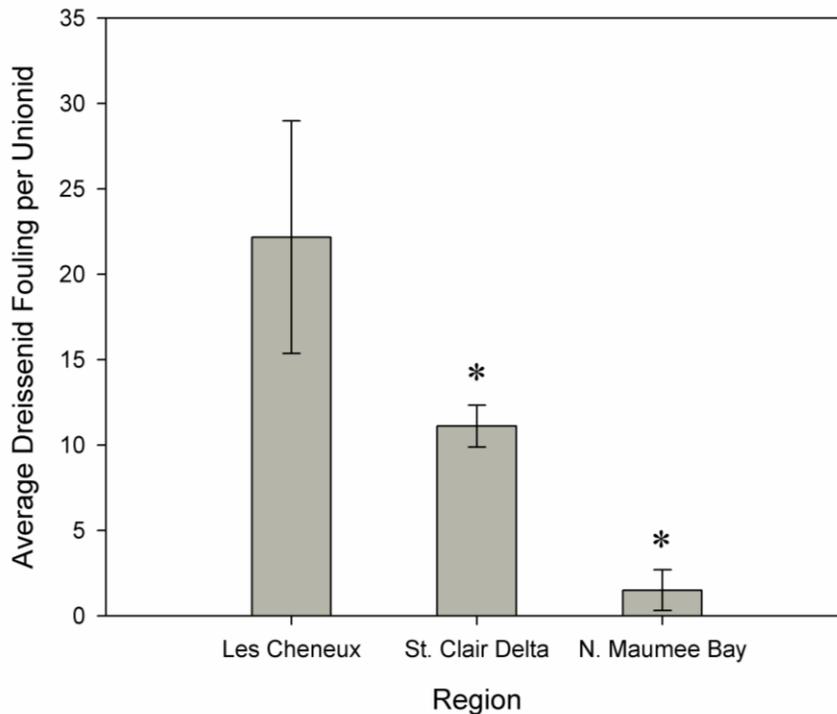


Figure 5. Mean dreissenid fouling on unionids for each study region where live unionids were found. Error bars denote standard error, asterisks represent significantly different fouling means ( $p = 0.05$ ).

Unionid densities were positively correlated with pH levels ( $r = 0.483$ ,  $p = 0.003$ ) and nitrate ( $r = 0.479$ ,  $p = 0.003$ ) at each site. Sites where unionids occurred had an average pH measurement of  $8.48 \pm 0.02$  (Les Cheneaux Islands),  $8.53 \pm 0.04$  (Lake St. Clair delta), and  $8.82 \pm 0.03$  (North Maumee Bay). The average nitrate levels for each of these sites was  $0.084 \pm 0.007$  mg/L (Les Cheneaux Islands),  $0.27 \pm 0.01$  mg/L (Lake St. Clair), and  $0.402 \pm 0.05$  mg/L (North Maumee Bay). Unionid densities were not correlated with dreissenid densities ( $r = -0.088$ ,  $p = 0.654$ ). No significant difference was found between dreissenid fouling and unionid species composition ( $F = 1.27$ ,  $p = 0.264$ ) (Figure 6).

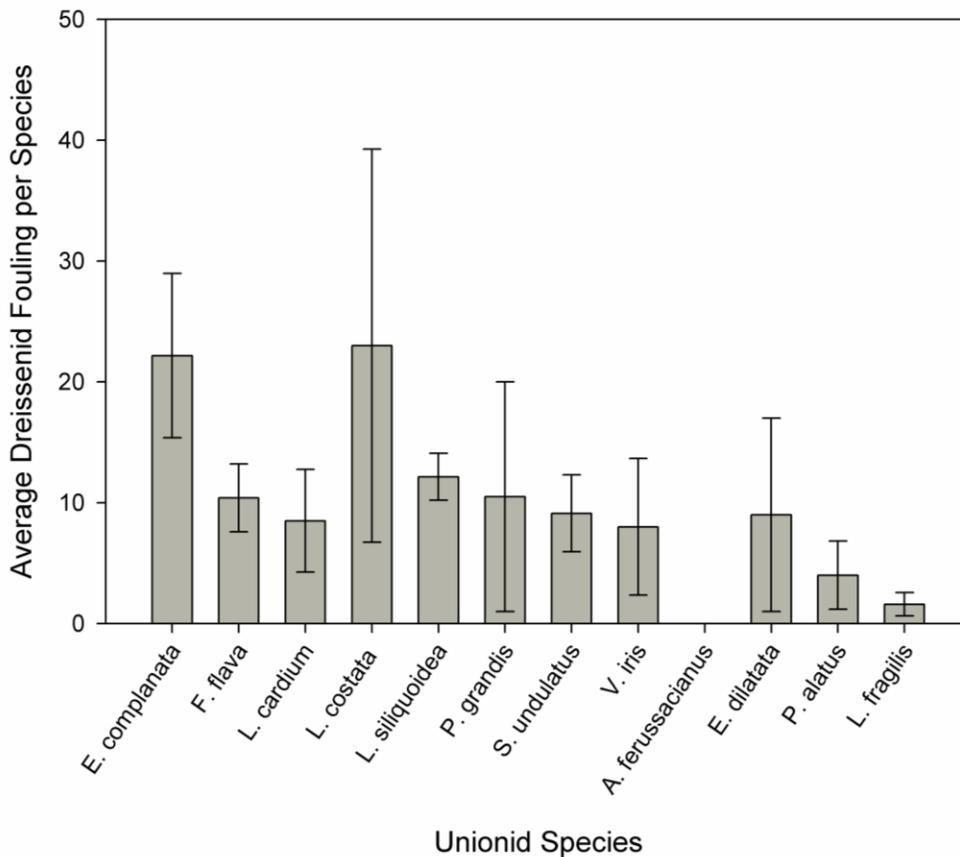


Figure 6. Mean number of fouling dreissenids on unionid species surveyed during this study. Error bars represent standard error.

#### *Dreissenid Colonization*

Dreissenid colonization occurred on the artificial substrates in Saginaw Bay at an average density of  $2327.4 \pm 1003.9 \text{ m}^{-2}$  with the highest colonization occurring in the outer wetland of site two at 12 weeks of colonization time and was  $20,741 \pm 1387.2 \text{ m}^{-2}$  (Table 1). Colonization also occurred in the North Maumee Bay wetlands at an average density of  $5635.9 \pm 2094.7 \text{ m}^{-2}$ . The highest colonization measured in this region occurred at site 2 in the outer wetland during the 6 week colonization period and was  $31,007 \pm 3513.4 \text{ m}^{-2}$ . Within the two regions where colonization occurred, dreissenid densities were highly variable among each site (Figure 7). Dreissenid densities

documented in North Maumee Bay during this study ( $179 - 31,007 \text{ m}^{-2}$ ) were similar to those found in Western Lake Erie by Berkman et al. (1998) where densities were measured between  $1500 - 32,500 \text{ m}^{-2}$ . Saginaw Bay site 1 had an average of  $1289 \pm 1009.3$  dreissenids  $\text{m}^{-2}$ , while site 2 averaged  $5668.4 \pm 2646.9 \text{ m}^{-2}$ , and site 3 only had an average of  $24.6 \pm 8.7$  dreissenids  $\text{m}^{-2}$ . North Maumee Bay site 1 showed no colonization during the study, while site 2 had an average colonization of  $10,724 \pm 3691.3 \text{ m}^{-2}$ , and site 3 had  $547 \pm 118.6$  dreissenids  $\text{m}^{-2}$ .

Table 1. Mean (SEM) dreissenid colonization throughout the study period.

<b>Site Name</b>	<b>6 Week</b>	<b>12 Week</b>	<b>Study Duration</b>	<b>Whole Site</b>	<b>Regional</b>
<b><i>N. Maumee Bay</i></b>					5635.9 (2094.7)
Site 2 Inner	2951.4 (1272.3)	1522 (260)	2236.7 (662.8)	10724.8 (3691.3)	
Site 2 Outer	31006.9 (3513.4)	7419 (1423)	19213 (5540.2)		
Site 3 Inner	179.4 (57.9)	468.8 (177.3)	324.1 (105.6)	546.9 (118.6)	
Site 3 Outer	717.6 (228)	821.8 (315.8)	769.7 (175.7)		
<b><i>Saginaw Bay</i></b>					2327.4 (1003.9)
Site 1 Inner	11.6 (11.6)	52.1 (10)	31.8 (11.4)	1289.1 (1009.3)	
Site 1 Outer	5.8 (5.8)	5086.8 (3577.3)	2546.3 (1962.2)		
Site 2 Inner	509.3 (306.9)	1313.7 (540.2)	911.5 (330.9)	5668.4 (2646.9)	
Site 2 Outer	110 (57)	20740.7 (1387.2)	10425.3 (4654.8)		
Site 3 Inner	0	46.3 (20.9)	23.1 (13.9)	24.6 (8.7)	
Site 3 Outer	5.8 (5.8)	46.3 (15.3)	26 (11.6)		

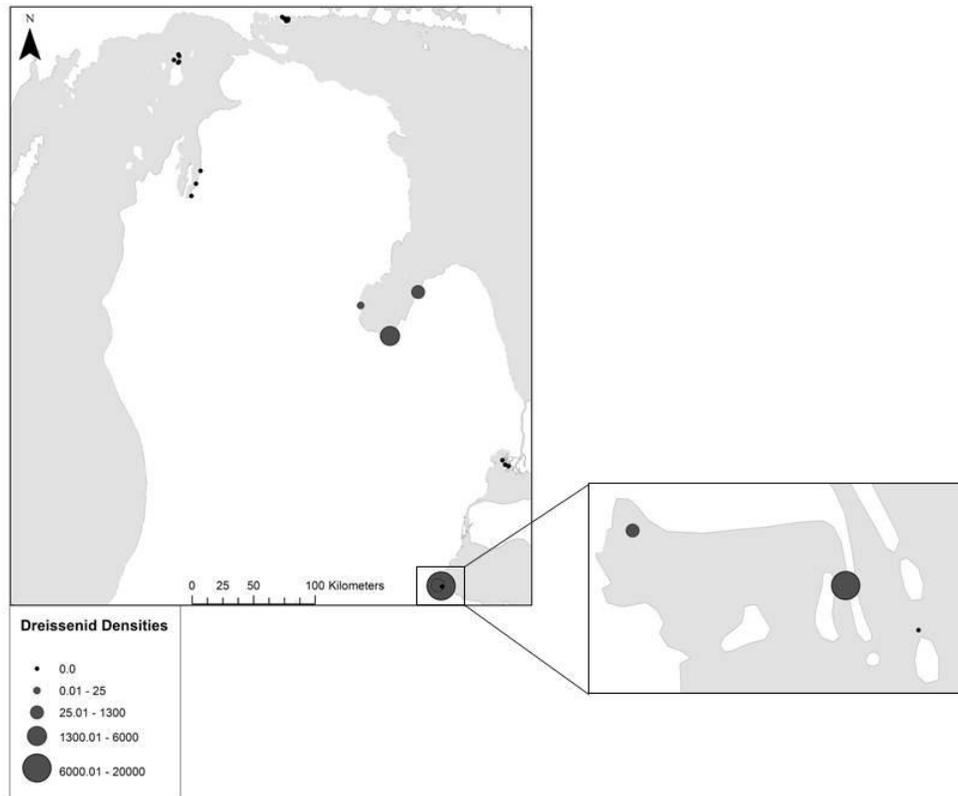


Figure 7. Dreissenid colonization densities on artificial substrates at each sampling location.

Aside from one individual *Dreissena polymorpha* documented on one tile in both the Lake St. Clair delta (site 2, outer wetland, six week colonization period) and on one tile in Grand Traverse Bay (site 3, outer wetland, 12 week colonization period), dreissenid colonization did not occur on the artificial substrates at any of the other study regions. Their presence, however, was noted in the open water regions off all study sites and within some of the wetlands in the Les Cheneaux islands. For the purpose of this study, the sole dreissenid attached to one artificial substrate in the Lake St. Clair delta and Grand Traverse Bay did not constitute true dreissenid colonization in these areas and were regarded as random colonization.

Colonization was significantly higher in the outer wetlands than in the inner wetlands ( $F = 6.78, p = 0.011$ ) (Figure 8) with the average colonization in the outer wetland among all regions being  $5497.7 \pm 1668.7 \text{ m}^{-2}$  and  $705.4 \pm 207.7 \text{ m}^{-2}$  in the inner wetlands. Dreissenid colonization was positively correlated to chlorophyll ( $r = 0.619, p = <0.001$ ), turbidity ( $r = 0.424, p = <0.001$ ), conductivity ( $r = 0.388, p = <0.001$ ), total dissolved solids ( $r = 0.363, p = <0.001$ ), water level fluctuation ( $r = 0.324, p = 0.003$ ), alkalinity ( $r = 0.264, p = 0.015$ ), and low water levels ( $r = 0.226, p = 0.033$ ) and was negatively correlated to oxidation reduction potential ( $r = -0.263, p = 0.046$ ).

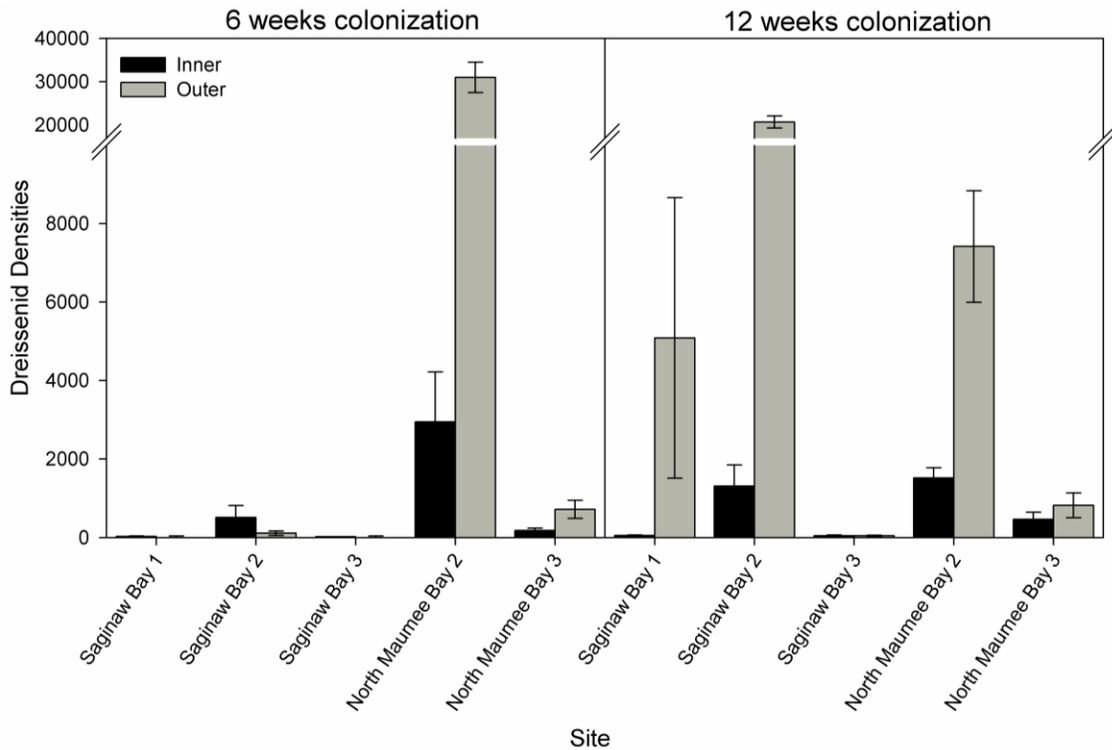


Figure 8. Dreissenid colonization in wetlands at six and 12 week time periods with the inner wetland and the outer wetland compared side by side for each site.

Upon review of the average number of dreissenids colonizing the artificial substrates, species composition and age categories were assessed for each region. The

dreissenid colonization in Saginaw Bay consisted of 7% (111 individuals) adults and 93% (1497 individuals) juveniles (measured as < 7 mm). Of the 7% adults, 88% (98 individuals) were *Dreissena polymorpha* and 12% (13 individuals) were *D. rostriformis bugensis*. At the North Maumee Bay sites, 18% (478 individuals) of the colonizing dreissenids were adults and 82% (2119 individuals) were juveniles. Only *D. polymorpha* were identified colonizing North Maumee Bay.

#### *Physical and Chemical Habitat Measurements*

The average high and low water levels, along with average fluctuation, were analyzed with an ANOVA GLM for significant differences among each region studied. High water levels were not significantly different across the regions ( $F = 2.13$ ,  $p = 0.0599$ ), but low water levels differed ( $F = 6.56$ ,  $p = <0.001$ ) (Figure 9). North Maumee Bay sites had the lowest average low water level (0.05 m) and the Lake St. Clair Delta had the highest average low water level (0.39 m). Water level fluctuation was significantly different across all regions ( $F = 2.72$ ,  $p = 0.0192$ ) (Figure 10). Saginaw Bay, Garden Island, and North Maumee Bay wetlands displayed the greatest average fluctuation (0.69 m, 0.68 m, and 0.67 m, respectively), while Grand Traverse Bay and the Les Cheneaux Islands produced the lowest average water level fluctuations (0.52 m and 0.49 m, respectively).

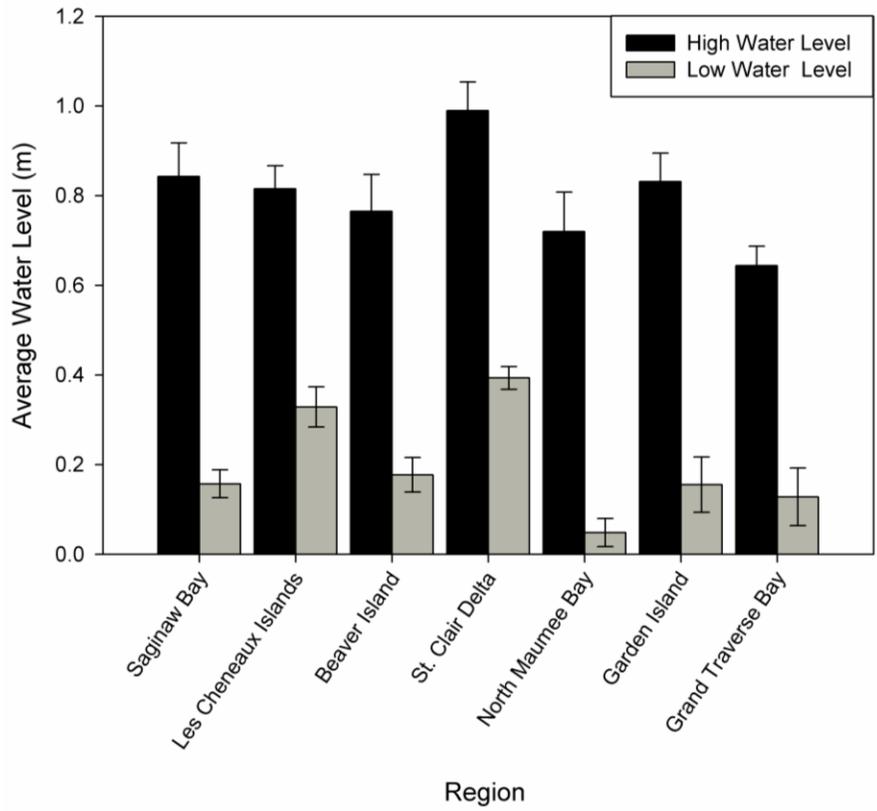


Figure 9. Mean high and low water levels for each study region. Error bars denote standard error.

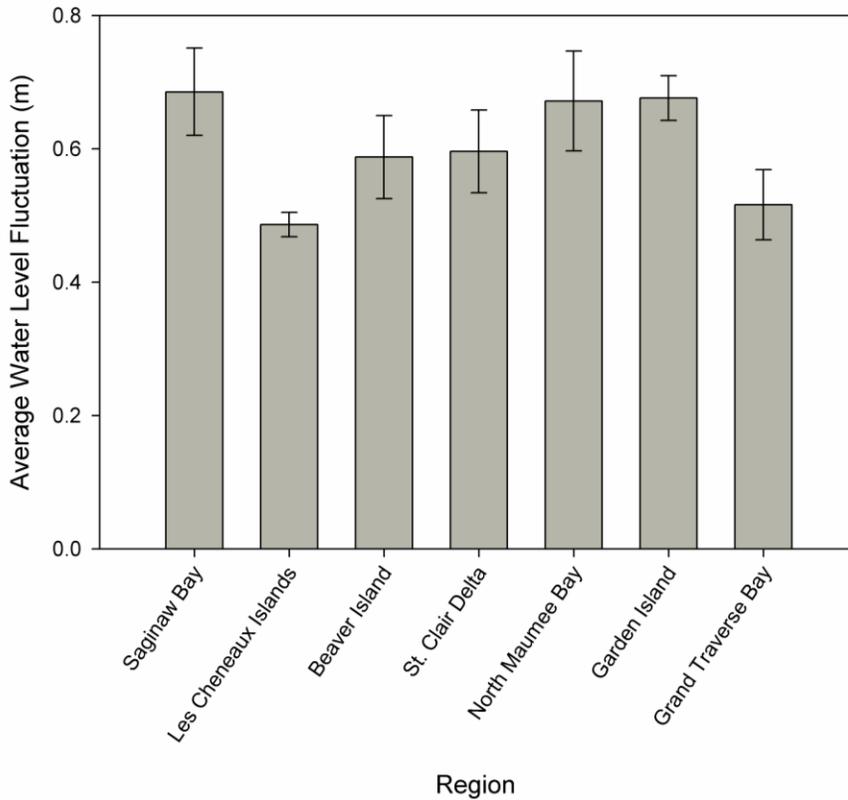


Figure 10. Mean water level fluctuations by region. Error bars denote standard error.

From the results of the principal components analysis, PC 1 explained 28% of the variation among each sampling region and was positively correlated with total dissolved solids ( $r = 0.957, p = <0.001$ ), alkalinity ( $r = 0.905, p = <0.001$ ), conductivity ( $r = 0.890, p = <0.001$ ), and ammonium ( $r = 0.629, p = <0.001$ ), and it was negatively correlated to pH ( $r = -0.597, p = <0.001$ ) and water depth ( $r = -0.197, p = 0.031$ ) (Figure 11). PC 2 explained 18.5% of the variation among each sampling region and was positively correlated with water depth ( $r = 0.489, p = <0.001$ ), and ammonium ( $r = 0.395, p = <0.001$ ), and negatively correlated with turbidity ( $r = -0.747, p = <0.001$ ), temperature ( $r = -0.693, p = <0.001$ ), pH ( $r = -0.618, p = <0.001$ ), oxygen ( $r = -0.370, p = <0.001$ ), nitrate ( $r = -0.337, p = <0.001$ ), and conductivity ( $r = -0.251, p = 0.006$ ). Dreissenid

colonization positively correlated to PC 1 ( $r = 0.26$ ,  $p = 0.022$ ), but negatively correlated to PC 2 ( $r = -0.236$ ,  $p = 0.038$ ). Unionid densities did not correlate significantly to either axis (PC1  $p = 0.064$ , PC2  $p = 0.321$ ).

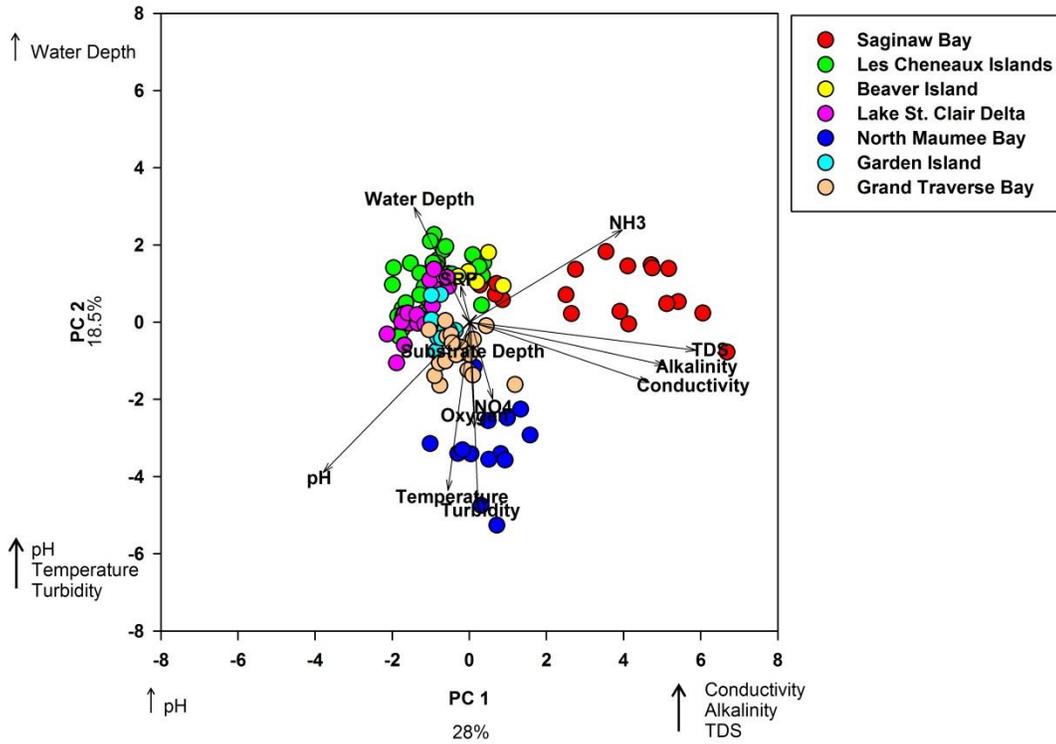


Figure 11. Principal Components Analysis of physical and chemical variables measured at each study region. For PC axis 1, the left side of the axis is characterized by high pH while the right side of the axis is characterized by high conductivity, alkalinity, and total dissolved solids. The upper portion of PC axis 2 is characterized by high water depth while the lower portion is characterized by high pH, temperature, and turbidity.

A discriminate analysis was conducted to determine which measured variables most accurately predicted dreissenid colonization presence or absence in a wetland (Figure 12). Twenty-five percent of the data (20 random data points, 4 sites with dreissenid presence and 16 where they were absent) were reserved for model validation. The remaining 75% of the data, or 60 data points, were used to construct the model. The model designated three parameters that strongly correlated with dreissenid colonization

presence and absence; conductivity ( $F = 73.92, p = <0.001$ ), turbidity ( $F = 18.19, p = <0.001$ ), and water level fluctuation ( $F = 13.46, p = <0.001$ ). The validation test correctly ascribed 19 of the 20 random points to their correct category (95% accuracy). The North Maumee site 1 (outer wetland) was incorrectly predicted to have dreissenid presence, and was, in fact, a site without dreissenid colonization (see discussion for potential explanation).

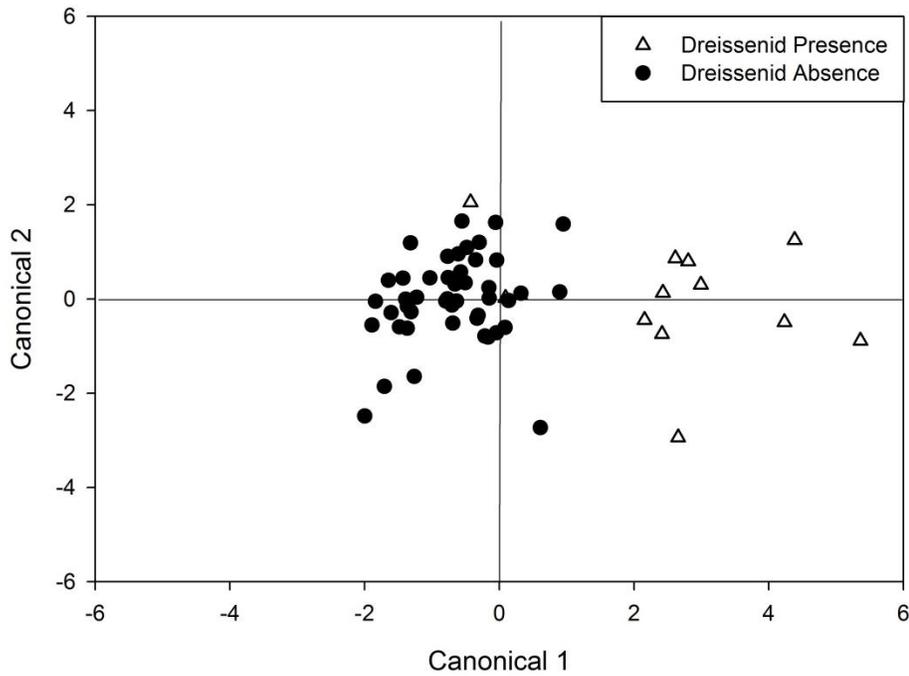


Figure 12. The distribution of study sites for dreissenid presence and absence as predicted by the Discriminate Analysis. Dominant factors for this model include conductivity, turbidity, and water level fluctuation.

## CHAPTER IV

### DISCUSSION

#### *Unionid Presence*

Live unionids were found in densities of  $0.015 - 0.056 \text{ m}^{-2}$  in the Les Cheneaux Islands in Lake Huron, the Lake St. Clair delta, and North Maumee Bay, Lake Erie. The densities from this project closely reflect those found in other studies (Zanatta et al. 2002, McGoldrick et al. 2009, Crail et al. 2011). Previous research in Great Lakes coastal wetlands described unionid refuge sites containing population densities of 0.09 individuals  $\text{m}^{-2}$  in the western basin of Lake Erie (Crail et al. 2011), densities of  $0.03 - 0.07 \text{ m}^{-2}$  in the Lake St. Clair delta (Zanatta et al. 2002), and  $0.02 - 0.12 \text{ m}^{-2}$  in the same region of the Lake St. Clair delta documented by McGoldrick et al. (2009). No live unionids were found in Saginaw Bay, although the area historically hosted 13 species (Goodrich and van der Schalie 1932). One *Potamilus ohioensis* (Rafinesque 1820) shell was recovered in infaunal position in the substrate with little weathering of the periostracum, and this may suggest that either the species could be present upon further investigation of the region, or that unionids have only recently been extirpated from the area.

McMahon and Bogan (2001) described a pH range of 5.6 – 8.3 to be the optimal range for unionid growth and reproduction, while the average pH levels for sites that contained unionids in this study were higher than this ascribed range. Unionids were found at sites that consisted of sand, silt or clay substrates. Previous habitat studies describe soft benthic substrates as a key to unionid survival because these substrates act as a mechanism for unionids to avoid or remove fouling dreissenids via burrowing

(Nichols and Wilcox 1997, Schloesser et al. 1997, Bowers and de Szalay 2004, Bowers et al. 2005).

Dreissenid fouling was variable among the regions where unionids were located. The unionids surveyed in North Maumee Bay had the lowest average fouling rate (1.5 dreissenid per unionid compared to 22 in the Les Cheneaux Islands and 11 in the Lake St. Clair delta) (see Figure 5). Water levels appear to be a driving force in reducing fouling by dreissenids. While North Maumee Bay did not demonstrate the greatest amount of fluctuation among the sites, this area did display the lowest average water levels (refer to Figure 9). This was partly due to site 1, which is an open shoreline site outside of the embayment area that experienced frequent dewatering from seiche events and/or seasonal water level declines and was dewatered during the second and third visit to the site. Sites 2 and 3 inside of the embayment did not appear to be as affected by the duration of seiche events or seasonal water level declines as site 1 and this may be attributed to their location inside of the embayment and an inflow of water from the Maumee River draining into this area. The majority of unionids were located at site 1 of North Maumee Bay and this may be attributed to either higher populations in the area from reduced fouling or also, in part, because the reduced water levels allowed surveys to be more successful than in other parts of the bay. The Les Cheneaux Islands experienced the least amount of water level fluctuation and this is most likely because all of the sites sampled were protected in the archipelago of islands and received less wave action due to this protective feature. This also lends explanation as to why 100% of the unionids surveyed in this area were fouled and why the highest average fouling rate occurred in this area.

The average number of attached dreissenids documented on individual unionids in the Lake St. Clair delta was 11, which follows a declining trend of fouling noted in this region by Zanatta et al. 2002, in which fouling was reduced from 61 to 31 to 17 in 1999, 2000, and 2001, respectively, and down to 15 dreissenids per unionid in 2003 and 2004 (McGoldrick et al. 2009). Based on the results of this study, water levels as well as chemical variables may be likely explanations for this decline. The Lake St. Clair delta had average fluctuation compared to the other regions of this study and it also had the highest low water level. The pelagic veligers of dreissenids rely on water currents to transport them to settlement areas and if the delta does not provide a high level of water fluctuations, this could impede the movement of veligers into the delta for colonization. Lake St. Clair sites, compared with other study sites by the PCA, displayed unrelated and inverse vectors for conductivity, TDS, alkalinity, and turbidity (Figure 11). The PCA serves to demonstrate that the St. Clair delta region, while hosting the highest unionid densities for this project and no dreissenid colonization, has lower levels of disturbance and possibly productivity, which appear to be important factors for dreissenids colonization to occur.

#### *Dreissenid Colonization*

Dreissenids were present in the open water areas nearby all sites in this study and on vegetation in the wetlands of the Les Cheneaux Islands, but artificial substrates were only colonized in Saginaw Bay and North Maumee Bay. Dreissenid colonization was positively correlated to several physical and chemical parameters measured in the wetlands and also to parameters demonstrated by the principal components analysis and discriminate analysis to be accurate predictors of dreissenids presence in coastal

wetlands. High conductivity and turbidity are strong indicators of disturbance in coastal wetlands (Uzarski et al. 2005), and the levels of both of these parameters indicates the presence of disturbance in Saginaw Bay and North Maumee Bay. Dreissenid colonization also displayed a strong positive correlation to chlorophyll levels and this indicates that productivity is also an important variable in dreissenid colonization. As suspension feeders, dreissenids will filter bacteria, algae, and detrital particulates from the water column (McMahon and Bogan 2001) and adequate amounts of these particles are necessary to support not only the high levels of colonization, but also the metabolism for veligers to transform to epifaunal juveniles and to sustain growth to adulthood.

North Maumee Bay sites had the highest documented dreissenid colonization of this study (31,007 m<sup>2</sup>; at site 2, outer wetland), but this region contained a site that had no colonization throughout the duration of this project (site 1). This is suspected to have been caused by the frequent dewatering at this open shoreline site. Low water levels also explain why the discriminate analysis incorrectly predicted site 1 of North Maumee Bay to have dreissenid presence when in reality, dreissenids did not colonize this site. The inner wetland of site 1 was de-watered during the 6 week sampling time period, while the outer wetland had a water depth of 0.12 cm. During the 12 week sampling period, the inner wetland at site 1 was again de-watered, while the water depth at the outer wetland measured 0.10 cm. This suggests that water level fluctuations are a driving factor in explaining why colonization did not occur at site 1.

The PCA, DA, and physical and chemical correlations suggest that dreissenid colonization is influenced by productivity, anthropogenic disturbance (indicated by high conductivity, turbidity, and TDS), and fluctuating water levels. The lack of colonization

at site 1 of North Maumee Bay (the region with the highest colonization) was most likely due to reduced water levels and aerial exposure of the colonization plates while other factors like low productivity, disturbance and water flow may have inhibited colonization in the Lake St. Clair delta, the Les Cheneaux Islands, the Beaver archipelago, and Grand Traverse Bay.

#### *Determination of Unionid Refugia*

Of the three sites with unionid presence, the Lake St. Clair delta had the highest density of unionids, the greatest species diversity, and medium fouling by dreissenids. North Maumee Bay surveys contained two species at lower densities than sites in the delta, but this region had the lowest fouling rates on unionids. The Les Cheneaux region contained the lowest diversity and density of unionids and had the highest fouling of dreissenids. Based on the findings of this study and supported by previous research, (Zanatta et al. 2002, McGoldrick et al. 2009) the Lake St. Clair delta and North Maumee Bay appear to be true refuges for unionids. Although live unionids were found in the Les Cheneaux region, the low diversity and density coupled with high dreissenid fouling indicate this is most likely a remnant population that is functionally extirpated and that this area does not appear to act as a true refuge.

#### *Conclusion and Management Implications*

The low densities of *E. complanata* found in the Les Cheneaux Islands coupled with this region having the highest average fouling rate indicate that these organisms are likely to be extirpated from the region in the near future. Based on these implications, Les Cheneaux Islands need immediate intervention by either government or private

conservation organizations to stabilize the populations and prevent extirpation. This area would also be a prime candidate for *in situ* removal of dreissenids, a technique suggested by Hallac and Marsden (2001) to help increase the chance of survival for unionids under high fouling conditions. Although the Les Cheneaux Islands are in need of conservation efforts, with the rapid decline of unionids across North America, all wetlands with remaining populations should be considered for monitoring and conservation efforts.

Based on the result of these surveys, North Maumee Bay in Lake Erie and the Lake St. Clair delta may be adequate habitats to use as potential nurseries or transplant sites for unionids. The water level fluctuations and productivity of North Maumee Bay appear to allow co-existence between unionids and dreissenids, a factor that Bowers and de Szalay (2004) suggest is an important aspect to identify for unionid conservation efforts. Although the delta region is very different chemically and physically from North Maumee Bay, this area may also serve as suitable habitat for co-existence due to the lack of high flow to carry in dreissenid veligers along with the lower levels of turbidity, alkalinity, and TDS which are needed to sustain high dreissenid colonization rates.

Michigan's coastal wetlands have historically received little consideration with regard to unionid populations, potential refuge habitats, and interactions with invasive dreissenid mussels. This study highlights that physical (water fluctuations) and chemical (i.e., turbidity, conductivity, and total dissolved solids) factors influence dreissenid colonization in coastal wetlands and dreissenid fouling on unionids. With unionid populations in rapid decline, it is imperative to examine this understudied fauna and recognize factors that can be used to conserve their habitats and numbers. Additional studies evaluating coastal wetlands as potential unionid habitat could greatly benefit

conservation efforts in the Great Lakes basin and this project provides a framework for future studies to achieve this goal.

## APPENDICES

**Appendix 1 Site Descriptions**

<b>Region</b>	<b>Site #</b>	<b>Hydrologic System</b>	<b>Dominant Substrate Type(s)</b>	<b>Field Season</b>
Saginaw Bay	1- Wildfowl Bay	Lacustrine, open embayment	Sand	2009
	2- Vanderbilt Park	Lacustrine, open embayment	Sand	2009
	3- Pinconning Park	Lacustrine, protected embayment	Silt	2009
Les Cheneaux	1- Sheppard Bay	Lacustrine, protected embayment	Clay	2009
	2- Urie Bay	Lacustrine, protected embayment	Clay-Detritus	2009
	3- Aldo Leopold Reserve	Lacustrine, protected embayment	Clay	2009
	4- Government Bay	Lacustrine, protected embayment	Sand	2010
	5- Muscallonge Bay	Lacustrine, protected embayment	Sand-Gravel	2010
	6- Mackinac Bay	Lacustrine, protected embayment	Clay-Sand	2010
Beaver Island 43	1- North	Lacustrine, open shoreline	Cobble	2009
	2- St. James Bay South	Lacustrine, open embayment	Detritus-Clay	2009
	3- St. James Bay East	Lacustrine, open embayment	Sand	2009
Lakes St. Clair	1- Big Muscamoot Bay	Riverine, delta	Sand-Silt	2010
	2- Goose Bay	Riverine, delta	Sand-Silt	2010
	3- Anchor Bay	Riverine, delta	Sand-Silt	2010
Lake Erie	1- North Maumee Bay Outer	Lacustrine, open shoreline	Silt	2010
	2- NMB- Inner East	Riverine, delta	Sand-Silt	2010
	3- NMB- Inner West	Riverine, delta	Sand	2010
Garden Island	1- Garden Harbor North	Lacustrine, protected embayment	Silt	2010
	2- Garden Harbor West	Lacustrine, protected embayment	Silt	2010
	3- Garden Harbor South	Lacustrine, protected embayment	Cobble	2010
Grand Traverse Bay	1- South Elk Rapids	Lacustrine, open shoreline	Cobble-Sand	2010
	2- North Elk Rapids	Lacustrine, open shoreline	Sand	2010
	3- Acme Roadside stop	Lacustrine, open shoreline	Sand	2010

## **Appendix 2** *Water Gauge Construction*

Water gauges were designed using a foam float constructed of 1.9 cm ( $\frac{3}{4}$  inch) housing insulation measuring 27.9 cm (11 inches) in diameter attached to a PVC pipe measuring 5.9 cm (2 inches) in diameter and 152 cm (5 feet) in length. The foam float had male and female pipe adaptors in the center of it that allowed the float to move freely up and down the PVC pipe. Pipe insulation for the PVC pipe, cut into 5.9 cm (2 inches) long sections, was affixed above and below the float to serve as the high and low water level markers. Cable ties were used to keep the pipe insulation held together as prolonged exposure to water and ultra-violet light caused the adhesive to break down and some of the water level markers to fall off during the initial sampling periods.

To add weight to the float so it could push down the low marker, a mass of 239.4 grams was added to the female adapter using 12, half inch stainless steel hex nuts. This allowed enough mass to surpass the friction of the low marker and push it down while still allowing the float to maintain buoyancy in the water. The PVC pipe was topped with a pipe cap adhered with PVC cement with a hole drilled through the center. A 91.4 cm (3 feet) piece of re-bar was hammered into the substrate to anchor the water gauge. The high and low markers were set directly above and below the float at the water level of each site to begin sampling. Measurements were obtained at six and 12 weeks during the sampling season. When the water gauges were checked, the top of the low marker was measured to the sediment line on the PVC pipe to determine the lowest water depth during the six week period. The bottom of the high marker was measured to the sediment line to determine the highest water level reached during the time period. The water gauge

was reset with each marker directly above and below the float to begin the next sampling interval.

**Appendix 3** *Unionid Diversity*

Site	Date	Species	N	Percent Dominance	Mean Length in mm (SEM)	Mean Fouling (SEM)	Fouling Range
Les Cheneaux, site 1	20-Jul-09	<i>Elliptio complanata</i>	5	100	91 (2)	22.8 (8.3)	3-49
Les Cheneaux, site 2	17-Aug-10	<i>Elliptio complanata</i>	1	100	79.0	19.0	
St. Clair Delta, site 1	12-Jul-10	<i>Fusconaia flava</i>	8	15.7	30.9 (2.3)	11.9 (3.3)	0-28
St. Clair Delta, site 1	12-Jul-10	<i>Lampsilis cardium</i>	4	7.8	76.3 (2.7)	8.5 (3.3)	3-18
St. Clair Delta, site 1	12-Jul-10	<i>Lasmigona costata</i>	2	3.9	64.8 (14.8)	23 (2)	21-25
St. Clair Delta, site 1	12-Jul-10	<i>Lampsilis siliquoidea</i>	27	52.9	52.3 (1.3)	12.4 (2.3)	0-39
St. Clair Delta, site 1	12-Jul-10	<i>Pyganodon grandis</i>	1	2.0	59.0	20.0	
St. Clair Delta, site 1	12-Jul-10	<i>Strophitus undulatus</i>	7	13.7	41.6 (1.7)	9.6 (3.6)	0-25
St. Clair Delta, site 1	12-Jul-10	<i>Villosa iris</i>	2	3.9	53.5 (6.5)	8 (2)	6-10
46 St. Clair Delta, site 2	13-Jul-10	<i>Anodontoides ferussacianus</i>	1	7.1	40.0	0.0	
St. Clair Delta, site 2	13-Jul-10	<i>Elliptio dilatata</i>	1	7.1	59.0	17.0	
St. Clair Delta, site 2	13-Jul-10	<i>Fusconaia flava</i>	2	14.3	43.8 (8)	4.5 (3.5)	1-8
St. Clair Delta, site 2	13-Jul-10	<i>Lampsilis siliquoidea</i>	7	50.0	54.6 (4)	12.9 (4.1)	1-35
St. Clair Delta, site 2	13-Jul-10	<i>Potamilus alatus</i>	2	14.3	63 (7)	4 (4)	0-8
St. Clair Delta, site 2	13-Jul-10	<i>Strophitus undulatus</i>	1	7.1	39.0	6.0	
St. Clair Delta, site 3	13-Jul-10	<i>Elliptio dilatata</i>	1	100	60.0	1.0	
St. Clair Delta, site 1	21-Aug-10	<i>Lampsilis siliquoidea</i>	1	100	48.0	0.0	
N. Maumee Bay, site 1	20-Jul-10	<i>Leptodea fragilis</i>	3	100	72 (4.6)	1.6 (1.7)	0-5
N. Maumee Bay, site 3	21-Jul-10	<i>Pyganodon grandis</i>	1	100	96.0	1.0	

## LITERATURE CITED

- Albert, D.A., Ingram, J., Thompson, T., and Wilcox, D. (2003). Great Lakes Coastal Wetland Classification. Great Lakes Coastal Wetland Consortium, Ann Arbor, Michigan.
- Alexander, J.E., Thorp, J.H. Jr., and Fell, R.D. (1994). Turbidity and temperature effects on oxygen consumption in the zebra mussel (*Dreissena polymorpha*). *Canadian Journal of Fisheries and Aquatic Sciences*, 51, 179-184.
- Allan, D.J. and Castillo, M.M. 2008. *Stream Ecology: Structure and function of running waters*. p. 41-42. 2<sup>nd</sup> ed. Springer, Dordrecht, The Netherlands.
- Anthony, J. L., Kesler, D. H., Downing, W. L., and Downing, J. A. (2001). Length-specific growth rates in freshwater mussels (Bivalvia: Unionidae): Extreme longevity or generalized growth cessation? *Freshwater Biology* 46, 1349-1359.
- APHA (American Public Health Association). (1998). *Standard Methods for the Evaluation of Water and Wastewater*. 20<sup>th</sup> ed. APHA, Washington, DC.
- Barnhart, M. C., Haag, W. R., and Roston, W. N. (2008). Adaptations to host infection and larval parasitism in Unionoida. *Journal of the North American Benthological Society*, 27(2), 370-394.
- Bauer, G. (1987). Reproductive strategy of the freshwater pearl mussel *Margaritifera margaritifera*. *Journal of Animal Ecology*, 56, 691-704.
- Bauer, G., and Wächtler, K, eds. (2000). *Ecology and Evolution of the Freshwater Mussels Unionoida*. Verlin: Springer-Verlag.
- Berkman, P.A., Haltuck, M.A., Tichich, E., Garton, D.W., Kennedy, G.W., Gannon, J.E., Mackey, S.D., Fuller, J.A., Liebenthal, D.A. (1992). Zebra mussels invade Lake Erie muds. *Nature*, 393, 27-28.
- Bookout, T.A. (1989). The Great Lakes marshes. In: L.A. Smith, R.L. Pederson, R.M. Kaminiski (Eds.), *Habitat Management for Migrating and Wintering Waterfowl in North America*, pp. 131-156. Texas Tech University Press, Lubbock, TX.
- Bowers, R., Sudomir, J. C., Kershner, M. W., and de Szalay, F. A. (2005). The effects of predation and unionid burrowing on bivalve communities in a Laurentian Great Lake coastal wetland. *Hydrobiologia*, 54, 93-102.
- Bowers, R. and de Szalay, F. A. (2004). Effects of hydrology on unionids (Unionidae) and zebra mussels (Dreissenidae) in a Lake Erie Coastal Wetland. *American Midland Naturalist*, 151, 286-300.

- Bowers, R. and de Szalay, F. A. (2005). Effects of water level fluctuations on zebra mussel distribution in a Lake Erie coastal wetland. *Journal of Freshwater Ecology*, 20(1), 85-92.
- Burlakova, L. E., Karatayev, A. Y., and Padilla, D. K. (2000). The impact of *Dreissena polymorpha* (PALLAS) invasion on unionid bivalves. *International Review of Hydrobiologia*, 85(5-6), 529-541.
- Burton, T. M., Uzarski, D. G., Gathman, J. P., Genet, J. A., Keas, B.E. Stricker, C. A. (1998). Development of a preliminary invertebrate index of biotic integrity for Lake Huron coastal wetlands. *Wetlands*, 19(4), 869-882.
- Campbell, D. C., Serb, J. M., Buhay, J. E., Roe, K. J., Minton, R. L., and Lydard, C. 2005. Phylogeny of North American amblesmines (Bivalvia, Unionoida): prodigious polyphyly proves pervasive across genera. *Invertebrate Biology*, 124(2), 131-164.
- Carlton, J. T. (2008). The zebra mussel *Dreissena polymorpha* found in North America in 1986 and 1987. *Journal of Great Lakes Research*, 34, 770-773.
- Crail, T.D., Krebs, R.A., and Zanatta, D.T. (2011). Unionid mussels from nearshore zones of Lake Erie. *Journal of Great Lakes Research*, 37, 199-202.
- Cummings, K. S., and Graf, D. L. (2010). Mollusca: Bivalvia. p. 309-384. In: J.H. Thorpe and A.P. Covich (ed.), *Ecology and classification of North American Freshwater Invertebrates*. 3<sup>rd</sup> ed. Academic Press, Inc., Burlington, MA.
- Dame, R. F. (1996). *Ecology of Marine Bivalves: an Ecosystem Approach*. CRC Press, New York.
- Downing, J. A., Amyot, J. P., Perusse, M., and Rochon, Y. (1989). Visceral sex, hermaphroditism, and protandry in a population of the freshwater bivalve *Elliptio complanata*. *Journal of the North American Benthological Society*, 8, 92-99.
- Downing, J.A., Van Meter, P., and Woolnough, D.A. (2010). Suspects and evidence: a review of the causes of extirpation and decline in freshwater mussels. *Animal Biodiversity and Conservation*, 3(2), 151-185.
- Ellis, A. E. (1978). British freshwater bivalve Mollusca. Keys and notes for the identification of the species. p.109. *Synopses of the British Fauna No. 11*. Academic Press, London.
- Garton, D. W. and Haag, W. R. (1993). Seasonal reproductive cycles and settlement patterns of *Dreissena polymorpha* in western Lake Erie, p. 111-128. In T.F. Nalepa and D.W. Schloesser [ed.] *Zebra mussels: biology, impacts, and control*. Lewis Publishers, Boca Raton, Fla.

- Gathman, J.P., Burton, T.M., and Armitage, B.J. (1999). Coastal wetland of the upper Great Lakes. Distribution of invertebrate communities in response to environmental variation. In: *Invertebrates in Freshwater Wetlands of North America*. D. P. Batzer, R.B. Rader, S.A. Wissinger (Eds.). pp. 949-994. John Wiley and Sons, New York.
- Gillis, P. L., and Mackie, G. L. (1994). Impact of the zebra mussel, *Dreissena polymorpha*, on populations of Unionidae (Bivalvia) in Lake St. Clair. *Canadian Journal of Zoology*, 72, 1260-1271.
- Goodrich, C. and van der Schalie, H. (1932). I. on an increase in the naiad fauna of Saginaw Bay, Michigan II. the naiad species of the Great Lakes. *Occasional Papers of the Museum of Zoology*, University of Michigan, 238, 1-14.
- Graf, D. L., and Cummings, K. S. (2006). Palaeoheterodont diversity (Mollusca: Trigonioida + Unionoida): what we know and what we wish we knew about freshwater mussel evolution. *Zoological Journal of the Linnaean Society*, 148, 343-394.
- Graf, D. L., and Cummings, K. S. (2007). Review of the systematics and global diversity of freshwater mussel species (Bivalvia: Unionoida). *Journal of Molluscan Studies*, 73, 291-314.
- Griffiths, R. W. (1993). Effects of zebra mussels (*Dreissena polymorpha*) on the benthic fauna of Lake St. Clair, p. 414-437. In T.F. Nalepa and D.W. Schloesser [ed.] *Zebra mussels: biology, impacts, and control*. Lewis Publishers, Boca Raton, Fla.
- Haag, W. R., Berg, D. R., Garton, D. W., and Farris, J. L. (1993). Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in western Lake Erie. *Canadian Journal of Fisheries and Aquatic Science*, 50, 13-19.
- Haag, W. R., Butler, R. S., and Hartfield, P. W. (1995). An extraordinary reproductive strategy in freshwater bivalves: Prey mimicry to facilitate larval dispersal. *Freshwater Biology*, 43, 471-476.
- Haag, W. R., and Warren, M. L. (2000). Effects of light and presence of fish on lure display and larval release behaviours in two species of freshwater mussels. *Animal Behaviour*, 60, 879-886.
- Haag, W. R., and Warren, M. L. (2003). Host fishes and infection strategies of freshwater mussels in large Mobile Basin streams, USA. *Journal of the North American Benthological Society*, 22, 78-91.
- Haag, W. R., and Rypel, A. L. (2011). Growth and longevity in freshwater mussels: evolutionary and conservation implications. *Biological Reviews*, 86, 225-247.

- Hallac, D. E., and Marsden, J. E. (2001). Comparison of conservation strategies for unionids threatened by zebra mussels (*Dreissena polymorpha*): periodic cleaning vs quarantine and translocation. *Journal of the North American Benthological Society*, 20(2), 200-210.
- Hebert, P. D. N., Muncaster, B. W., and Mackie, G. L. (1989). Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Science*, 46, 1587-1591.
- Herdendorf, E. (1987). The ecology of the coastal marshes of western Lake Erie: a community profile. US Fish and Wildlife Service, Washington, DC.
- Hincks, S. S., and Mackie, G. L. (1997). Effects of pH, calcium, alkalinity, hardness, and chlorophyll on the survival, growth and reproductive success of zebra mussel (*Dreissena polymorpha*) in Ontario lakes. *Canadian Journal of Fisheries and Aquatic Science*, 54, 2049-2057.
- Howard, J. K., and Cuffey, K. M. (2006). The functional role of native freshwater mussels in the fluvial benthic environment. *Freshwater Biology*, 51, 460-474.
- Hunter, R. D., and Simons, K. A. (2004). Dreissenids in Lake St. Clair in 2001: evidence for population regulation. *International Association of Great Lakes Research*, 30(4), 528-537.
- Jansen, W., Bauer, G., and Zahner-Meike, E. (2001). Glochidial mortality in freshwater mussels, in: Bauer, G. and Wächtler, K. (Eds.), Ecology and evolution of the freshwater mussels Unionoida. Springer-Verlag, Berlin, pp. 185-211.
- Jones, J. W., and Neves, R. J. (2002). Life history and propagation of the endangered fanshell pearl mussel, *Cyprogenia stegaria* Rafinesque (Bivalvia: Unionidae). *Journal of the North American Benthological Society*, 21, 76-88.
- Jokela, A., and Ricciardi A. (2008). Predicting zebra mussel fouling on native mussels from physical and chemical variables. *Freshwater Biology*, 53, 1845-1856.
- Jude, D.J. and Pappas, J. (1992). Fish utilization of Great Lakes wetlands. *Journal of Great Lakes Research*, 18, 651-672.
- Levinton, J. S. (1995). Bioturbators as ecosystem engineers: control of the sediment fabric, inter-individual interactions, and material fluxes. p. 29-38. In: *Linking Species and Ecosystems*. C.G. Jones and J.H. Lawton (eds.). Chapman and Hall, New York.

- Lydeard, C., Cowie, R. H., Winston, F. P., Bogan, A. E., Bouchet, P., Clark, S. A., Cummings, K. S., Frest, T. J., Gargominy, O., Herbert, D. G., Hershler, R., Perez, K. E., Roth, B., Seddon, M., Strong, E. E., and Thompson, F. G. (2004). The global decline of nonmarine mollusks. *Bioscience*, 54(4), 321-330.
- Mackie, G.L. (1984). 5. Bivalves. p. 351-418. In: K.M. Wilbur (ed.). *The Mollusca. Vol. 7. Reproduction* (eds. A.S. Tompa, N.H. Verdonk and J.A.M. van de Biggelaar), Academic Press, NY.
- Mackie, G.L. (1990). Early biological and life history attributes of the zebra mussel, *Dreissena polymorpha* (Bivalvia: Dreissenidae), and impacts on native bivalves in Lake St. Clair. p. 215-231. In: *Proceedings of the Technology Transfer Conference*, Toronto, Ontario, Nov. 19-20, 1990.
- Mackie, G. L. (1991). Biology of the exotic zebra mussel, *Dreissena polymorpha*, in relation to native bivalves and its potential impact in Lake St. Clair. *Hydrobiologia*, 219, 251-268.
- Mackie, G. L., and Schloesser, D. W. (1996). Comparative biology of zebra mussels in Europe and North America: an overview. *American Zoologist*, 36, 244-258.
- Masteller, E. C. and Schloesser, D. W. (1992). Infestation and impact of zebra mussels on the native unionid population at Presque Isle State Park, Erie, PA. *Journal of Shellfish Research*, 11, 232.
- May, B., and Marsden, J. E. (1992). Genetic identification and implications of another invasive species of dreissenid mussel in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Science*, 49, 1501-1506.
- McCune, B. and M. J. Mefford. (1999). PC-ORD. Multivariate Analysis of Ecological Data. Version 5.0 MjM Software, Gleneden Beach, Oregon, U.S.A.
- McGoldrick, D. J., Metcalfe-Smith, J. L., Arts, M. T., Schloesser, D. W., Newton, T. J., Mackie, G. L., Monroe, E. M., Biberhofer, J., and Johnson, K. (2009). Characteristics of a refuge for native freshwater mussels (Bivalvia: Unionidae) in Lake St. Clair. *Journal of Great Lakes Research*, 35, 137-146.
- McMahon, R. F. (1991). Mollusca: Bivalvia. p. 315-398. In: J.H. Thorpe and A.P. Covich (ed.), *Ecology and classification of North American Freshwater Invertebrates*. 2<sup>nd</sup> ed. Academic Press, Inc., Orlando, FL.
- McMahon, R. F. (1996). The physiological ecology of the zebra mussel, *Dreissena polymorpha*, in North America and Europe. *American Zoologist*, 36, 339-363.

- McMahon, R.F., and Bogan, A.E. 2001. Mollusca: Bivalvia. p. 331-429, *In* J.H. Thorp and A.P. Covich (Eds.). *Ecology and Classification of North American Freshwater Invertebrates*, 2<sup>nd</sup> Edition. Academic Press, New York, NY. 1056 pp.
- Mills, E. L., Dermott, R. M., Roseman, E. F., Dustin, D., Mellina, E., Conn, D. B., and Spindle, A. P. (1993). Colonization, ecology and population structure of the “quagga” mussel (Bivalvia: Dreissenidae) in the lower Great Lakes. *Canadian Journal of Fisheries and Aquatic Science*, 50, 2305-2314.
- Nichols, S. J. and Wilcox, D. A. (1997). Burrowing saves Lake Erie clams. *Nature*, 389, 921.
- Nichols, S. J. and Amberg, J. (1999). Co-existence of zebra mussels and freshwater unionids: population dynamics of *Leptodea fragilis* in a coastal wetland infested with zebra mussels. *Canadian Journal of Zoology*, 77, 423-432.
- Nichols, S.J. and Garling, D. (2000). Food-web dynamics and trophic-level interactions in a multispecies community of freshwater unionids. *Canadian Journal of Zoology*, 78, 871-882.
- Prince, H.H., Padding, P.I., and Knapton, R.W. (1992). Waterfowl use of the Laurentian Great Lakes. *Journal of Great Lakes Research*, 18, 673-699.
- Ram, J. L., and McMahon, R. F. (1996). Introduction: The biology, ecology, and physiology of zebra mussels. *American Zoologist*, 36, 239-243.
- Ramcharan, C.W., Padilla, D.K., and Dodson, S.L. (1992). Models to predict potential occurrence and density of the zebra mussel, *Dreissena polymorpha*. *Canadian Journal of Fisheries and Aquatic Science*, 49, 2611-2620.
- Ricciardi, A., Whoriskey, F. G., and Rasmussen, J. B. (1995). Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density. *Canadian Journal of Fisheries and Aquatic Science*, 52, 1449-1461.
- Ricciardi, A., Whoriskey, F. G., and Rasmussen, J. B. (1996). Impact of the *Dreissena* invasion on native unionid bivalves in the upper St. Lawrence River. *Canadian Journal of Fisheries and Aquatic Sciences*, 53(6), 1434-1444.
- Schloesser, D. W. and Nalepa, T. F. (1994). Dramatic decline of unionid bivalves in offshore waters of western Lake Erie after infestation by the zebra mussels, *Dreissena polymorpha*. *Canadian Journal of Fisheries and Aquatic Science*, 51, 2234-2242.
- Schloesser, D. W., Smithee, R. D., Longton G. D., and Kovalak, W.P. (1997). Zebra mussel induced mortality of unionids in firm substrata of western Lake Erie and a habitat for survival. *American Malacological Bulletin*, 14(1), 67-74.

- Schloesser, D. W. and Masteller, E. C. (1999). Mortality of unionid bivalves (Mollusca) associated with dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) in Presque Isle Bay, Lake Erie. *Northeastern Naturalist*, 6(4), 341-352.
- Strayer D. L., Downing, J. A., Haag, W. R., King, T. L., Layzer, J. B., Newton, T. J., and Nichols, S. J. (2004). Changing perspectives on pearly mussels, North America's most imperiled animals. *BioScience*, 54(5), 429-439.
- Strayer, D. L. (1999). Effects of alien species on freshwater mollusks in North America. *Journal of the North American Benthological Society*, 18, 74-98.
- Strayer, D. L. and Smith, L. C. (1996). Relationships between zebra mussels (*Dreissena polymorpha*) and unionid clams during the early stages of zebra mussel invasion of the Hudson River. *Freshwater Biology*, 36, 772-779.
- Uzarski, D. G., Burton, T. M., and Genet, J. A. 2004. Validation and performance of an invertebrate index of biotic integrity for Lakes Huron and Michigan fringing wetlands during a period of lake level decline. *Aquatic Ecosystem Health and Management*, 7(2), 269-288.
- Uzarski, D.G., Burton, T.M., Cooper, M.J., Ingram, J.W., and Timmermans, S.T.A. 2005. Fish habitat use within and across wetland classes in coastal wetlands of the five Great Lakes: Development of a fish-based index of biotic integrity. *Journal of Great Lakes Research*, 31(1), 171-187.
- Vaughn, C. C., and Hakenkamp, C. C. (2001). The functional role of burrowing bivalves in freshwater ecosystems. *Freshwater Biology*, 46, 1431-1446.
- Watters, G. T., Hoggarth, M. A., and Stansbery, D. H. (2009). *The freshwater mussels of Ohio*. The Ohio State University Press, Columbus, OH. 421 pp.
- Weeber, R.C. and Vallianatos, M. (Eds). *The Marsh Monitoring Program 1995-99: Monitoring Great Lakes Wetlands and their Amphibian and Bird Inhabitants*. Bird Studies Canada, Port Rowan, Ontario.
- Whillans, T. (1979). Historic transformations of fish communities in three Great Lakes Bays. *Journal of Great Lakes Research*, 5, 195-215.
- Williams, J. D., Warren, M. L., Cummings, K. S., Harris, J. L., and Veves, R. J. (1993) Conservation status of freshwater mussels of the United States and Canada. *Fisheries*, 18, 6-22.
- Zanatta, D. T., Mackie, G. L., Metcalfe-Smith, J. L., and Woolnough, D. A. (2002). A refuge for native freshwater mussels (Bivalvia: Unionidae) from the impacts of the exotic zebra mussel (*Dreissena polymorpha*) in Lake St. Clair. *Journal of Great Lakes Research*, 28(3), 479-489.

Zanatta, D. T., and Murphy, R. W. (2006). The evolution of active host-attraction strategies in the freshwater mussel tribe Lampsilini (Bivalvia: Unionidae). *Molecular Phylogenetics and Evolution*, 41, 195-208.