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Spatial and Temporal Variation of Macroinvertebrate Communities in the Muskegon River and Bigelow Creek, Michigan

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Spatial and Temporal Variation of Macroinvertebrate Communities in the Muskegon River and Bigelow Creek, Michigan

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Abstract

The first objective of this study was to determine the relationship between zebra mussel densities/biomass and benthic macroinvertebrate composition and density in the Muskegon River at a site near Croton Dam, Thirteen benthic quadrat samples were taken along a range of zebra mussel and macroinvertebrate densities at a single sample location. Turbellaria was the only taxa to have a significant positive relationship with zebra mussel density and biomass, Simuliidae had a positive, non-significant relationship with both. No macroinvertebrate taxa decreased because of zebra mussel density/biomasss. The other objectives of this study were to compare current macroinvertebrate communities in the Muskegon River and Bigelow Creek, as well as between the1998 and 2011 samples. Benthic samples were taken at six sites (in summer and fall) in a 22.5 km reach downstream of Croton Dam of the Muskegon River, and two sites on Bigelow Creek, using Hess samples and five-rock clusters. Macroinvertebrate community richness, EPT richness, Shannon-Wiener diversity, and evenness were calculated for each site, as well as zebra mussel densities. Macroinvertebrate and zebra mussel densities were highest in the upper sample sites on the Muskegon River. Macroinvertebrate production shifted from the mid-river sites in 1998 to the upper sites near Croton Dam in 2011 on the Muskegon River. *Cheumatopsyche* increases in the Muskegon River were the driving taxa in community changes from 1998 to 2011. Bigelow Creek also experienced changes between the 1998 and 2011 samples, primarily due to a shift in taxa from *Protoptila* and Hydropsychidae to *Baetidae* and *Simuliidae*. A single factor could not be found for the cause in the change in macroinvertebrate communities from 1998 to 2011 with the data studied, but is likely due to the invasion of zebra mussels in the Muskegon River as well as environmental changes in both Bigelow Creek and Muskegon River.

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CHAPTER I

INTRODUCTION

Rivers and streams are found on every continent on Earth, and vary in size from a trickle during precipitation events or snowmelt, to a raging river the size of the Amazon. They are unique ecosystems that can span large geographic areas and have unidirectional flow from the source to the mouth. Although streams themselves are unique ecosystems, the shape, size, and chemical makeup of a stream are products of the area immediately surrounding the stream, known as its catchment. For example, the composition of rock in a stream's catchment determines the type of substrate in and around the stream, ion availability to the stream's inhabitants, as well as the slope of the streambed (Hynes, 1975).

However, even as each stream is representative of the terrain around it, it has only been relatively recently that the study of streams and their catchments has been developed. Many important studies and major concepts in stream ecology have only been discerned in the past 30 years and most studies researched different physical zones of streams, which include: the longitudinal flow from headwaters to mouth, the lateral spread of a river into its flood plain, the vertical flow of a river into the hyporheic zone, and the physical change of rivers through time (Ward, 1989).

The first dimension stream ecologists identified is based on the longitudinal flow of a river. Vannote et al. (1980) expanded on the concept by Strahler (1952) for classifying streams based on tributary connections. Vannote et al. (1980) examined how streams generally changed from upstream to downstream, and derived three overall river classifications, how each size-class differed, and how macroinvertebrate communities segregate themselves by river-size, which is known as the river-continuum concept (RCC) (Vannote et al., 1980). Headwater streams are generally small in size (order 1-3) and will have high allochthonous input but minimal autochthonous production due to heavy shading from the riparian zone (Vannote et al., 1980). As the stream gets larger in size and order, dependence on riparian input is reduced and autochthonous production as well as use of organic matter from upstream increases (Vannote et al., 1980).

Vannote et al. (1980) also proposed the groundbreaking concept that the community composition of organisms as well as functional feeding groups (FFGs) will shift from headwaters to mouth, due to changes in stream size and available food resources (Vannote et al., 1980). FFGs can be a useful measure to assess stream conditions, and was first described for use in streams by Cummins (1973). Vannote et al. (1980) expanded on Cummins (1973) and identified four main functional feeding groups in streams: shredders, collectors, grazers, and predators. Shredders use allochthonous litter (coarse particulate organic matter, CPOM) as a food source, and generate fine particulate organic matter which will be available for use downstream by collectors (Vannote et al., 1980). Grazers eat periphyton, fungi, and bacterial colonies off objects such as rocks or leaves in the streams (Vannote et al., 1980). Collectors utilize small debris (fine particulate organic matter, FPOM), such as the scraps from CPOM, dislodged periphyton from scrapers, small algae, and waste from upstream organisms (Vannote et al., 1980). Predators eat small fish, crustaceans, and other macroinvertebrates throughout the stream (Vannote et al., 1980). Along with the previous changes from allochthonous to autochthonous input, the macroinvertebrate communities will change as well with increasing stream order (Vannote et al., 1980). This is considered the longitudinal dimension of streams and rivers, and the RCC was an attempt to explain how rivers will change from headwaters to mouth.

The second dimension that is identified by stream ecologists is the latitudinal axis: a stream's floodplain and corresponding riparian zone. Streams are invariably connected to terrestrial environments, and cannot be thought of simply as a pipe or conduit. The riparian zone is an important feature connecting streams to the land and vice versa, through mechanisms such as nutrient transfers, water movement, and sediment transfers. During flood events, high water levels create a connection to the flood plain, which can then be utilized by biota, such as fish spawning grounds, or seed dispersal from terrestrial plants (Junk et al., 1989). During a flood event, and the eventual recession of water, terrestrial nutrients will enter the stream system to be utilized by the downstream biota (Junk et al., 1989). The riparian zone (or aquatic/terrestrial transition zone (ATTZ)) is a unique habitat that is sometimes terrestrial and sometimes aquatic. Both terrestrial and aquatic organisms can utilize the riparian zone, and both depend on the transfer of nutrients, recycling of organic matter, and physical space that the ATTZ provides. Due to the uniqueness of the riparian zone, Junk et al. (1989) proposes that it should be considered a specific ecosystem.

The third dimension of streams and rivers is the vertical dimension known as the hyporheic zone or corridor. The hyporheic corridor is defined as the vertical penetration of river water into fluvial deposits within the floodplain and active river channel (Triska et al., 1990; as cited in Stanford and Ward, 1993). Stanford and Ward (1993) found that the hyporheic corridor influences many aspects of the river system itself including species richness, structure of riparian zones, transfer of bioavailable resources, and bioproduction through the biogeochemical and microbial processes that occur in the corridor (Stanford and Ward, 1993). Because of the abundance of nutrients (and in turn food items) and protection from predators as well as disturbances, some macroinvertebrates utilize the hyporheic corridor to complete many life stages, or as a permanent residence place (Stanford and Ward, 1993). The hyporheic zone is an integral and permanently connected part of a river, but still inadequately studied. Stanford and Ward (1993) suggest that the hyporheic corridors are so unique that they should be considered a dynamic ecotone.

With the progression of time, everything changes in some way, and rivers are no exception. The above processes are altered and shifted through time to coincide with the changing physical aspects of a river and its boundaries. The changes through time in a river can be as brief as a recolonization event on a patch of stream after a disturbance, to many hundreds of years shifting the flow of the river itself (Ward, 1989). In essence, scientists must not only look at the physical characteristics of a river, but should also investigate how time (weeks, seasons, or years) will affect how the stream changes (Ward, 1989). The streams around the Mount St. Helens crater, provide excellent insight into temporal changes in streams after an extreme disturbance (Hawkins et al., 1988; Lamberti et al., 1992,)

Because of the four-dimensional nature of streams, particularly the unidirectional flow, nutrients in streams do not just cycle in place. Rather they are transferred downstream in the form of a spiral. A nutrient spiral is the time an atom of a nutrient (such as nitrogen) takes to move from the inorganic to the organic phase and back again, with a shorter spiral length being more efficient and desirable for a stream (Newbold et al., 1981). Unless nutrient spirals are really efficient, they normally do not recycle these nutrient atoms in place, nutrients recycled at one point in a stream are unable to be utilized by organisms at that location, instead the nutrients get transported downstream for further use and recycling (Newbold et al., 1983).

Nutrient spirals are often complex, and there are many ways that nutrients are transferred to a stream. The particulate organic matter (POM, which is matter > 0.45μm that is undissolved in the water column) input from the riparian zone, as well as in-stream, is shredded by aquatic macroinvertebrates and then transported from upstream to downstream. This POM (and the microbial ‘peanut butter’ that covers it) is nutritionally loaded and utilized by the flora and fauna throughout the river (Cummins, 1974).

Disturbances are important factors in almost every ecosystem, including rivers and streams. A disturbance can be defined as a damaging force that is applied to a habitat occupied by a population, community, or ecosystem and can be thought of in three ways (Lake, 2000). A pulse disturbance is typically short, with clearly defined start and end points, such as a flood (Lake, 2000). A press disturbance is maintained for a long time, with a distinct and sharp start, which levels off, such as increased sedimentation in a river after a landslide or persistence of heavy metal pollution in a system (Lake, 2000). The third type of disturbance, the ramp, is maintained for a long period and typically keeps increasing in strength unless it reaches an endpoint (Lake, 2000). An example of a ramp disturbance would be a drought, or the spread of an invasive species (Lake, 2000). Many riverine organisms have adapted to predictable natural disturbance events, as described earlier, but large disturbance events are also an integral part of the natural cycle of a river system (Junk et al., 1989). One of the main concepts regarding disturbances is the intermediate disturbance hypothesis which states that at an intermediate level of disturbance, species richness will be highest; whereas at low disturbance dominant species would overtake weaker competitors, and at high disturbance, disturbance-intolerant species would become locally extinct (Connell, 1978). This intermediate disturbance hypothesis (IDH) has been found to be applicable to many ecosystems including intertidal communities (Sousa, 1979), and desert communities (Guo, 1996). Although the IDH has been widely accepted for many years, it is not the only disturbance hypothesis. For example, Tilman and Downing (1994) found that a diversity-stability hypothesis was more appropriate for drought-disturbed grassland in which a more diverse grassland community would better withstand a major drought. Collins et al. (1995) found that neither the IDH nor any other hypothesis could explain how grassland species richness was affected by fire, but instead suggested the use of multiple theories. These examples attempt to explain natural disturbances, but disturbances can also be anthropogenic in origin.

The impacts of humans on an ecosystem vary widely in severity and cause. It is important to consider the spatial scale of disturbances being studied. For example, the effects of these human disturbances can be localized (such as washing clothes in a specific location on a river (Mathooko, 2001)) or widespread (the 31 dams throughout the Columbia River watershed), and the proper scale must be taken into account for the study being conducted.

For example, anthropogenic disturbances in the John Day River Basin, Oregon, are quite different from the disturbances of streams in Appalachia, and both will differ from disturbances in the Smoky Mountains National Park; due to geography and population size. The three main factors of human disturbance on the John Day River are: cattle grazing, forestry and logging practice, and dredge mining; whereas in Appalachia the disturbances are energy generation, forestry practices, and sewage/industrial effluents (Resh et al., 1988). In the Smoky Mountains National Park, there is no permanent human residence, but logging occurs frequently, and it negatively affects streams around the logging area in the park (Silsbee and Larson, 1983).

In Michigan, anthropogenic disturbances are different depending on stream types. A survey of warm-water streams in Michigan found that 38.1% had anthropogenic disturbances that were detectable to severe (on a scale of undetectable, detectable, moderate, heavy, and severe) (Wang et al., 2008). For warm-water streams the top three anthropogenic disturbances were urban land use, nitrogen and phosphorous inputs, and residential population density (Wang et al., 2008). In cold-water streams 18.2% had anthropogenic disturbances that were detectable to severe (Wang et al., 2008). The three most significant anthropogenic disturbances of the cold-water streams in this study were: nitrogen and phosphorous input, road density, and urban land use (Wang et al., 2008). Most of the streams in this study were in the Upper Peninsula and northern Lower Peninsula of Michigan, which are more natural streams, so these conclusions may not be applicable to the southern Lower Peninsula that has much more urbanization and agricultural use around streams (Wang et al., 2008). Along with heavy urbanization, one of the largest problems with rivers in the Lower Peninsula are dams. Many of the large rivers and their tributaries in the southern Lower Peninsula with dams include the Grand, Kalamazoo, Muskegon, Rogue, Thornapple, and St. Joseph River (Morman, 1979).

Although dams are built for many reasons such as generating electricity, transporting goods, and fisheries management, the existence of a dam on a river has been shown to affect a number of pathways within a river, both upstream and downstream. Ward and Stanford (1983) studied the disruptions that dams create in a river and developed the serial discontinuity concept from their findings. They predicted that a dam acts as a ‘reset-button’ for the processes defined by the RCC, for both abiotic and biotic processes (Ward and Stanford, 1995). In their work, they identified three typical reaches in a natural river: the straight headwater reach, a braided middle reach, and a meandering lower reach (Ward and Stanford, 1995). When a dam is placed in a straight headwater reach, the abiotic factors of the stream such as channel stability and thermal regimes are minimally affected (Ward and Stanford, 1995). However, many biotic factors are affected; ecological connectivity, POM ratios, and biodiversity all will be negatively impacted in an impeded headwater area. In fact, the POM ratio in a headwater reach will behave more like a braided reach with little coarse detritus being transported (Ward and Stanford, 1995). A dam installed in the braided middle area of a river will radically impact both the abiotic and biotic components (Ward and Stanford, 1995). Channel stability, thermal regimes, ecological connectivity, POM ratios, and biodiversity all are ‘reset’ downstream of the dam to resemble and operate more like a straight-flowing headwater reach than a braided type reach (Ward and Stanford, 1995). If a dam is constructed in a meandering lower reach, there is a large change in most of the abiotic and biotic processes (Ward and Stanford, 1995). Again, an impoundment will act as a reset-button for most processes, with channel stability, thermal regimes, ecological connectivity, and biodiversity returning to a more headwater-like state (Ward and Stanford, 1995). The CPOM/FPOM ratio will return to a more braided-type state with low CPOM amounts (Ward and Stanford, 1995). A human-made dam or impoundment will have considerable ramifications for the downstream reaches in a river.

Dams have many negative effects on the structure and function of streams; however, they do provide a few unintended benefits. For example, in a few instances, they can help to limit the expansion of invasive species. Rood et al. (2010) found that a dam on the Snake River in Idaho restricted the downstream expansion of invasive riparian plants due to drought and flood stress from the reservoir. Pratt et al. (2009) showed that dams and other barriers stop the invasive sea lamprey (*Petromyzon marinus*) from invading Great Lakes tributaries. Nevertheless, for the few benefits that are gained from dams, there are many detriments. For example, dams are known to trap and accumulate sediment from upstream in their reservoirs, they change natural temperature regimes, reduce water quality, and change biological communities.

Changes in thermal regimes of rivers downstream of a dam are common and geographically widespread across the world (Patric and Kakela, 1983). For example, Preece and

Jones (2002) found that the water discharged in spring and summer from the deep-release Keepit Dam on the Namoi River, Australia, cooled the water downstream, causing disruptions in native fish spawning cues. These temperature conditions lasted for 100 km downstream of the dam until it was restored to natural regimes (Preece and Jones, 2002). Warmer downstream temperatures caused by dams are also disruptive. Goniea et al. (2006) found that in the Columbia River below and between dams, migrating salmon chose to temporarily use cooler water tributaries that were 2-7°C cooler than the warm mainstream (20°C) due to the dams. They found that as the water temperature rose, the number of salmon using the cooler tributaries grew exponentially (Goniea et al., 2006). Baxter (1977) found that the hypolimnic layer of a stratified reservoir stays cool in the summer, thus having an abnormal cooling effect on the stream below the dam. During the winter when the reservoir is no longer stratified, the stored solar heat from the epilimnion layer gets mixed, and when it flows over the dam has an abnormal warming effect on the stream water (Baxter, 1977). Because water temperature and density are correlated, the summer-cooled water released downstream drifts to the bottom, whereas the winter-warmed water flows on the top of the stream, creating a thermally stratified river (Baxter, 1977). The abnormal temperature regimes can lead to dense currents (currents differing from regular flow by differing temperature, organic matter, etc.) from the dam, flowing into mainstream tributaries below the dam, reducing water quality in those tributaries and affecting the biota (Baxter, 1977). Temperature will also effect dissolved oxygen concentrations in an impounded river. Below the Capivara Reservoir Dam, Brazil, reduced oxygen concentrations were found due to eutrophication, thermal stratification, and the position of the spillway (de Oliveira Naliato et al., 2009). The temperature and dissolved oxygen concentrations downstream of the Capivara Dam were similar to the reservoir stratum at which the turbines were pulling water, changing the water quality in the river (de Oliveira Naliato et al., 2009).

Impoundments also affect water quality downstream of a dam. Dams change the chemistry and amount of total dissolved solids (TDS) available to the river below the dam. Kurunc et al. (2006) found that the Kilickaya Dam in Turkey reduced the concentration of many essential ions (K^+, Ca^{2+}, Mg^{2+}, etc.) of the downstream water. They suggest the reservoir is the cause of this change, as the water has a long residence time (on average 264 days) and ions are transformed by organisms (Kurunc et al., 2006).

These changes to the water chemistry in a river will affect plant and animal metabolism and growth rates. Kurunc et al. (2006) mention that microorganisms (bacteria, fungi, algae) will be affected by reductions in necessary chemical compounds and nutrients, because most microorganisms have the same nutritional requirements as higher organisms living in the same environment. Since many microorganisms can convert inorganic forms of elements to usable organic forms that are necessary for organism growth, they are an essential part of an ecosystem (decomposers, primary producers, etc.) and without the necessary nutrients, could cause a cascade effect through higher trophic levels reducing biodiversity (Kurunc et al., 2006).

Invertebrates are also affected by dams. On the South Saskatchewan River in Canada, Lehmkuhl (1972) found a reduction in macroinvertebrate abundances 70 miles downstream of Gardiner Dam as compared to upstream of the reservoir. Takao et al. (2008) found a somewhat different result in the Yahagi River, Japan. The authors found low taxa richness but high abundances of macroinvertebrates below the dam (Takao et al., 2008). This reduction of macroinvertebrate richness and diversity, but high abundance right below a dam is a general trend observed in many studies, and coincides with the alteration of the environment as described above (Doeg et al., 1987; Munn and Brusven, 1991; Lessard and Hayes, 2003; Santucci Jr. et al., 2005; Maloney et al., 2008; Growns et al., 2009).

More recently, studies have found that dam construction can facilitate the introduction of invasive species (Johnson et al., 2008). Impoundments have significantly more (2.5 to 7.8 times) established populations of invaders than a natural lake system, leading to changes in the community and reduced biodiversity in river systems (Johnson et al., 2008). The authors suggest that this could be because impoundments are typically larger than natural lakes, and more easily accessed by humans, thus promoting invasion (Johnson et al., 2008).

One notorious invader of many freshwater systems including the Mississippi River, Ohio River, Hudson River, and Great Lakes basin is the zebra mussel *Dreissena polymorpha*. Zebra mussels are prolific broadcast spawners, with a single female able to produce over a million eggs during one spawning season, making them formidable invaders (Snyder et al., 1999). Since the introduction of zebra mussels into the Great Lakes and their tributaries, mussels have impacted the ecosystem and its inhabitants. As a single zebra mussel can filter water at a rate of up to 1 $L \cdot day^{-1}$, this can cause cascades in many food webs (Reeders et al., 1989). Padilla et al. (1996) found that in Lake Michigan at Green Bay, WI, zebra mussels had a strong negative effect on large phytoplankton during the summer months. The study also found that even if phytoplankton were too large to be eaten by the zebra mussels, they were still withdrawn from the plankton and expelled as pseudofeces (Padilla et al., 1996). This withdrawal of large phytoplankton reduces the competition for nutrients by smaller plankton leading to an indirect positive effect from the zebra mussels (Padilla et al., 1996).

Zebra mussels effect not only phytoplankton communities but also modify the benthic environment that they colonize (Strayer et al., 1999; Strayer, 2009). Considerable research has been done into how zebra mussels affect benthic macroinvertebrates in lentic systems. Wisenden and Bailey (1995) found that in Lake Erie, zebra mussels at a turbulent site increased the abundance of amphipods due to microhabitat stability and a steady food supply, although the abundance of midges, caddisflies, and snails decreased as a result of the mussels. Ricciardi et al. (1997) observed that zebra mussels increased the number of macroinvertebrates (deposit-feeding organisms, small predatory invertebrates, and small gastropods) in lakes and canals on the St. Lawrence River system, due to habitat complexity (shell architecture) and the increase in organic matter the mussels bio-deposit in their beds. However, the zebra mussel colonies reduced biodiversity, displacing certain taxa (large snails and large filterers) that were prevalent before invasion (Ricciardi et al., 1997). Horvath et al. (1999) found similar results in Christiana Creek (a lake outlet); zebra mussels increased certain types of macroinvertebrates due to the complex substrate the mussel shells create.

Somewhat less research has focused on how zebra mussels affect river systems, although this topic has received considerable attention more recently (see Caraco et al., 1997; Horvath et al., 1999; Strayer et al., 2004; Bartsch et al., 2005; Strayer and Malcolm, 2007; Ward and Ricciardi, 2007). Most studies of this nature have been done on large river systems like the Hudson River or St. Lawrence River system. As these two rivers were some of the earliest invaded by zebra mussels, the studies from these rivers have helped to shape our understanding of what to expect in a newly invaded system; such as how zebra mussels affect macroinvertebrate communities (Strayer et al., 1998), fish communities (Strayer et al., 2004), native unionid communities (Ricciardi et al., 1996; Strayer and Malcolm, 2007), and the aquatic environment in general (Strayer et al., 1999; Jones and Ricciardi, 2005; Strayer, 2009).

Zebra mussels were discovered in the Muskegon River, MI in 2000, with a density of 8500 m^{-2}, and by 2001 had increased to 25,000 m^{-2} (M. Luttenton, unpublished data). Fuentes (2003) suggested that initially, zebra mussels were introduced into Croton Reservoir (a dam on the Muskegon River) by boaters and subsequently established populations downstream of the dam. Zebra mussels reduced phytoplankton biomass, which likely reduced available food sources to downstream communities, leading to shifts in invertebrate communities (Fuentes, 2003). The most profound shifts were seen in the family Hydropsychidae, with densities of *Hydropsyche* plummeting throughout the river, while *Cheumatopsyche* increased at the Croton sample site, but were reduced at the other sample locations (Luttenton et al., 2006).

The current studies were conducted to better understand how zebra mussel densities/biomass affect benthic macroinvertebrate communities. Specifically, I wanted to investigate macroinvertebrate composition and density, as well as classify the current macroinvertebrate community in the Muskegon River and Bigelow Creek, a tributary of the Muskegon River. I also sought to examine how the present macroinvertebrate communities have changed from the historical, pre-zebra mussel invasion macroinvertebrate communities studied by Godby (2000) in the Muskegon River and Bigelow Creek, Michigan.

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CHAPTER II

THE RELATIONSHIP BETWEEN MACROINVERTEBRATE COMMUNITIES AND THE INVASIVE ZEBRA MUSSEL (*DREISSENA POLYMORPHA*) IN THE MUSKEGON RIVER, MI, BELOW CROTON DAM

ABSTRACT

Zebra mussels invaded the Muskegon River via Croton Dam reservoir in the early 2000s and have changed the river ecosystem drastically in ways such as water-clarity, plankton reductions/taxa modifications, and substrate alterations. These environmental changes have had impacts on the macroinvertebrate community; in order to characterize these changes, thirteen benthic samples representing a range of zebra mussel densities were taken in one area of the Muskegon River, downstream of Croton Dam. Total macroinvertebrate density had no significant relationship with zebra mussel density or biomass. Positive significant relationships were found with Turbellaria and increasing zebra mussel density and biomass. Commonly affected macroinvertebrate taxa such as Amphipoda, Gastropoda, Chironomidae, and Hydropsychidae had no significant relationship with zebra mussels. No macroinvertebrate taxa significantly decreased because of zebra mussel density/biomass, which may indicate that macroinvertebrates are responding more to the sample environment than to the zebra mussels themselves.

INTRODUCTION

Zebra mussels (*Dreissena polymorpha*) were introduced into the Great Lakes around 1986 through ballast water discharge into Lake St. Clair from European ocean-crossing vessels (Griffiths et al., 1991). Since then, zebra mussels have spread across North America and have irreversibly changed the ecology of the Laurentian Great Lakes. Zebra mussels have caused economic damage in excess of $1 billion per year due to declines in commercial and recreational fisheries, impacts to water and power facilities, loss of tourism, and boating damages, as well as other similar problems (Pimentel, 2005; Connelly et al., 2007; Strayer, 2009). The zebra mussel invasion has also caused ecological damage; zebra mussels increase greenhouse gas emissions (Svenningsen et al., 2012), outcompete native fauna (Strayer and Malcom, 2007; Strayer 2009), reduce phytoplankton and zooplankton populations, and cause blooms of toxic cyanobacteria (Caraco et al., 1997; Vanderploeg et al., 2001; Miller and Watzin, 2007;Fishman et al., 2009; Higgins and Vander Zanden, 2010).

Many of these changes are due to the fact that zebra mussels are prodigious feeders, with a single zebra mussel able to filter up to 1 $L \cdot day^{-1}$ (Snyder et al., 1997) which will increase water clarity and light penetration, allowing macrophytes to grow excessively and spread to locations in a waterbody that they could not previously colonize (Caraco, 2000; Sabater et al., 2008). Nutrient ratios can shift as phytoplankton decline; phosphorus and soluble nitrogen may increase, although not consistently due to feeding times/rates of the zebra mussels (Fishman et al., 2009). Trophic structure may be altered due to changes at the base of the aquatic food chain leading to declines in many groups of herbivores (Strayer, 2009).

Zebra mussels also act as ecosystem engineers. They change benthic substrates by adding habitat complexity via their shell architecture and clumped distribution, providing shelter from predators, altering flow, and moving energy from the water column to the benthos via their waste (Ricciardi et al., 1997, Horvath et al., 1999). These habitat changes affect many macroinvertebrate communities. For example, certain macroinvertebrate taxa (such as gastropods, flatworms, and Ephemeropterans) seem to increase in abundance after a zebra mussel invasion (see Wisenden and Bailey, 1995, Ricciardi et al., 1997, Ward and Ricciardi, 2007). In contrast, native unionids are outcompeted for resources, or are directly fouled by zebra mussels colonizing on them, which interfere with feeding, movement, and reproduction. This leads to a noticeable loss in abundance and density (Strayer, 1999).

Studies that have investigated the effects of zebra mussels have reported significant changes in both structure and function of river systems (Ricciardi et al., 1997; Strayer et al., 1998; Horvath et al., 1999; Strayer et al., 2004). Our understanding of how zebra mussels affect rivers is still relatively limited, particularly for moderate-size rivers. This is the case for many impounded Michigan rivers, which have seen zebra mussel invasions in the past decade, and which are an important economic resource for many areas through recreation, sport, and aesthetics.

Zebra mussels were found in 2000 in the Muskegon River, Michigan, a large impounded river system (Fuentes, 2003). By 2001, zebra mussel densities below Croton Dam on the Muskegon River reached approximately 25,000 m^{-2} (Fuentes, 2003), and changes in macroinvertebrate communities were linked to this increase (Luttenton, personal communication). The greatest densities of zebra mussels are found in a 2 km section below Croton Dam, although there are small, isolated pockets of zebra mussels further downstream. The potential impacts on the Muskegon River are of particular concern given the very popular sport fisheries. For example, the U.S. Environmental Protection Agency states the Muskegon

River fishery is worth $5 million annually (EPA, 2008). The objectives of this study were to determine the relationship between zebra mussel densities/biomass and benthic macroinvertebrate composition and density in the Muskegon River near Croton Dam.

METHODS

Study Area

The Muskegon River, one of the largest rivers in Michigan, is 341 km long, has a watershed of approximately 6086 km^2, and has approximately 94 tributaries (O'Neal, 1997). The river is regulated by a series of three impoundments: Rogers Dam, Hardy Dam, and Croton Dam, which are ordered from upstream to downstream. Average discharge was 55.01 $m^3 \cdot s^{-1}$ in November and December of 2011 at Croton Dam (US Geological Survey, 2013).

My sampling site was located in a wadeable run habitat approximately 600 m downstream of Croton Dam (Figure 1). This sample site was chosen because there was relatively little human disturbance at this site compared to areas closer to the dam. The site had an average depth of 0.39 m and an average velocity of 0.14 $m \cdot s^{-1}$. River width at this location was approximately 78 m on December 1, 2011. The substrate consisted primarily of cobble and gravel, and the sample quadrats had physical and chemical characteristics that were relatively similar (Table 1).

Field Sampling

To evaluate the relationship between zebra mussel densities and macroinvertebrate community composition, I collected 13 benthic samples from a single study reach on December 1, 2011. Within the reach, sampling sites were randomly chosen from a 50 m long by 2 m wide zone that was parallel to shore. Benthic samples were collected by placing a 0.25 m^2 x 0.25 m^2 quadrat on the substrate and removing all of the sediment within the quadrat to a depth of approximately 2 cm. A 150 µm mesh D-frame net was placed directly downstream of the quadrat as the substrate was collected. In the field, the macroinvertebrates, algae, and zebra mussels were removed from the collected rocks. The rocks were then washed with ethanol over a 212 µm sieve to detach any macroinvertebrates that were not removed by forceps. The macroinvertebrates, algae and zebra mussels collected were placed in 95% ethanol.

A YSI multiparameter water quality sonde (model 556 MPS) was used to measure dissolved oxygen, percent saturation, pH, conductivity, and temperature directly above the substrate within each sampling quadrat. Sensors were calibrated the night before field sampling took place. I measured flow velocity at a point halfway between the surface and benthos in each quadrat using a Marsh-McBirney Flo-Mate™ (model 2000) flowmeter. A qualitative benthic substrate analysis (percentage) was done within each 0.25 m^2 x 0.25 m^2 quadrat for substrate types, and included: cobble, gravel, zebra mussel hash, and sand.

Laboratory Procedures

I used an elutriation method to separate most of the macroinvertebrates from the residual substrate collected. A sample was poured into a tray and 2 – 4 cm of water was added, depending on the amount of substrate in the sample. The sample was gently mixed by hand until most organic particles were suspended in the water. The suspension was then gently decanted from the tray through a 212-µm sieve. This process was repeated a total of four times to remove most macroinvertebrates from the substrate. The substrate was then examined under a Nikon SMZ1500 dissecting scope to remove zebra mussels and any macroinvertebrates that may have clung to the substrate. The macroinvertebrates were identified to the lowest level reasonable, usually to order or family; Hydropsychid caddisflies were identified to genus (using Merritt et al. 2008), because hydropsychids accounted for a significant portion of the community. Samples were analyzed using a Nikon SMZ1500 dissecting scope. Zebra mussels were counted and assigned to one of three size categories: small (≤7 mm); medium (7.01 – 13 mm); or large

(≥13.01 mm). Biomass of each zebra mussel size-category was then measured on a Mettler Toledo NewClassic MF scale that is accurate to thousandths of a gram.

Community Indices and Statistical Analyses

For each quadrat, I calculated taxa richness, density, Shannon-Wiener diversity, and Pielou's evenness index (eveness). Evenness and the Shannon-Wiener diversity index were calculated following the methods presented in Merritt and Cummins (2006).

Regression analyses were performed to detect relationships between the total density of macroinvertebrates and densities of specific macroinvertebrate taxa, and zebra mussel densities or biomass. Total macroinvertebrate, Chironomidae, Simuliidae, and Turbellaria densities were log transformed to meet normality assumptions (Shapiro-Wilk test). Gastropod and amphipod data were normally distributed. I used a Spearman Rank correlation to analyze Oligochaeta density data, which could not be normalized. For all statistical tests, significance was judged at $\alpha=0.05$. All analyses were done using R software, version 2.14.1 (R Development Core Team, 2011).

Multivariate canonical correspondence analysis (CCA) was used to evaluate relationships among macroinvertebrate taxa densities and zebra mussel biomass, dissolved oxygen, temperature, flow, and depth. Distance scaling was used to observe associations between the environmental vectors and macroinvertebrate taxa. Taxa included in this analysis were Turbellaria, Simuliidae, Hydropsychidae, Gastropoda, and Oligochaeta. The environmental variables used in the analysis were not correlated to one another (established using a matrix scatterplot).

RESULTS

A total of 35 macroinvertebrate taxa were found (excluding zebra mussels) in the thirteen samples. Sample richness ranged from 18 to 31 (Table 2). Shannon-Wiener Diversity values ranged from 1.119 to 2.185, and evenness values ranged from 0.387 to 0.742 (Table 2). However, the greatest taxa richness did not correspond to the highest diversity index value or greatest evenness (Table 2).

Total macroinvertebrate density varied widely across sample quadrats ranging from 5024 to 51,504 m^{-2}, with an average density (±SE) of 16,689±3209 m^{-2} (Figure 2). In contrast, zebra mussel densities (Table 2, Figure 2) were less variable, ranging from 464 to 3424 m^{-2}, with an average of 1319±217 m^{-2}. Zebra mussel biomass (Table 2) ranged from 17.60 to 172.75 $g \cdot m^{-2}$, with an average biomass of 70.00±12.82 $g \cdot m^{-2}$. Zebra mussel density and zebra mussel biomass was significantly correlated (Spearman Rank test, $\rho=0.90$, $p<0.0001$), however I have used both density and biomass in my analyses because some taxa were correlated with one term more than the other. There was no significant relationship between total macroinvertebrate densities (log transformed, excluding Simuliidae and Turbellaria, as they were found to be closely correlated with zebra mussels) and zebra mussel biomass ($p=0.325$, $R^2=0.087$) (Figure 3a) nor between total macroinvertebrate density and zebra mussel density ($p=0.172$, $R^2=0.162$) (Figure 3b).

Excluding zebra mussels, five taxa accounted for the majority of the invertebrates collected during the study (see Figure 7). Chironomidae were most abundant, with densities ranging from 1440 to 31,472 m^{-2} and an average density of 10,227±2062 m^{-2}. Simullidae were the second most abundant taxa, and had densities ranging from 208 to 6336 m^{-2} with an average density of 1139±449 m^{-2}. Turbellarians ranged from 368 to 4320 m^{-2} with an average density of 1050±288 m^{-2} whereas average Hydropsychidae density was 920±281 m^{-2} with densities ranging from 144 to 3312 m^{-2}. Oligochaete density ranged from 160 to 3696 m^{-2} with an average density of 890±330 m^{-2}.

Total constrained variability explained with CCA was 74.2 %. The first two axes of the CCA explained 62.4% of the variability (Figure 4). Both axes were controlled by three main vectors: dissolved oxygen, flow, and zebra mussel biomass (Axis 1: eigenvalue=0.244, 48.2% of variation, Axis 2: eigenvalue=0.072, 14.1% of variation, Table 3). Axis 1 represents a gradient of increasing zebra mussel biomass and decreasing dissolved oxygen, depth and flow. Axis 2 was interpreted as a gradient of increasing dissolved oxygen and decreasing flow, depth and zebra mussel biomass. There seems to be an association between the zebra mussel biomass vector and Simuliidae (Figure 4). Hydropsychidae seemed to be loosely associated with dissolved oxygen. Dissolved oxygen had an inverse relationship with zebra mussel biomass; depth was uncorrelated with zebra mussel biomass (Figure 4).

Of the five dominant taxa (see Figure 7), only one was significantly associated with zebra mussel density and/or biomass. There was a significant positive linear relationship between Turbellaria density and both zebra mussel biomass ($p=0.004$, $R^2=0.543$) and zebra mussel density ($p=0.0002$, $R^2=0.720$) (Figure 5). There was a non-significant positive linear relationship between Simuliidae abundance and zebra mussel biomass ($p=0.055$, $R^2=0.294$) as well as zebra mussel density ($p=0.053$. $R^2=0.298$) (Figure 6). Chironomidae and Hydropsychidae densities had no relationship with zebra mussel biomass ($p=0.351$, $p=0.992$) or zebra mussel density ($p=0.220$, $p=0.908$). Oligochaeta likewise had no significant correlation with zebra mussel density ($p=0.799$, $\rho= 0.079$) or zebra mussel biomass ($p=0.816$, $\rho=0.071$).

Amphipods and Gastropods were not considered common taxa during this study, although they are commonly correlated with zebra mussels. Amphipods showed no significant relationship with zebra mussel density (p=0.647, R^2=0.019) or zebra mussel biomass (p=0.888, R^2=0.001), but both tests showed a slight negative trend. Gastropoda had a positive but non-significant relationship with zebra mussel biomass and density (p=0.234, p=0.088 respectively). There was also no relationship between algal biomass and zebra mussel biomass (p=0.870) or density (p=0.787).

Relative abundance of the five dominant taxa also varied across sample sites (Figure 7). Chironomidae accounted for the greatest proportion of individuals in all samples ranging from 28% (Sample 11) to 75% (Sample 1). Turbellaria comprised 2% (Sample 4) to 26% (Sample 11) of samples. Hydropsychidae abundances ranged from 1% (Sample 4) to 15% (Sample 12). Oligochaetes composed 1% (Sample 3) to 21% (Sample 4) of samples. Simuliidae abundances ranged from 1% (Sample 2) to 12% (Sample 13). There was no obvious visual relationship between the relative abundance of the five dominant macroinvertebrate taxa and zebra mussel density (Figure 7).

DISCUSSION

Previous studies have generally identified changes in macroinvertebrate communities in response to the introduction of zebra mussels. The intent of this study was to evaluate the relationship between macroinvertebrate communities and the abundance of zebra mussels more than 10 years after initial colonization by zebra mussels. Zebra mussel populations in the Muskegon River have entered a cyclic phase, shifting from relatively high to relatively low densities. It appears that this study was conducted when zebra mussels were at a relatively low population density. I found only a weak association between zebra mussel density (or biomass) and macroinvertebrate densities, thus, they may have little to no clear influence on macroinvertebrates at low population densities. Indeed, at low zebra mussel densities, substrate composition and other environmental factors may be more important in determining macroinvertebrate community density and composition in the Muskegon River.

Total macroinvertebrate density had no significant relationship with zebra mussel density or biomass (Figure 3), which contrasts with results of other studies. Increases of total macroinvertebrate densities in zebra mussel beds are common and have been observed in many studies in both rivers and lakes (Botts et al., 1996; Horvath et al., 1999; Strayer et al., 1999; Mayer et al., 2002; Ward and Ricciardi, 2007). For example, Horvath et al. (1999) found significantly greater abundances of macroinvertebrates on higher (1000 m^{-2}) zebra mussel density rocks, than on lower densities in Christiana Creek, MI. However, Christiana Creek's substrate is composed mostly of sand and small gravel so the addition of zebra mussel covered rocks added a great deal of stable substrate allowing a strong reaction from the macroinvertebrates in the river (Horvath et al., 1999). Conversely, the substrate in the Muskegon River has been stable, and composed mostly of cobble, gravel, and boulders pre- and post-zebra mussel invasion, which may have explain the diminished response of some macroinvertebrates to zebra mussels.

There were five dominant taxa present in the Muskegon River at my sample reach, as compared to three taxa in Christiana Creek, MI. In my study reach, Chironomidae was the most abundant taxa present, and Simuliidae had extensive numbers as well (Figure 7). In contrast, within Christiana Creek, MI, Hydridae, Trichoptera, and Gastropoda were the most abundant taxa present in zebra mussel beds, while Simuliidae was a rare species (Horvath et al., 1999). There are ample differences between Christiana Creek and Muskegon River. For example, the zebra mussel beds added a lot of solid substrate to the unstable benthos of Christiana Creek. Outside of the zebra mussel beds on the benthos, Christiana Creek had a substrate consisting of small gravel and depositional sediments (such as sand) (Horvath et al., 1999), whereas in the Muskegon River, the substrate was mostly gravel, cobble, and boulders. Other differences include the size of the rivers; Christiana Creek had a channel width of 15 m, and had discharge of 2.0 m^3/s (Horvath et al., 1999), while the Muskegon River had an average discharge of 52.5 m^3/s (on the sample date), and had a channel width of 78 meters. The physical differences previously mentioned, as well as others such as canopy cover (Hawkins et al., 1982), salinity (Piscart et al., 2005), and human activity (Woodcock and Huryn, 2006; Yates and Bailey, 2010) between streams such as Christiana Creek and Muskegon River, will accommodate different macroinvertebrate communities. Nevertheless, Horvath et al., (1999) did find similar patterns with higher macroinvertebrate abundance with increasing zebra mussel abundance. The data presented in this study revealed that most macroinvertebrate taxa in this sample location on the Muskegon River tended to increase (although most increases were not significant) at a certain point with zebra mussel density or biomass. However, more samples would help broaden the range of macroinvertebrate and zebra mussel densities.

Zebra mussels create a large amount of organic matter through their daily metabolic activities, creating layers of feces and pseudofeces in the bed. Many filter-feeding and detrital-feeding macroinvertebrates are able to use the mussels' waste as an abundant food-source (Ricciardi et al., 1997; Gergs and Rothhaupt, 2008a). Predatory taxa also utilize the zebra mussel beds for a high density of prey items to feed on (Stewart et al., 1998). Zebra mussels emit kairomones, which may attract some macroinvertebrate taxa (Gergs and Rothhaupt, 2008b).

Both the biotic and physical factors in a zebra mussel bed add important complexity to benthic substrates and can lead to increases in macroinvertebrate taxa richness, diversity, and density (Ricciardi et al., 1997; Thayer et al., 1997; Stewart et al., 1998; Ward and Ricciardi, 2007). Every waterbody is different, however there are some common taxa that seem to adapt to zebra mussel beds. Botts et al. (1996) found that turbellarians, amphipods, chironomids, oligochaetes, and hydrozoans increased when zebra mussel shells (dead or alive) were present. Thayer et al. (1997) observed more of an increase in oligochaetes and crustaceans in enclosed ponds with zebra mussels than ponds without zebra mussels. In a meta-analysis of 47 sites, Ward and Ricciardi (2007) discovered that after a zebra mussel invasion, the most common taxa to increase in density were Hirudinea, Turbellaria, and Ephemeroptera.

In this study, Turbellaria was the only taxa to significantly increase with zebra mussel density/biomass (Figure 5). Simuliidae densities had a p-value close to α with both zebra mussel densities and biomass, which may indicate an ecological significance even if the tests are not statistically significant. An abundant food source is likely the reason that these taxa were able to flourish in the zebra mussel beds. Fuller et al. (1988) found that bacteria growing in organic matter were an important energy source for *Simulium vittatum*, allowing it to grow and complete its life cycle in a very short time. The predatory Turbellaria thrives in zebra mussel beds because the beds allow for abundant prey and a refuge from other predators (Stewart et al., 1998).

Many past studies have found a positive relationship between amphipod densities and zebra mussel densities (Ricciardi et al., 1997; Stewart et al., 1998; González and Downing, 1999; Gergs and Rothhaupt, 2008b). However, the current study found low numbers of amphipods in all samples and they were shown to have no significant interaction with zebra mussels. Because of the diversity of microhabitats in the Muskegon River, these findings should not be extrapolated to other areas unless sites are similar in substrate and flow to my sample area.

The increase of Turbellaria (and Simuliidae although not significantly) associated with an increase in zebra mussel density/biomass could have trophic ramifications. Prior to ZM invasion, steelhead parr were found to consume mainly amphipods (41.8%), and trichopterans (26.6%), of which most were hydropsychids (17.3%), and other groups (14.3%) which were mainly cladocerans, terrestrial items, and unidentifiable items (Giuliano, 2011). Parr diet post-mussel invasion (2003) changed to mainly dipterans (50.1%, which were mainly chironomids), amphipods (30.4%), and ephemeropterans (7.2%) (Giuliano, 2011). Turbellaria were not a part of the steelhead parr diet at all either pre- or post-zebra mussel invasion, and although dipterans are a large part of parr diet, simulids seem to be a small portion. However, Giuliano (2011) sampled during a different season (summer, fall) from this study (winter), which may account for differences in abundance of taxa.

An ecological threshold may exist within the Muskegon River between the macroinvertebrate and zebra mussel communities. An ecological threshold is a turning point in an ecosystem where small changes in the environment (such as a certain density of zebra mussels) will produce large responses (such as the sudden increase in macroinvertebrate densities) in the surrounding area (Groffman et al., 2006). There was no apparent effect of zebra mussel densities affecting the macroinvertebrate densities until zebra mussel densities were approximately 1.5 times greater than the next highest zebra mussel density (Figure 2). This could denote that until the density of zebra mussels is approximately 3500 per m^2, or have a biomass of approximately 178 $g \cdot m^{-2}$ that the macroinvertebrate community may not have any (or a muted) response to the changes in the habitat in the Muskegon River. This threshold effect is suggested by one high-density sample (Sample 13), and is problematic for making more general conclusions about the river.

Macroinvertebrates in Christiana Creek, MI seemed to have a threshold response in zebra mussel beds; macroinvertebrate densities had no significant difference on control (0 zebra mussels), low (200 mussels m^{-2}), and medium (500 mussels m^{-2}) zebra mussel densities (Horvath et al., 1999). However, macroinvertebrate response to high zebra mussel densities (1000 mussels m^{-2}) were significantly different from the other treatments (Horvath et al., 1999), and may have shown an ecological threshold in Christiana Creek.

Continuing research will be necessary to improve and clarify the patterns seen in this study. Additional quadrat samples from the study area on the Muskegon River would help to define macroinvertebrate communities in more detail. More quadrat samples with high zebra mussel density (3500 per m^2 or greater) would aid in identifying an ecological threshold between zebra mussels and macroinvertebrates in the Muskegon River. The use of other sampling areas, although not comparable to each other, would assist in illustrating if these relationships occur all over the Muskegon River or are unique to one area. Sampling in a different season (such as summer and fall) in the same sampling area may produce different abundances of taxa, which may produce different relationships.

Conclusions

The macroinvertebrate communities in the Muskegon River have changed through time from pre- to post-zebra mussel invasion, and may continue to change and affect the trophic dynamics of the river. My analyses have shown that even at relatively low densities, zebra mussels in the Muskegon River may influence some macroinvertebrate taxa. Turbellarian densities had a significant positive relationship with both zebra mussel densities and biomass. Simuliidae had a positive but non-significant relationship with zebra mussel biomass and density, but still may have ecological significance. There was a non-significant positive relationship between Gastropoda and zebra mussel biomass and density. Amphipods, chironomids, hydropsychids, and algae had no relationship with either zebra mussel density or biomass. Five macroinvertebrate taxa dominated the zebra mussel substrate in my sample site in the Muskegon River: Chironomidae, Simuliidae, Oligochaeta, Hydropsychidae, and Turbellaria. An ecological threshold may exist in the Muskegon River between zebra mussel densities and macroinvertebrate densities; however, only one sample (Sample 13) is responsible for this potential threshold and more samples would help to clarify this relationship.

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Table 1. Physical and chemical characteristics of macroinvertebrate sample locations on the Muskegon River, near Croton, MI. Samples were taken on December 1, 2011. Depth is in (m), Flow is in (m·s^{-1}), Temp is temperature (°C), Cond is conductivity (µS·cm^{-1}), DO% is percent dissolved oxygen, DO mg is dissolved oxygen concentration (mg·L^{-1}).

Sample	*Depth*	*Flow*	*Temp*	*Cond*	*pH*	*DO%*	*DO mg*
1	0.396	0.30	6.31	0.381	8.02	101.9	12.55
2	0.396	0.46	6.57	0.377	7.31	107.5	13.16
3	0.366	0.41	7.57	0.377	8.31	108.5	14.16
4	0.305	0.45	6.66	0.377	7.31	106.0	12.93
5	0.411	0.49	6.52	0.378	7.51	103.3	12.66
6	0.366	0.51	6.66	0.377	7.35	101.1	12.36
7	0.427	0.51	6.57	0.378	7.41	100.3	12.30
8	0.366	0.37	6.57	0.377	7.28	103.7	12.70
9	0.366	0.40	6.62	0.377	7.28	105.5	12.89
10	0.472	0.36	6.36	0.380	7.62	98.8	12.16
11	0.427	0.46	6.32	0.381	7.80	98.7	12.17
12	0.442	0.53	6.61	0.377	7.39	104.0	12.71
13	0.335	0.41	6.67	0.377	7.36	101.3	12.39
Mean±SE	0.390±0.01	0.435±0.01	6.616±0.09	0.378±0.0	7.535±0.09	103.12±0.87	12.70±0.15

Table 2. Richness (R), Shannon-Wiener Diversity Index (H'), Evenness (J) values for macroinvertebrates (excluding zebra mussels) in each sample taken from the Muskegon River, December 2011. Zebra mussel density (m^{-2}), and zebra mussel biomass ($g \cdot m^{-2}$) are given for each sample. Sample numbers correspond to Figure 2.

Sample	*R*	*H'*	*J*	*ZM Density*	*ZM Biomass*
1	18	1.119	0.387	464	17.60
2	24	2.134	0.672	464	18.59
3	23	1.838	0.586	608	37.22
4	22	1.409	0.456	848	18.62
5	22	1.668	0.540	1072	57.36
6	24	1.813	0.570	1104	67.12
7	22	1.358	0.439	1120	43.20
8	23	1.307	0.417	1248	107.31
9	24	1.524	0.479	1600	60.56
10	21	1.667	0.548	1680	116.26
11	19	2.185	0.742	1696	91.38
12	23	1.722	0.549	1824	102.05
13	31	1.343	0.391	3424	172.75
Mean±SE	22.8±0.86	1.622±0.09	0.521±0.03	1319.4±217.49	70.00±12.82

Table 3. Biplot scores of the vectors used in the canonical correspondence analysis.

Vector	*CCA 1*	*CCA 2*
ZM Biomass	0.3819	-0.3121
Algae	0.0665	0.1672
Depth	-0.5295	-0.8083
Flow	-0.3066	-0.1205
DO	-0.7020	0.6489

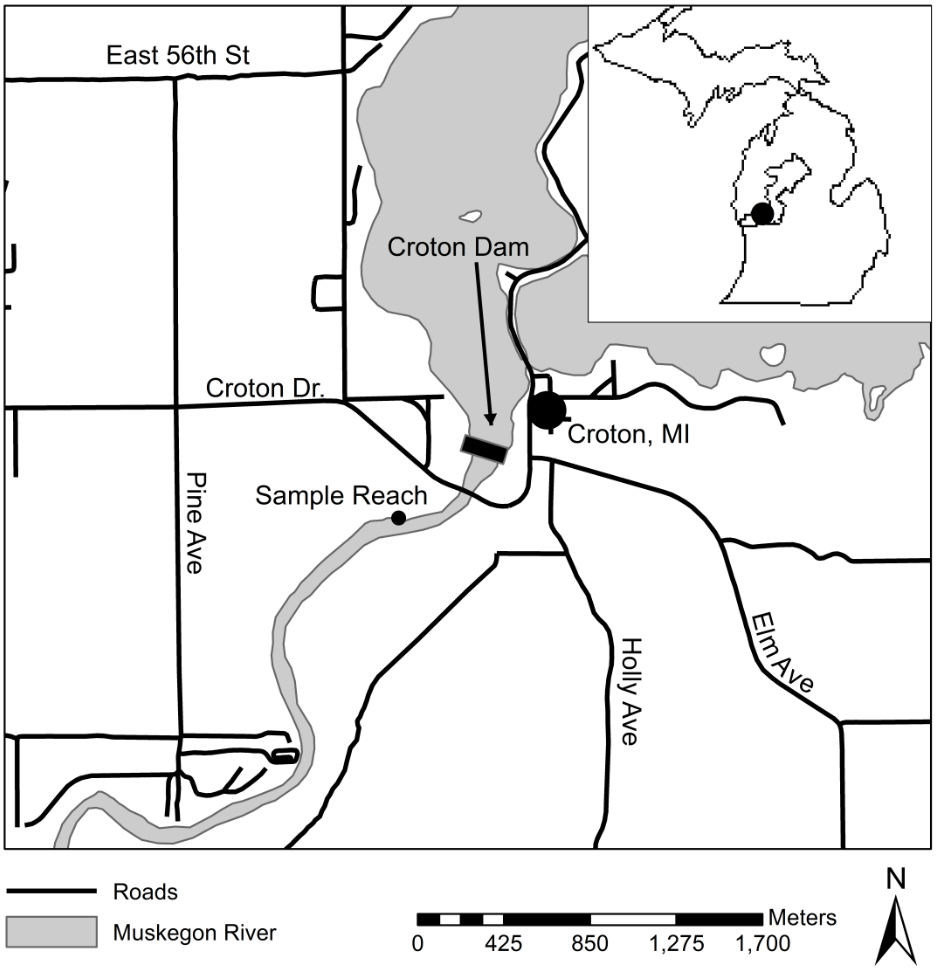

Figure 1. Macroinvertebrate sampling location on the Muskegon River in Croton, MI, approximately 600 river meters below Croton Dam.

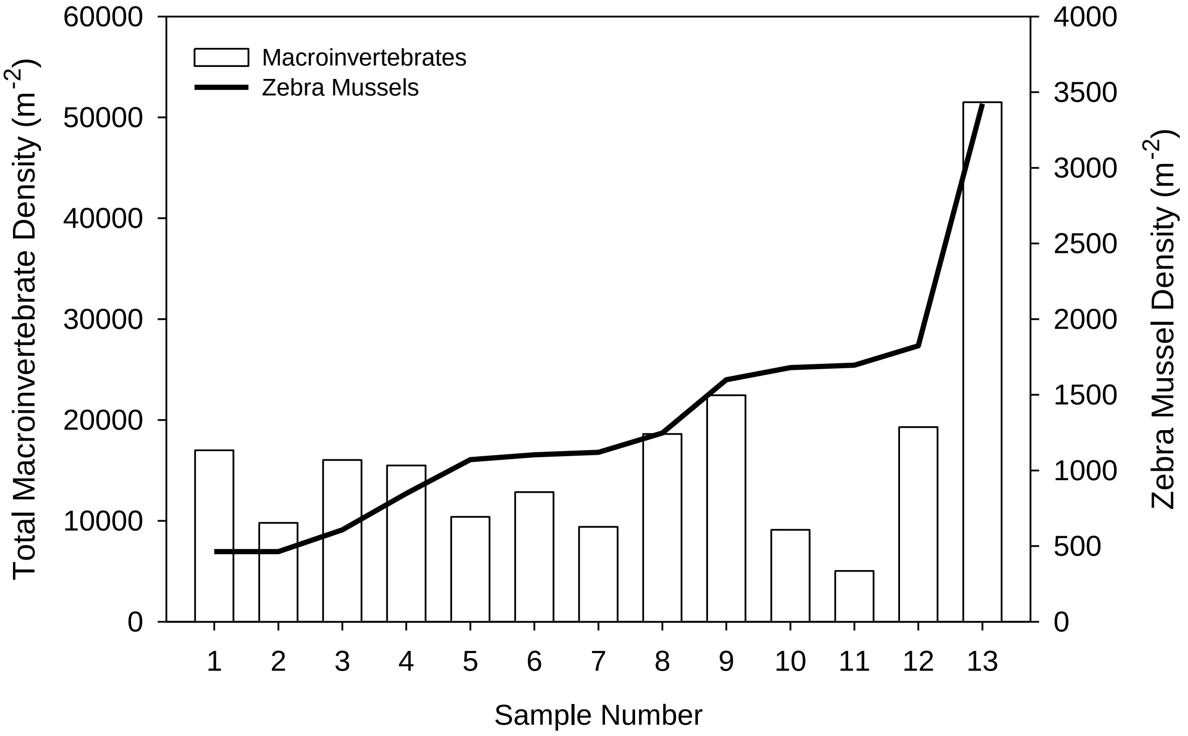

Figure 2. Total macroinvertebrate density (bars, left axis) and zebra mussel density (right axis) for thirteen samples collected from the Muskegon River near Croton, MI. Samples were collected December 1, 2011.

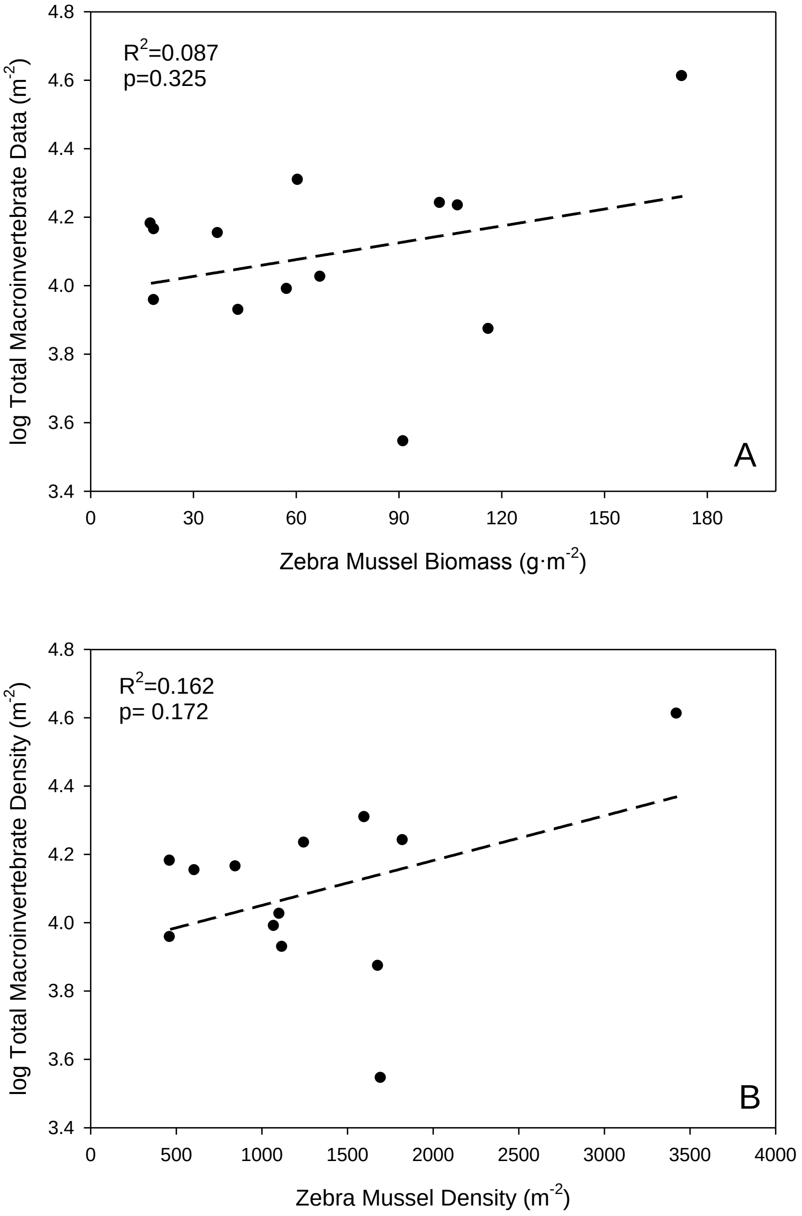

Figure 3. Regression plots of zebra mussel biomass (g·m^{-2}) (A) and density (m^{-2}) (B) against log-transformed total densities of macroinvertebrates. Simuliidae and Turbellaria densities were excluded from these regressions. Samples were collected from the Muskegon River near Croton, MI on December 1, 2011.

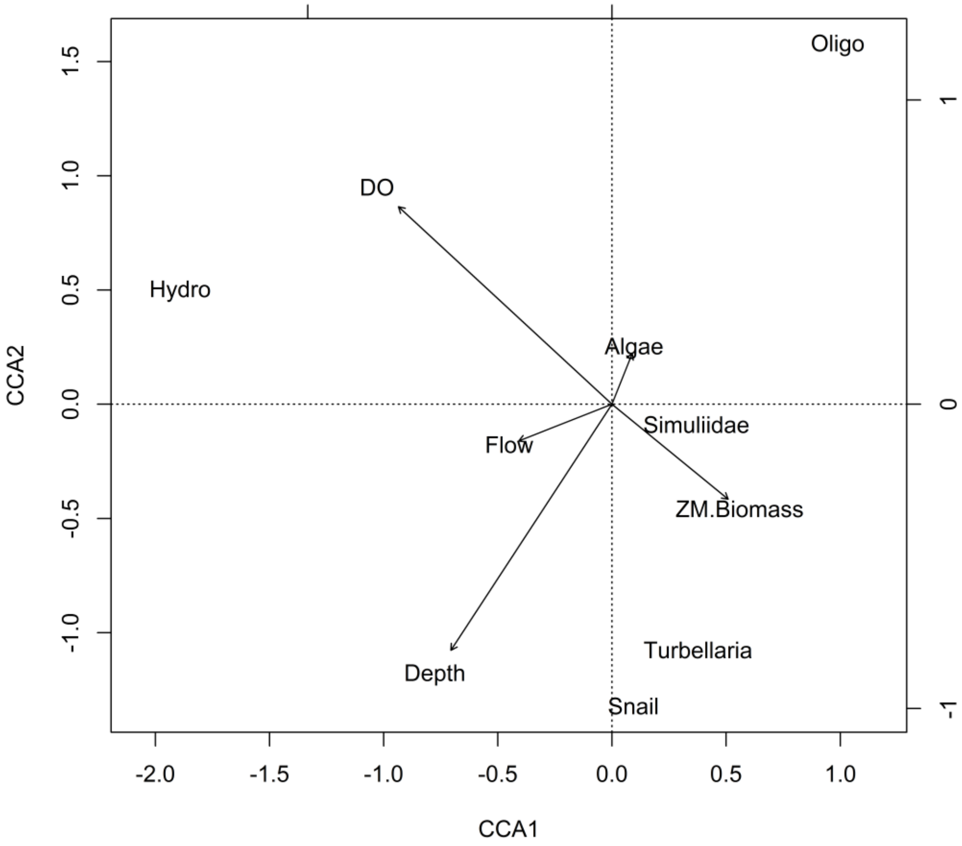

Figure 4. Canonical correspondence analysis (CCA) of taxa abundance and environmental variables. Data are from the Muskegon River on December 1, 2011. The taxa included are: Gastropoda (Snails), Oligochaeta (Oligo), Turbellaria, Simuliidae, and Hydropsychidae (Hydro).

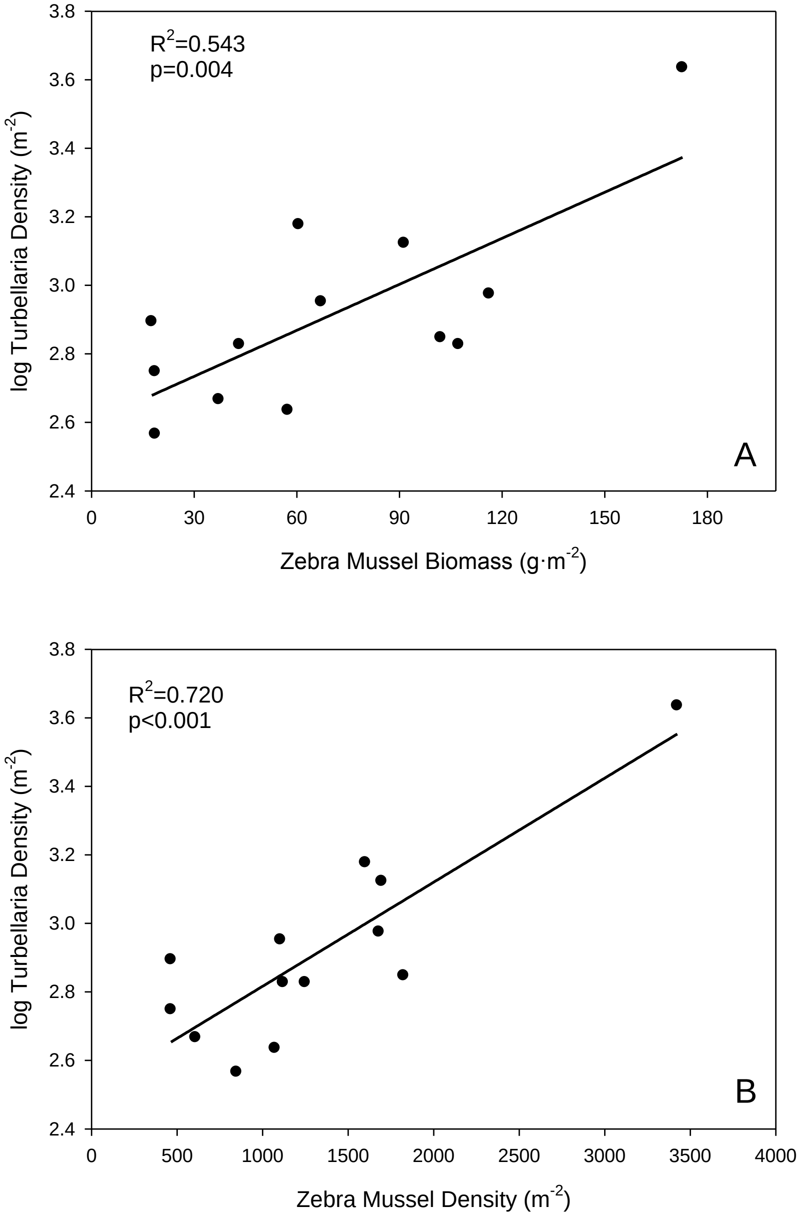

Figure 5. Regression plots of zebra mussel biomass ($g \cdot m^{-2}$) (A) and density (m^{-2}) (B) against log-transformed densities of Turbellaria. Samples were collected from the Muskegon River near Croton, MI on December 1, 2011.

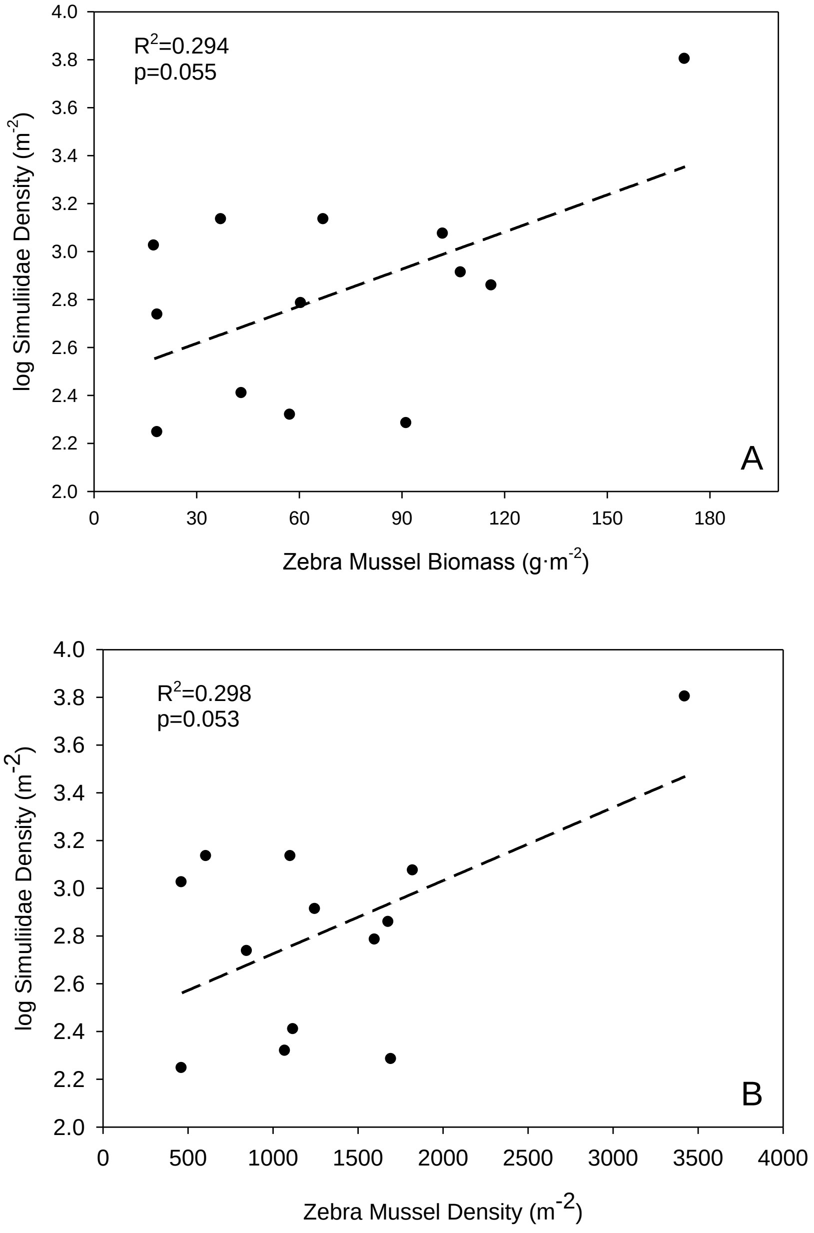

Figure 6. Regression plots of zebra mussel biomass (g·m^{-2}) (A) and density (m^{-2}) (B) against log-transformed densities of Simuliidae. Samples were collected from the Muskegon River near Croton, MI on December 1, 2011.

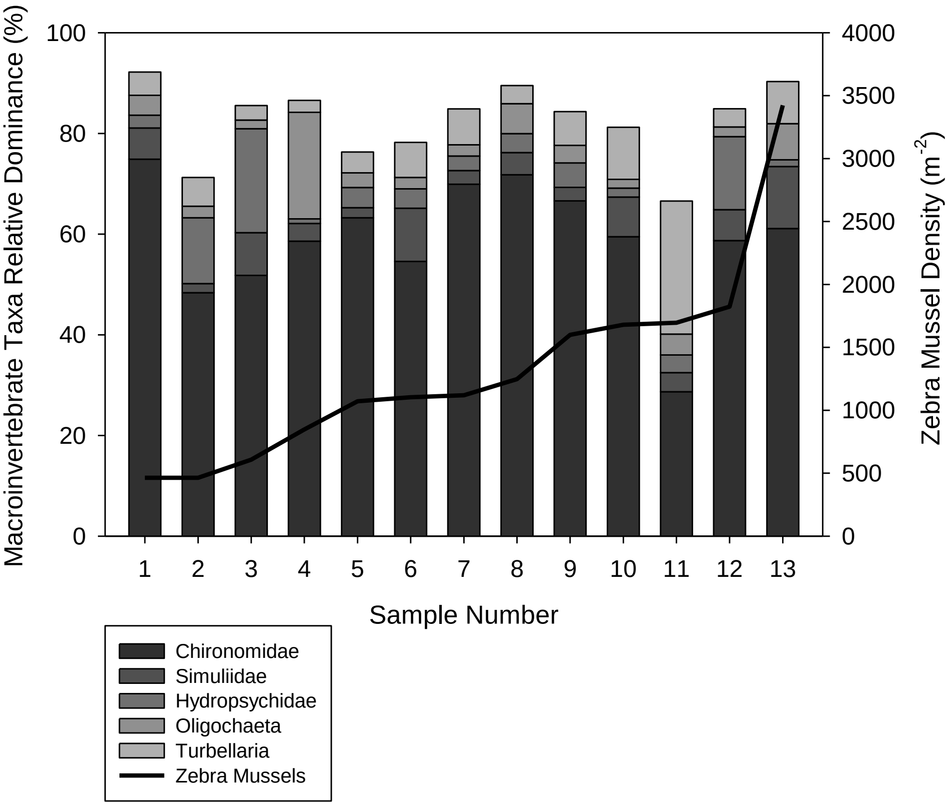

Figure 7. Relative abundance (bars) of the five dominant taxa found in the thirteen samples from the Muskegon River (left axis), and zebra mussel density in each sample is also shown as a line plot (right axis). Samples were collected on December 1, 2011 from the Muskegon River near Croton, MI.

CHAPTER III

MACROINVERTEBRATE COMMUNITIES IN THE MUSKEGON RIVER, MI AND IN BIGELOW CREEK, A COLD-WATER TRIBUTARY

ABSTRACT

Macroinvertebrate communities have shifted in richness, density, and diversity in the Muskegon River since 1998. The invasion of zebra mussels (*Dreissena polymorpha*) in the early 2000s has changed the Muskegon River drastically, leading to water clarification, substrate alterations, as well as a reduction and taxa modification of plankton. To distinguish some of the variation that has occurred in the macroinvertebrate community since 1998, both Hess and five-rock cluster sampling methods were used at six sample sites on the Muskegon River and two sample sites on Bigelow Creek, a cold-water tributary, for both summer and fall seasons. Macroinvertebrate community richness, EPT richness, Shannon-Wiener diversity, and evenness were calculated for each site, as well as zebra mussel densities. Hydropsychidae and *Cheumatopsyche* increases in the Muskegon River were the driving taxa in community changes from 1998 to 2011. In Bigelow Creek a shift in the taxa from *Protoptila* and Hydropsychidae to *Baetidae* and *Simuliidae* were responsible for the shift from 1998 to 2011.

INTRODUCTION

Aquatic macroinvertebrates are one of the most pervasive and ecologically diverse groups in freshwater systems; they encompass many different phyla including Mollusca, Arthropoda, Platyhelminthes, Annelida, and Nematoda. They are adapted to a range of aquatic ecosystems and contribute significantly to the structure and function of aquatic systems. Specifically, macroinvertebrates are found at multiple trophic levels and play a key role in processing organic matter. In some systems, macroinvertebrates may influence the structure of communities by functioning as a keystone species, and often facilitate the transfer of energy from primary producers to higher trophic levels. Recognizing the importance of macroinvertebrates, aquatic ecologists have placed a premium on understanding the role of macroinvertebrates in streams (Merritt and Cummins, 2006).

Due to their relative importance and their sensitivity to environmental factors, macroinvertebrates are often used as indicators of stream condition; as some taxa are quite intolerant of change, they can show degradation of habitat or habitat loss that other methods may not identify. Thus, macroinvertebrates may serve as surrogates for stream condition and many commonly used metrics (including functional feeding groups and EPT richness among others) have been developed (Barbour et al., 1999).

Numerous factors may cause shifts in macroinvertebrate communities. Changes in water quality, impoundments, loss of riparian vegetation, and exotic species have all been shown to alter macroinvertebrate communities (Lehmkuhl, 1979; Cummins and Klug, 1979; Quinn and Hickey, 1990; Leland and Fend, 1998; Lessard and Hayes, 2003; Santucci Jr. et al., 2005; Correia and Anastácio, 2008; Huff et al., 2008; Takao et al., 2008; Growns et al., 2009; Rosin et al., 2009; Kokeš, 2011). For example, the introduction of zebra mussels into the Muskegon

River corresponded to a decline in some invertebrate taxa such as Chironomidae and *Hydropsyche*, but led to a rise in *Cheumatopsyche* (Luttenton et al., 2006). Stewart et al. (1998) found that the three-dimensional habitat created by zebra mussels was important for the rise of certain macroinvertebrate taxa such as *Dugesia*, *Gammarus*, and *Hydridae*, but the organic matter created by the mussel beds was essential for other taxa such as *Physella*, and *Microtendipes*. In the Hudson River, New York, the benthic communities declined shortly after zebra mussels invaded (approximately 1990) (Strayer et al., 2011).

Streams, however, streams are often impacted my multiple factors. For example, the Muskegon River, Michigan has experienced numerous changes during the past 150 years. The legacy of several factors (logging, development, impoundments) continues to influence this system. In addition, several exotic species such as sea lamprey (*Petromyzon marinus*), rusty crayfish (*Orconectes rusticus*), spiny water flea (*Bythotrephies cederstromii*), curly pond weed (*Potamogetan crispus*), and Eurasian water milfoil (*Myriophyllum spicatum*) have become well-established members of the benthic community (Luttenton, personal observation). Unfortunately, pre-disturbance or pre-introduction data is not available for these factors, so estimating the overall impacts is difficult.

More recently, the introduction of new invasive species may complicate this already complex aquatic community. Specifically, zebra mussels (*Dreissena polymorpha*) were discovered below Croton Dam in 2000 (Luttenton et al. 2006) and round gobies (*Neogobius melanostomus*) were discovered in the Muskegon River below Croton Dam in 2011 (personal observation). In addition, the operators of Croton Dam (Consumers Energy) modified dam operation to reduce thermal loading below the dam. Fortunately, data collected just prior to the discovery of zebra mussels (2000) are available (Godby, 2000) and provide the opportunity to compare pre-invasion and post-invasion invertebrate communities.

The objectives of this study were to characterize current macroinvertebrate communities in the Muskegon River (altered) and Bigelow Creek (relatively unaltered) and to compare current macroinvertebrate communities to those present during the late 1990's (Godby, 2000). These data provide a unique opportunity to compare macroinvertebrate communities following several environmental changes over a relatively short temporal scale.

METHODS

Study Area

The Muskegon River watershed extends from mid-central to west central Michigan and incorporates about 6086 km^2 of land (Figure 1). The Muskegon River originates at Houghton Lake and Higgins Lake, and flows 341 km to Lake Michigan making it the second longest river in the state (O'Neal, 1997). With a drowned river mouth lake (Muskegon Lake) at its mouth, and roughly 94 tributaries, the Muskegon River system exhibits an extraordinary array of aquatic habitats (O'Neal, 1997). There are three hydroelectric dams in succession on the Muskegon River; Rogers Dam is the most upstream, then Hardy Dam, and finally Croton Dam. Croton Dam blocks the upstream movement of resident fish as well as adfluvial fish.

The study reach for this project extended about 22.5 km, and is located from Croton Dam on the Muskegon River to the town of Newaygo, at Henning Park (official name Ed H. Henning County Park) (Figure 1). This section of the Muskegon River reach has been divided into six strata based on a 1989 principal components analysis of stream substrate and riparian vegetation (Icthyological Associates, 1991, as used by Godby, 2000). The strata are defined as distinct habitats within the Muskegon River (Table 1) (Icthyological Associates, 1991, as used by Godby, 2000). Through this section the Muskegon River is approximately 50 meters wide and had an annual mean discharge of 48 m^3·s^{-1} in 2011 below Croton Dam. In the summer (June, July, August) the mean discharge was 49 m^3·s^{-1}, and in the fall (September October, November) the mean discharge was 44 m^3·s^{-1}. The physical and chemical characteristics (temperature, pH, conductivity, etc.) varied slightly among Muskegon River sample sites (Table 2). I also sampled Bigelow Creek, a small cold-water tributary of the Muskegon River that connects to the main channel just above the town of Newaygo (Figure 1). Bigelow Creek is approximately 5.3 meters across on average and had a discharge of 2 $m^3 \cdot s^{-1}$ (high-water) in late October 2011 at the mouth. The upstream site was dominated by sand, whereas the downstream site was dominated by gravel (Table 3). The riparian zone is intact at both sites and there are many areas of large woody debris in the stream. The upstream section of Bigelow Creek was warmer than the downstream section during the summer sampling period (Table 4).

Field Sampling

Macroinvertebrates were collected at six sites in the Muskegon River and two sites in Bigelow Creek (Figure 1). Muskegon River sites were partitioned between the 6 strata with one site in strata 1 (at the Croton boat launch), one site at the boundary between strata 1 and strata 2 (above the Pine Street access), two sites in strata 4 (upstream and downstream of the Thornapple access), and 2 sites in strata 5 (upstream and downstream of Henning Park). All Muskegon River sites were located in riffle areas. Bigelow Creek sites were located at 58th street, and at the mouth. Invertebrate communities were sampled during summer (late July to early August) and again in fall (early October to early November). Sampling sites and seasons correspond to the sample regime used by Godby (2000).

Macroinvertebrate samples were collected at each sample site following the protocol outlined by Godby (2000). I collected three replicate benthic invertebrate samples with a 33.5cm diameter Hess sampler (sample area of 0.881 m^2) with a 242 µm net at each of the 6 Muskegon River sites, (one in Stratum 1, one in Stratum 2, two in Stratum 4, and two in Stratum 5) and the two sites in Bigelow Creek on both sampling dates. Invertebrates were dislodged by disturbing the sediment and rocks to a two centimeter depth inside the sampler. In addition, three replicate five-rock cluster samples were collected at each of the six sampling sites. A 150 µm mesh D-frame net was placed downstream while each rock was retrieved so any invertebrates dislodged from the substrate would be caught. All macroinvertebrates, zebra mussels, and algae were removed from the rocks using forceps, and preserved in 95% ethanol. Chosen rocks were then washed with 95% ethanol over a 212 µm sieve to ensure all macroinvertebrates were removed from the rock. After picking, the rock clusters were placed into individual labeled bags.

A YSI multiparameter sonde (model 556 MPS) was used to measure dissolved oxygen percent and concentration, pH, conductivity, and temperature at each of the macroinvertebrate sampling sites. Flow velocity was measured at each sampling site using a Marsh-McBirney Flo-Mate™ (model 2000) portable flow meter.

Laboratory Procedures

I used an elutriation method to separate macroinvertebrates from the substrate collected with the Hess samples. A sample was poured into a tray and 2-4 cm of water was added, depending on the amount of substrate in the sample. The sample was gently disturbed by hand to suspend particles and macroinvertebrates in the water. The suspension was then gently decanted from the tray through a 212-µm sieve, with as little substrate as possible going into the sieve. This process was repeated a total of 4 times to remove most macroinvertebrates from the substrate. The remaining substrate was then examined microscopically to remove zebra mussels and any remaining macroinvertebrates. The macroinvertebrates were then identified to the lowest practical taxonomic level (using Merritt et al. 2008) and counted using a Nikon SMZ1500 dissecting scope. Rock surface areas were calculated using the aluminum foil method described in Lamberti et al. (1991).

Density, Diversity Indices, and Taxa Richness

Densities of each taxon were estimated for both the Hess samples and rock cluster samples. The sample method that generated the highest density estimate for a given taxon was then used to calculate total density (sample n=3). Generally, Hess samples were used to estimate the density of large, rare taxa and rock cluster samples were used to estimate smaller, common taxa. Macroinvertebrate densities, richness, diversity indices, and evenness were calculated using these estimates and are referred to as ‘density’, ‘richness’, ‘diversity’ or ‘evenness’ respectively in the tests where they are used. For each sample site and season, taxa richness, common taxa percentage, density, EPT (Ephemeroptera, Plecoptera, Trichoptera) richness, EPT index, Shannon-Wiener diversity, and Pielou’s evenness index (evenness) were calculated. The Shannon-Wiener diversity index (H') and evenness (J) were calculated following the methods presented in Merritt and Cummins (2006). I also determined the common taxa richness (CTR) of each site. I have defined CTR as the number of taxa that had ≥5% relative abundance at a site, as the few dominant taxa provided almost all of the percent composition. Taxa were considered to be rare if they accounted for <5% relative abundance.

EPT analyses followed methods described in Merritt and Cummins (2006). These analyses are based on the presumption that a high-quality aquatic system should have higher counts of Ephemeroptera, Plecoptera, and Trichoptera than a low quality system. The EPT richness is the total number of Ephemeroptera, Plecoptera, and Trichoptera species in each sample. The EPT index is calculated by dividing the EPT richness by the total species richness in a sample.

Functional Feeding Group Metrics

The ecological function of river systems can be characterized by assigning each macroinvertebrate taxon to a functional feeding group (FFG) (Barbour et al. 1999, Merritt and Cummins 2006, and Merritt et al. 2008). I chose to use the method outlined by Merritt and Cummins (2006) to categorize taxa into FFG. Although this method uses more general categories than alternative methods (Barbour et al. 1999, Merritt et al. 2008), it provided a sufficient level of detail for this study (as I was looking for general trends of the macroinvertebrate communities in Muskegon River and Bigelow Creek), even if it resulted in a small reduction in resolution. This method distinguishes four main groups including: scrapers, collectors, predators, and shredders. Thus, I combined filterer-collectors and gatherer-collectors into the collector group and I combined scrapers and piercers into the scraper group. I used FFGs to assess several stream attributes including the autotrophy to heterotrophy index, where a stream is considered autotrophic if the ratio of scrapers to shredders and total collectors is greater than 0.75. The coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM) index was calculated as the ratio of the abundance of shredders to the abundance of collectors. The criterion value for the spring to summer months is greater than 0.25, and in the fall to winter months the criterion value is greater than 0.5. I calculated the suspended to stored FPOM index using the ratio of filtering collectors to gathering collectors. When transport of FPOM exceeds deposited FPOM the index value is >0.5. Channel stability was also characterized from the ratio of scrapers and filtering collectors to shredders and gathering collectors. The benthic substrate is considered stable if the ratio is greater than 0.50. I also examined top-down predator control in the system, where a normal predator-to-prey (all other FFG groups) ratio is between 0.10 – 0.20.

Statistical Analyses

I used regression analysis to determine relationships for combined sample seasons between Muskegon River macroinvertebrate density, zebra mussel density, and distance from Croton Dam. Data were first fit to a linear model, but if the data did not fit a linear relationship, a quadratic regression was used. All samples (Hess and rock cluster, sample n=6) were used for the macroinvertebrate density and distance from Croton Dam regression.

I also analyzed for differences among sites and seasons using one-way or two-way ANOVAs, or their nonparametric test equivalent if data did not meet normality or variance parameters. Variables included: mean macroinvertebrate densities, Chironomidae densities, and Hydropsychidae densities, zebra mussel densities, and EPT richness. Chironomidae and Hydropsychidae densities were log transformed to meet normality assumptions. T-tests, or their nonparametric test equivalents were used to compare Muskegon River and Bigelow Creek macroinvertebrate communities.

A goal of the current study was to compare macroinvertebrate community structure during 2011 to that reported by Godby (2000). Regression analyses were used to compare relationships between 1998 and 2011 seasonal all-sample macroinvertebrate densities, combined season taxa richness, and distance downstream from Croton Dam. For regressions comparing 1998 samples (Godby 2000) and 2011 samples, I included both sample types as replicates (Hess and rock cluster, sample n=6). These analyses are labeled as 'all sample' in each figure or table legend whenever it is used. It is important to note that this approach differs from how Godby (2000) presented this information. T-tests (or non-parametric alternatives) were used to compare seasonal Chironomidae and Hydropsychidae densities in the 1998 and 2011 samples. A multivariate non-metric multidimensional scaling analysis (NMDS) test was used to investigate differences in macroinvertebrate communities collected from the Muskegon River and Bigelow Creek by Godby (2000) and during the current study. All macroinvertebrate taxa densities in both studies were used with the exception of zebra mussels and Chironomidae. Chironomidae were excluded because their abundance obscured differences among sites. The NMDS was performed using Bray-Curtis distance measures, and 999 iterations. I used two dimensions in my analysis, as a stress plot showed that stress was not reduced significantly with more than two dimensions. A multivariate ANOVA post-hoc test (adonis, 5000 permutations) was performed to analyze differences in macroinvertebrate community composition between sampling years. A similarity percentage (SIMPER) post-hoc test was performed if the adonis test was significant. A SIMPER test evaluates the percent contribution of dissimilar taxa to the percent contribution of similar taxa between samples, and calculates an average. Taxa with the largest average to dissimilarity ratios are responsible for the observed differences between samples (Quinn and Keough, 2002). There were too many possible crosses in the SIMPER test to include all of the sites for both years, so the upper site (Croton) and lower site (Henning DS) on the Muskegon River, for both sample years, were chosen for the test.

RESULTS

Muskegon Macroinvertebrate Communities

There was a significant negative linear relationship ($p=0.046$, $R^2=0.671$) between macroinvertebrate density and distance below Croton Dam when data for both seasons were combined (Figure 2). A two-way ANOVA indicated that there were significant differences between seasons ($p<0.05$, summer mean (±SE) macroinvertebrate densities were 14804±2386 m^{-2}, fall mean macroinvertebrate densities were 199534±1918 m^{-2}) and sites ($p<0.05$, macroinvertebrate densities ranged from 24887±4440 m^{-2} at the upstream site Croton to 9679±2580 m^{-2} at Henning US), and the interaction between season and site was significant ($p<0.05$) (Table 5).

Mean macroinvertebrate densities (excluding zebra mussels) varied among sample sites on the Muskegon River and in the summer, were highest (31,359 m^{-2}) at the upstream site (Croton) with densities generally lower at mid-reach and downstream sites (Figure 3). Linear regression analysis of summer macroinvertebrate density and downstream distance was not significant ($p=0.074$, $R^2=0.589$, Figure 4). A one-way ANOVA showed there were no significant differences among sites during summer ($F_{5,12}=2.668$, $p>0.05$).

In the fall, the highest (26,637 m^{-2}) mean macroinvertebrate densities (excluding zebra mussels) were generally at upstream and mid-reach sites and lowest (10,893 m^{-2}) at downstream sites (Figure 3). The relationship between fall total invertebrate densities and distance from Croton Dam was not significant (linear regression, $p=0.500$, $R^2=0.120$) (Figure 5). In addition, a one-way ANOVA indicated that differences among sites during fall ($F_{5,12}=1.382$, $p>0.2$) were not significant.

The combination of summer and fall samples yielded 74 total macroinvertebrate taxa found in the Muskegon River samples. There was a significant positive relationship (p=0.035, R^2=0.707) between macroinvertebrate species richness and distance below Croton Dam for both sample seasons (Figure 6**)**. Species richness ranged from 31 to 43 taxa during the summer, with a mean (±SE) of 37.5±1.7. During the fall, richness ranged from 36 to 55, and the mean species richness per site jumped to 44.5±2.8 (Table 6). Common taxa richness (CTR, taxa density $\geq$ 5% of total relative abundance) had a range of 3 to 6 in the summer and 2 to 5 in the fall, with mean CTR slightly higher in the summer (4.66±0.42) than in the fall (3.5±0.50) (Table 6).

Taxa diversity and evenness followed the same general pattern as taxa richness, with highest values at downstream sites and lowest values closer to Croton Dam. The upstream sample site at Henning Park had the greatest diversity and evenness throughout both seasons, the Croton site had the lowest during both seasons (Table 6). Shannon-Wiener Diversity index values and evenness values were similar in both the summer (ranging from 1.419 to 2.460) and fall (1.821 to 2.855) samples (Table 6). The mean (±SE) Shannon-Wiener Index value was 2.192±0.160 in the summer and 2.246±0.138 in the fall. Evenness values ranged from 0.413 to 0.712; the mean evenness value for summer samples was 0.603±0.038, and the mean fall value was 0.591±0.028 (Table 6).

The total EPT richness for the Muskegon River was 41, and the EPT index value was 0.554, when both sample season data were combined. EPT richness increased in a downstream direction, although not significantly (linear regression p=0.091, R^2=0.549, Figure 7). EPT richness was higher in the fall compared to the summer (two-way ANOVA, Tables 7 & 8). The greatest summer EPT richness and index values were observed at mid-reach sample sites

(Thornapple US) whereas the highest fall EPT richness and EPT index values were recorded at sites farthest downstream (Thornapple DS, Henning US, and Henning DS) (Table 7).

Average zebra mussel densities ranged from 0 to 6302.70 m^{-2} and were highest near Croton Dam (Croton sample site) regardless of season (Table 9). The two downstream sites (Henning DS and Henning US) had the lowest zebra mussel densities during summer and fall respectively (Table 9). Mean zebra mussel density had a non-significant ($p=0.063$, $R^2=0.619$) negative linear relationship with distance from Croton Dam. A quadratic regression was found to have a better fit, and a significant positive relationship ($p=0.043$, $R^2=0.876$) with increasing distance from Croton Dam (Figure 8). Zebra mussel densities were significantly different among sites (Kruskal Wallis, $p=0.001$), but a Mann-Whitney post hoc test (with Bonferroni correction) could not identify which sites differed. Zebra mussel densities in the Muskegon River did not significantly differ between seasons (Kruskal Wallis, $p=0.398$). Mean total macroinvertebrate density had a significant ($p=0.001$, $R^2=0.946$) logarithmic relationship with mean zebra mussel density, although this relationship appears to be driven by one sample point (Figure 9).

Chironomidae and Hydropsychidae were the most abundant taxa during both seasons (Appendix A). Chironomidae mean density was highest during the summer, with the maximum mean densities closest to Croton Dam (Croton and Pine sites) (Figure 10). A one-way ANOVA on log-transformed Chironomidae densities indicated there were significant differences among sites during the summer ($F_{5,11}=14.93$, $p<0.001$). A Tukey’s HSD post hoc test using the summer data revealed significant differences between Croton and Thornapple US ($p<0.001$), Thornapple DS ($p<0.001$), Henning US ($p<0.001$), and Henning DS ($p=0.002$) as well as between Pine and Thornapple US ($p=0.029$), and Pine and Thornapple DS ($p=0.013$). The comparison between Pine and Henning US was not significant ($p=0.055$).

During fall, the mean densities of chironomids declined to almost half of the summer mean density with maximum mean densities shifting toward mid-reach and downstream sample sites (Thornapple DS, and Henning DS) (Figure 10). A one-way ANOVA on log-transformed Chironomidae densities reported significant differences among sites in the fall ($F_{5,12}$=4.29, p<0.05). A Tukey's HSD post-hoc test for fall data indicated significant differences between Croton and Henning US (p=0.028), Pine and Henning US (p=0.041), Thornapple DS and Henning US (p=0.039), and Henning US and Henning DS (p=0.020). A statistically significant difference was not found between Thornapple US and Henning US (p=0.078).

Hydropsychidae mean densities were highest at upstream sites (Croton and Pine) in the Muskegon River (Table 10). This pattern was observed for both summer and fall sampling seasons with summer values somewhat higher (Figure 11). Although differences among sites were significant (two-way ANOVA, p<0.01, Table 10), a Tukey's HSD test could not distinguish significant differences among sites. Separate one-way ANOVAs found that there was a significant difference among sites in summer ($F_{5,11}$=4.436, p<0.05) but not fall ($F_{5,12}$=1.396, p >0.10). A Tukey's HSD post-hoc test for summer sites found that the Croton and Henning US sites were significantly different (p=0.036).

Bigelow Creek Macroinvertebrate Communities

Mean macroinvertebrate densities varied seasonally in Bigelow Creek. During summer, mean macroinvertebrate densities were highest at the downstream site (10,729 m^{-2}) and lowest in the upstream site (4,350 m^{-2}) (Figure 3). This pattern was reversed in the fall, with highest mean macroinvertebrate densities at the upstream site (9,534 m^{-2}) and lowest densities at the downstream site (4,450 m^{-2}) (Figure 3). Separate two-tailed t-tests found that there was no significant difference between seasons (p=0.871), or sites (p=0.681) on Bigelow Creek.

There were 58 total macroinvertebrate taxa found in Bigelow Creek, when summer and fall samples were combined. The upstream and downstream sites had approximately equal richness during both sampling periods (Table 11). The Bigelow Upstream site had a greater diversity and evenness in the summer sample season (1.722 and 0.496 respectively),

Bigelow Creek had a total EPT richness of 37 and an EPT index value of 0.637. The Bigelow Downstream site had the greatest EPT richness and index value throughout both sample seasons (Table 12). EPT richness was significantly different between seasons (two-way ANOVA, $p<0.05$), but not between sites (Table 13). One-way ANOVAs showed no significant difference between sites in summer ($F_{1,4}=0.045$, $p=0.842$) or fall ($F_{1,4}=0.729$, $p=0.441$).

Overall, Chironomidae and Hydropsychidae had the highest density in all samples compared to other taxa (Appendix A). Chironomid densities were not significantly different between sites in summer (Kruskal-Wallis, $p=0.083$) or fall (Kruskal-Wallis, $p=0.275$). Hydropsychidae densities followed the same pattern with no significant difference between sites in summer samples (Kruskal-Wallis, $p=0.083$) or fall samples (Kruskal-Wallis, $p=0.275$).

Comparison of Macroinvertebrate Communities in the Muskegon River and Bigelow Creek

Macroinvertebrate taxa density, richness, diversity, and EPT richness varied between Muskegon River ($n=36$) and Bigelow Creek ($n=12$), evenness values were similar. The macroinvertebrate densities between Muskegon River and Bigelow Creek were significantly different (two-tail t- test, $p=0.001$). Muskegon River macroinvertebrate richness was significantly different from Bigelow Creek macroinvertebrate richness for combined seasons (two-tail t-test, $p=0.007$). The Shannon-Wiener Diversity Index for the Muskegon River was significantly different from the Diversity Index of Bigelow Creek (two-tail t-test, $p=0.018$). There was a significant difference in EPT richness between the Muskegon River and Bigelow

Creek (two-tail t-test, p=0.006). Evenness values between the Muskegon River and Bigelow Creek had no significant difference (Welch's t-test, p=0.342).

Functional Feeding Groups

Macroinvertebrate functional feeding groups indicated that most Muskegon River sites were autotrophic (>0.75 ratio value, Figure 12), with a mean combined season value of 0.814 (based on the ratio of scrapers and shredders to collectors in the Muskegon River).This ratio implies that the Muskegon River's base food supply comes largely from algae, plankton, and rooted vascular plants. The CPOM/FPOM index (the ratio of shredders to collector macroinvertebrates) values for the Muskegon River were much lower than the criterion values (>0.25 summer-spring, >0.50 fall-winter) for both sample seasons; the combined season mean for sites was 0.079. This value indicates that there are low amounts of CPOM and more FPOM in the river. The transported FPOM to benthic FPOM (TFPOM/BFPOM) ratio (the ratio of filtering to gathering collectors) indicated that there was a higher than normal loading of FPOM in suspension (>0.50 criterion value, mean combined season ratio of 0.777) in the Muskegon River. The large value indicates an abundance of FPOM in transport, and low benthic storage of FPOM in the Muskegon River. The FFG ratio index estimating channel stability (the ratio of scrapers and filtering collectors to shredders and gathering collectors) determined that the Muskegon River had very stable substrates (>0.50 criterion value, mean combined season value of 2.001). Top-down predator trophic controls (predators to all other functional feeding groups) for most sites on the Muskegon River were within parameters ($0.1 \leq x \leq 0.2$ criterion value, mean combined season value of 0.162). However, the few sites that had above-normal criterion values for Muskegon River indicated that there were more predatory taxa to the prey taxa at those sites and seasons. The ratio values within parameters indicate a nominal predator-prey ratio.

During the summer sampling season, the values for the P/R ratio in the Muskegon River ranged from 0.625 (Croton) to 0.928 (Henning DS), and were mostly autotrophic. The only sites that were not autotrophic were Croton (0.625) and Thornapple DS (0.684) during the summer season (Figure 12). The CPOM/FPOM ratios for the Muskegon River had a range of 0.055 (Thornapple DS) to 0.076 (Henning DS) (Figure 13). The summer TFPOM/BFPOM Muskegon River values ranged from 0.50 (Croton, Thornapple US and DS) to 0.875 (Pine) (Figure 14). Muskegon River benthic channel stability ratios for the summer ranged from 1.363 (Croton) to 2.375 (Henning DS) (Figure 15). The predator prey ratio in the Muskegon River had values ranging from 0.10 (Pine) to 0.272 (Henning US) (Figure 16). Only the Henning US (0.272) and Henning DS (0.25) were above the criterion values in the summer season.

In the fall season, the Muskegon River P/R values ranged from 0.761 (Thornapple DS) to 1.000 (Croton) (Figure 12). The CPOM/FPOM values ranged from 0.066 (Thornapple US) to 0.117 (Pine) (Figure 13), while the fall TFPOM/BFPOM values ranged from 0.666 (Croton) to 1.0 (Thornapple US and DS, and Henning DS) for the Muskegon River (Figure 14). Channel stability ratios for fall ranged from 2.0 (Croton and Henning US) to 2.555 (Thornapple US) (Figure 15). Predator/prey ratios in the fall for the Muskegon River ranged from 0.076 (Pine) to 0.209 (Henning US); Pine was the only site in the fall season that had low predator/prey values and was not in the criterion range (Figure 16).

Bigelow Creek exhibited a heterotrophic state for both seasons and sites (<0.75 ratio, mean combined season value of 0.625). This ratio implies that the base food-supply for macroinvertebrate communities in Bigelow Creek comes from allochthonous input (such as leaf litter) from the riparian zone. Bigelow Creek exhibited a below-typical CPOM/FPOM ratio, with a mean combined season value of 0.126; this value suggests that there are low food resources from the riparian zone (CPOM), and more FPOM available in-stream, when the seasons were combined. Bigelow Creek had a high TFPOM/BFPOM loading value (>0.50 criterion value, mean combined season value of 0.634). The large ratio value of transported to benthic FPOM indicates there is an abundance of FPOM in transport in Bigelow Creek, and a low abundance of benthic-stored FPOM. Bigelow Creek had a stable substrate for macroinvertebrates to live in and cling onto (criterion value of >0.50, mean combined season value of 1.485). The overall predator/prey ratio in Bigelow Creek was slightly higher than the criterion value (0.10 to 0.20) with a mean combined season value of 0.244, suggesting that there were slightly more macroinvertebrate predators than prey taxa.

In the summer sampling season, Bigelow Creek had heterotrophic P/R values of 0.470 at Bigelow US, while Bigelow DS had a value of 0.642, (Figure 12). Summer CPOM/FPOM FFG ratios were comparable for Bigelow Creek, with a value of 0.062 at Bigelow US and slightly greater downstream with a value of 0.076 at Bigelow DS (Figure 13). Bigelow Creek had high TPOM/BFPOM loading values during the summer samples, with the Bigelow US site having a value of 0.777, while Bigelow DS site had a value of 0.625 (Figure 14). Bigelow Creek had a benthic channel-stability summer value of 1.50 at Bigelow US, and 1.555 at Bigelow DS (Figure 15). During the summer, Bigelow Creek exhibited high predator/prey ratio values of 0.240 at Bigelow US and 0.304 at Bigelow DS (Figure 16).

For the fall sampling season of Bigelow Creek, the P/R ratio remained heterotrophic, with Bigelow US having a ratio value of 0.666 and Bigelow DS having a value of 0.722 (Figure 12). CPOM/FPOM ratios increased from summer values to 0.166 at Bigelow US and 0.200 at Bigelow DS in the fall (Figure 13). In the fall, the Bigelow US site had a TFPOM/BFPOM ratio value of 0.636, while Bigelow DS had a value of 0.50 (Figure 14). In the fall, channel stability values at Bigelow US stayed at 1.50, whereas Bigelow DS changed to 1.384 (Figure 15). Predator/prey ratios of the Bigelow US site fell to be within the criteria to 0.142, while Bigelow DS was still above the criteria values, at 0.290 (Figure 16).

Comparison Between 1998 and 2011Macroinvertebrate Communities

A significant positive quadratic relationship was found between all-sample macroinvertebrate densities and distance downstream of Croton Dam for summer 2011 samples on the Muskegon River (p=0.024, R^2=0.916); whereas the summer 1998 data displayed a significant negative relationship (p=0.015, R^2=0.938) (Figure 17). In the fall, no significant relationship was found between all-sample macroinvertebrate densities and distance from Croton Dam for 2011 samples (p=0.301, R^2=0.583) or 1998 samples (p=0.515, R^2=0.357). Both sample-years displayed a negative quadratic trend (Figure 18).

The 1998 Muskegon River all-sample macroinvertebrate taxa richness had a significant positive linear relationship with distance downstream from Croton Dam (p=0.040, R^2=0.690). The 2011 Muskegon River samples followed the same trend, although more macroinvertebrate taxa were present in the samples (p=0.035, R^2=0.707) (Figure 6).

In 2011, Chironomidae mean densities were highest near Croton Dam, whereas the 1998 summer samples had the highest densities of chironomids in the mid-reach sample sites (Thornapple and Henning) (Figure 19a). There was not a significant difference between the mean 1998 and 2011 summer chironomid densities in the Muskegon River (two-tail t-test, p =0.695).

Fall 2011 samples had slightly higher mean Chironomidae densities than summer samples, and had the highest densities closest to Croton Dam (Figure 19b). The 1998 fall samples had the highest chironomid density near Croton Dam as well (Figure 19b). Fall 1998 mean Chironomidae densities were significantly greater than the fall 2011 mean chironomid densities in the Muskegon River (Wilcoxon test, $p<0.01$).

Summer 2011 Hydropsychidae mean densities were highest near Croton Dam in summer, and in 1998, the densities were highest in the mid-reach sample sites (Figure 20a). There was no significant difference between summer 2011 and summer 1998 mean Hydropsychidae densities in the Muskegon River (Welch's t-test, $p=0.120$).

Hydropsychidae mean densities were highest in the sites close to Croton Dam for both 1998 (Croton site) and 2011 (Pine site) samples (Figure 20b). However, there was a large increase in Hydropsychidae densities in a mid-reach sample site (Thorn DS) in 1998 (Figure 20b). There was not a significant difference between fall 1998 and 2011 mean Hydropsychidae densities in the Muskegon River (Wilcoxon test, $p=0.179$).

In general, samples separated by sample year based on the NMDS analysis. There was a significant difference between the macroinvertebrate communities as a whole on the Muskegon River from the total samples taken in 1998, and the current study's total samples taken in 2011 (NMDS stress=0.148 and subsequent adonis analysis, $R^2=0.111$, $p<0.001$) (Figure 21). There was a significant difference between macroinvertebrate communities for the upstream (Croton) and downstream (Henning DS) sites between the 1998 Muskegon River samples, and the 2011 samples (NMDS plot, stress=0.105, and adonis post-hoc test $R^2=0.116$, $p<0.001$) (Figure 22). A SIMPER test on the upstream and downstream Muskegon River sites revealed the macroinvertebrate taxa driving the variation between communities differed between year and site. The macroinvertebrate taxa with the greatest cumulative contribution for the comparison between Croton 1998 and Henning DS 1998, Croton 1998 and Croton 2011 samples, and Croton 2011 and Henning DS 2011 samples were Hydropsychidae and *Cheumatopsyche*. The taxa that were driving the differences in macroinvertebrate communities between the Henning DS 1998 and Henning DS 2011 sample were *Protoptila* and Hydropsychidae (Appendix B).

Bigelow Creek also had a significant difference between the macroinvertebrate communities between the two sampling years 1998 and 2011 (NMDS stress = 0.134, adonis R^2=0.118, p<0.001), and sites (p<0.001, R^2=0.090) (Figure 23). However, I should note that there was no Bigelow downstream sample collected during summer 1998 which may affect the clarity of these tests. I should also note that the vertical line of Bigelow Upstream 1998 sample points near the middle of Figure 19 were the Hess samples collected at that sample site during summer and fall of 1998. I suggest that the arrangement of these points is probably due to the similar taxa richness and densities in those samples, especially *Brachycentrus, Cheumatopsyche, Ceratopsyche, and Hydropsyche*. A SIMPER test showed that macroinvertebrate taxa responsible for the difference in the communities between sites changed by year (Appendix B). Taxa with the greatest cumulative contribution to differences between the Bigelow Upstream site during 1998 (US) and the Bigelow Downstream site during 1998 (DS), were *Protoptila* and Hydropsychidae. Comparing 2011 sites, differences between the upstream and downstream sites were due to Baetidae and Simuliidae. Differences between the Bigelow US 1998 sample and the Bigelow US 2011 sample were driven by Hydropsychidae and *Protoptila*. The taxa that accounted for the greatest cumulative contribution when comparing the Bigelow DS site between 1998 and 2011 samples shifted from *Protoptila* and Hydropsychidae to *Protoptila* and Baetidae.

DISCUSSION

The objectives of this study were to examine current macroinvertebrate communities in the Muskegon River and Bigelow Creek and to compare current macroinvertebrate communities to those studied by Godby (2000). I found clear differences in the density, richness, and diversity of macroinvertebrate communities in both rivers since 1998, and a possible ecological threshold relationship with zebra mussel densities and biomass. These changes in the macroinvertebrate communities may have trophic effects for higher organisms, such as the many game fish in the Muskegon River.

Muskegon Macroinvertebrate Communities

I found a significant negative linear relationship between macroinvertebrate densities and distance downstream of Croton Dam when sample seasons were combined (Figure 2) and this trend continued (although not significantly) when the summer and fall samples were analyzed separately (Figure 4, 5). Lehmkuhl (1972) found a similar reduction in macroinvertebrate densities up to 70 miles downstream of Gardiner Dam on the Saskatchewan River. He suggested that the cause of the drop in macroinvertebrate density downstream of the dam was attributed to lower water temperatures from the Gardiner Dam reservoir (Lehmkuhl, 1972). The Croton Dam on the Muskegon River does not produce lower water temperatures going into the river, but instead raises water temperatures downstream of the dam; this may be a part of the reason for low macroinvertebrate densities in this section of river, but I would suggest that the food availability and benthic substrate composition are the main factors. The most upstream site (Croton) on the Muskegon River had the highest density of zebra mussels on the benthos (6303 ± 4186 m^{-2} in summer, 1688 ± 567 m^{-2} in fall), while the Henning DS site had very few zebra mussels (0 m^{-2} in summer, 37.04 ± 29.39 m^{-2} in fall, Table 9). Zebra mussels create a complex benthic environment when they invade a system, allowing for a localized increase in some benthic fauna (Horvath et al., 1999; Strayer, 2009). Dead zebra mussel shells also create a complex habitat (Horvath et al., 1999) and the piles of shells downstream of Croton Dam provide many places for exploitation by macroinvertebrates. The Croton site (right below Croton Dam) will be the first to receive any phytoplankton (and any POM) to come through the dam, giving the macroinvertebrates and zebra mussels living closest to the dam the best accessibility to food. As the water passes over the zebra mussel beds and macroinvertebrates at Croton, it is suggested that most of the POM and phytoplankton is depleted, thus not allowing for high densities of zebra mussels (and a reduced amount of macroinvertebrates) to survive downstream such as at Henning DS.

Macroinvertebrate taxa richness for the Muskegon River samples significantly increased further downstream of Croton Dam (Figure 6). The recovery of organism richness (and diversity) with increasing downstream distance is a common characteristic of an impounded river, and many organisms display this trend as well including: macroinvertebrates (Vinson, 2001; Takao et al., 2008; Growns et al., 2009), primary producers (Bernez et al., 2004; Cibils Martina et al., 2013), and fish (Lessard and Hayes, 2003; Santucci Jr. et al., 2005). The fall Muskegon River samples had higher macroinvertebrate richness (including EPT richness) than the summer samples (Table 6, 7). This seasonal effect is likely due to the emergence of more taxa (shredders and collectors) able to utilize the abundant leaf litter introduced to the system.

Zebra mussel densities in the Muskegon River followed a positive quadratic trend with distance downstream of Croton Dam (Figure 8). This trend approximately follows a source-sink type model of invasion, with Croton reservoir acting as the source, and the Muskegon River acting as the sink. The source-sink model has been shown as a useful descriptor for zebra mussel population expansion in a flowing-water system (Horvath et al., 1996). The zebra mussel densities decrease until the furthest downstream sample sites (Figure 8, Table 9). This downstream decrease in zebra mussel density is most likely due to a lack of available food (Fuentes, 2003). The small rise in zebra mussel densities at the Thornapple DS and Henning sample sites does not quite fit into the source-sink model from Croton Dam. However as the Thornapple and Henning sample sites are public boat launches, these sites could be acting as another source for the zebra mussel population (if infected boats are put into the river at those locations). The Muskegon River macroinvertebrate communities followed a logarithmic relationship with zebra mussel density when both seasons were combined (Figure 9). This logarithmic relationship shows that macroinvertebrate densities plateau after about 350 zebra mussels m^{-2}, which may imply that after a certain zebra mussel density, macroinvertebrate communities are not as influenced by the zebra mussels. This could show that high zebra mussel densities do not influence macroinvertebrate communities as much as lower zebra mussel densities in this section of the Muskegon River; the addition of the three-dimensional habitat at low zebra mussel populations may allow more macroinvertebrates to use that substrate, but at higher densities may not attract as many macroinvertebrates. However, caution must be taken in analyzing this relationship, only six sample locations were used for this analysis and this relationship appears to be driven by one sample point. More data would help to reveal if the logarithmic relationship of zebra mussel to total macroinvertebrate density is true over multiple locations and years.

Bigelow Creek Macroinvertebrate Communities

There was no significant difference between macroinvertebrate densities the upstream and downstream sample sites on Bigelow Creek for either sample season. This similarity between the two sites could be because Bigelow Creek is much smaller in size and discharge than the Muskegon River, and there was much less distance between the two sample locations in Bigelow Creek. Although Bigelow Creek had less total taxa richness than the Muskegon River when the seasons were pooled, the taxa richness for each season was remarkably similar from Bigelow US to Bigelow DS (Table 11). Even though the taxa richness was similar between the seasons, there were still taxa that were site-specific (Table 18, Appendix A); *Hydropsyche* and *Baetisca* were exclusive to the Bigelow US samples, whereas *Tipula* and *Seratella* were unique to the Bigelow DS samples.

Bigelow Creek was restored from 2004 to 2009 and included adding woody habitat structures, flow modifiers, and other habitat improvements (Muskegon River Watershed Assembly, 2013). This work was mainly for improving habitat for game fish; however stream restoration usually has an effect on macroinvertebrate communities as well, typically through a change in composition, diversity, or densities (Gørtz, 1998; Moerke et al., 2004; Sariquett et al., 2007; Miller et al., 2010). The restoration work on Bigelow Creek in previous years, may have influenced the macroinvertebrate communities that were found in the river in 2011.

Comparison of Macroinvertebrate Communities in the Muskegon River and Bigelow Creek

Macroinvertebrate densities in the Muskegon River were significantly higher than macroinvertebrate densities in Bigelow Creek ($p<0.001$), but that is to be expected as the Muskegon River is a much larger river than Bigelow Creek and has a more diverse range of environments for macroinvertebrates to inhabit.

The Muskegon River had significantly higher macroinvertebrate taxa richness, than Bigelow Creek. However, even though the Muskegon River and Bigelow Creek share a watershed, there are inherent differences between the two streams in substrate, flow, temperature, and riparian coverage (Tables 1-4).

Mid-order streams (such as the Muskegon River) have been shown to have higher diversity and richness than low-order (such as Bigelow Creek), or high-order streams (Vannote et al., 1980; Minshall et al., 1985). This is partially because in low-order streams, there is typically a consistent temperature regime between seasons, which only some macroinvertebrate taxa will be able to tolerate. High-order streams have a large volume of water, and hence tend to also have a consistent temperature throughout. Mid-order streams have fluctuating temperatures and water flow, and thus are able to provide a better environment for more thermally diverse macroinvertebrate taxa (Vannote et al., 1980). Both Vannote et al. (1980) and Minshall et al. (1985) state that there are many other factors including temperature, benthic substrate, and riparian influence that have effects on the diversity and richness of macroinvertebrate taxa in streams.

Bigelow Creek and Muskegon River varied greatly in temperature. The Muskegon River had higher temperatures than Bigelow Creek in both the summer and fall samples (Table 2, 4). This positive trend of greater taxa richness corresponding to higher temperature conforms to the trend found by Jacobsen et al. (1997). Their global study of rivers showed that macroinvertebrate family richness and diversity follow a positive linear trend with temperature, i.e. the higher the temperature in a river, a greater number of macroinvertebrate families. A study examining Michigan rivers found a different trend; Lessard and Hayes (2003) found macroinvertebrate community similarity values, not richness values, had a linear trend with increasing temperature. Friberg et al. (2009) found that macroinvertebrate communities in Icelandic streams lost diversity but increased in density with higher stream temperatures.

Dams also affect macroinvertebrate community richness and diversity. This study found a positive linear relationship between macroinvertebrate richness and distance from Croton Dam, which conforms to the trend found in Godby et al. (2000). The recovery of organism richness and diversity with increasing distance from a dam is a common characteristic of impounded rivers, and can be seen in macroinvertebrate communities (Vinson, 2001; Takao et al., 2008; Growns et al., 2009), fish (Lessard and Hayes, 2003; Santucci Jr. et al., 2005), and primary producers (Bernez et al., 2004; Cibils Martina et al., 2013).

The Muskegon River has varied substrates throughout its length, including zebra mussel hash, cobble, and boulder, whereas Bigelow Creek is comprised of mostly sand and some woody debris, although there is some cobble substrate near the mouth (Table 1, 3). Macroinvertebrate richness and diversity tends to be higher in a river with heterogeneous substrate such as the Muskegon River, than in a river with homogeneous or almost homogeneous substrate such as Bigelow Creek (Vannote et al., 1980; Miller et al., 2010). The macroinvertebrate richness and diversity found in this study between the two rivers conforms to the trend seen in other studies, where larger substrate size (Muskegon River) up to a point (i.e. sand to cobble to boulder) increases richness and diversity (Minshall, 1984; Quinn and Hickey, 1990). A study by Kokeš (2011) had a different outcome for Czech rivers; higher habitat diversity did not lead to an increase in macroinvertebrate diversity, but was still shown to be an important contributing factor for invertebrate assemblages through a multivariate redundancy analysis.

Utilizing rock clusters and Hess samples to obtain a perspective of macroinvertebrate communities in each river is a favorable option, as these two methods get a broader view of the communities in the river; however, it introduces bias. Bigelow Creek is comprised mostly of sand and woody debris, but there were no woody debris samples taken. There were also no woody debris samples taken in the Muskegon River, but as mentioned previously, the Muskegon River has a much more heterogenic substrate, which is favorable for more macroinvertebrate diversity. Since woody debris is one of the only permanent habitats in Bigelow Creek, not having sampled this environment severely overlooked the taxa that may have actually been in the river. In the Satilla River, snag habitats (woody debris) were found to have the highest diversity and macroinvertebrate standing stock biomass compared to sandy or mud habitats on the same river (Benke et al., 1984). Miller et al. (2010) found that adding large woody debris tends to increase macroinvertebrate richness in impaired streams, and while Bigelow Creek is not impaired, the woody debris was not sampled, which resulted in low total taxa richness in the river. However even without sampling the woody debris, it was found that Bigelow Creek did support some macroinvertebrate taxa not found in the Muskegon River, such as *Polycentropodidae spp.*, and *Tipula spp.* (Appendix A).

Seasonality has an effect on when certain taxa will be found in aquatic systems. The life cycles of macroinvertebrates are diverse, and can range from just a few weeks to several years to complete (Merritt et al., 2008). Some macroinvertebrate species only have one complete life cycle per year (univoltine) while others (such as many chironomidae) have several completions during one year (multivoltine) and are found in rivers during every season. In temperate climates, the life cycles of certain taxa (i.e. fall-winter shredders and some collectors) revolve around the addition of allochthonous input during the fall season as a food source (Cummins, 2002). There was an increase in both shredders and collectors during the fall sample in both Bigelow Creek and Muskegon River. Dieterich et al. (1997) discovered a significant positive relationship, life-cycle synchronization, between shredders and collectors. The authors found that shredders seemed to emerge first in a temporary Oregon stream, and collectors would emerge sometime after, once there was an adequate food-source for those taxa, generated from the shredders (Dieterich et al., 1997). The timing of the emergence of these fall-winter seasonal shredders and collectors could be the reason for an increase in taxa richness during our fall sample in both the Muskegon River and Bigelow Creek.

Functional Feeding Groups

Using the ratios of different functional feeding groups is an inexpensive and commonly used approach to getting a basic view of the health of a river and the pathways that transpire within a river. Even though Bigelow Creek and the Muskegon River are in the same watershed, there are distinct differences in their macroinvertebrate communities, and the proportion of taxa in each FFG.

One of the main differences between the two rivers is the production / respiration ratios. The Muskegon River was almost exclusively autotrophic, except for the Croton and Thornapple DS summer samples. Bigelow Creek was shown to be exclusively heterotrophic (Figure 12). The two P/R ratios of the different streams correspond almost exactly to the River Continuum Concept (Vannote et al., 1980). The Muskegon River is a mid-order river, and relies less on allochthonous input from the riparian zone than a head-water stream or a small tributary (such as Bigelow Creek). Mid-order streams employ more autochthonous primary production (from macrophytes and phytoplankton), and organic transport from upstream (Vannote et al., 1980).

The CPOM/FPOM ratios for the Muskegon River were below criterion levels and indicate that there is a low-functioning riparian zone on the Muskegon River; this is likely because there are a series of three dams directly upstream of our first sample site, Croton (Figure 13). Dams are known to modify CPOM/FPOM transportation from the headwaters to mouth. Normally, allochthonous input from the headwaters gets shredded by macroinvertebrates, and is used by collector macroinvertebrates downstream in the mid-order reaches. However, in a dammed river, allochthonous input from the riparian zone upstream cannot get past the barrier (dam), and thus severely limits, and changes, the ratio of macroinvertebrate taxa that utilize POM as their main food source (shredders and collectors) beneath the dam (Ward and Stanford, 1983).

The TFPOM/BFPOM (T/B) ratio established that all of the sites on the Muskegon River had higher values than the criterion ratio, which suggests excess FPOM loading in the water column, throughout all the sites and seasons (Figure 14). This is unusual because the CPOM/FPOM FFG analysis indicated that there was little CPOM or FPOM in the river (Figure 13). The T/B ratio could be inflated due to the abundant presence of zebra mussels at the most upstream site, Croton. Zebra mussels are known to produce considerable OM through their metabolic activities, and this OM may get caught in the current before it settles and moves downstream where collector macroinvertebrates may be able to use it. This flow of OM could be why there is a high number of TFPOM macroinvertebrates at the Pine site, but is reduced again at the Thornapple sites. An additional reason that the T/B ratio in the Muskegon River may be unusual is the distance between certain sites. For example, the Pine and Thornapple US site are approximately 8.18 km apart. This distance may allow for collectors to filter out most of the FPOM within the water column between the high TFPOM Pine summer sample and the normal-range Thornapple US and DS summer samples. The Thornapple DS site and the Henning US site are approximately 9.78 km apart. The Thornapple sites are in Stratum 4, which has many deep and shallow runs and the substrate consists of mostly sand/silt and gravel, which is not a preferred substrate for many macroinvertebrates. The Henning US and DS sites are located in Stratum 5, which, highly urbanized, may input OM from runoff of impermeable surfaces. Many grass lawns are mowed straight to the river bank (or retaining wall) with no buffer zone to stop runoff from the civilized areas.

The FFG values for the substrates of the Muskegon River and Bigelow Creek demonstrated that the channels were quite stable, with all of the sites having a value much higher than the 0.5 value given for plentiful stable substrate (Figure 15). However, this is an artifact of the sampling method used to gather the macroinvertebrates. I used rock clusters (which are a stable substrate) as well as Hess samples as the main source of macroinvertebrate taxa; most taxa that utilize the rocks as habitat are going to be the few that are present in stable substrate. The sample methods inflated the channel stability ratios, and this FFG test should not be used to make expansive claims of the stability of both rivers. Bigelow Creek is a mostly sandy-bottom river (Table 3) that has fast stream flow (discharge of 2.14 m^3/s at high-water mark), so the stability of the channel is actually much less than the value given with the FFG ratios.

Top-down control from predators in the Muskegon River was within the normal range at most sites for both seasons (Figure 16). The summer 2011 Henning US and DS sites were above criterion values for the predator-prey ratio (PPR). The fall 2011 sample season shows that the Pine sample site has lower predator-prey ratio values, but Henning US is still above the criteria value. Bigelow Creek had a similar pattern; in the summer both US and DS sites were above the PPR criteria value, but in the fall only the Bigelow DS site was above the value (Figure 16). Jeffries and Lawton (1985) conducted a meta-analysis of freshwater macroinvertebrates in North America and Britain; they found an average PPR of 0.36, higher than the criteria range used in the FFG metrics. Furthermore, the average PPR of a species-poor community was 0.48, and the ratio for a species-rich community was 0.29 (Jeffries and Lawton, 1985).

The criteria values that Merritt and Cummins (2006) presented for the FFG metrics are not absolute. Different geographic regions may have different “normal” ranges from the generalized FFG metric. A FFG metric developed for different geographic regions would help account for ecosystem variability throughout the United States.

Comparison Between 1998 and 2011 Macroinvertebrate Communities

The summer 2011 Muskegon River macroinvertebrate samples differed from the summer 1998 macroinvertebrate samples. The summer 2011 macroinvertebrate densities had a significant positive quadratic slope with increasing distance from Croton Dam, whereas the 1998 summer data from Godby (2000) showed a significant negative quadratic relationship with increasing distance from Croton Dam (Figure 17). The fall Muskegon River samples from 1998 and 2011 also differed; although neither regression was significant, the 1998 samples had higher mean densities than the 2011 samples.

Chironomidae and Hydropsychidae density changed between 1998 and 2011. Chironomidae density was higher in the middle portions of the Muskegon River (Pine, Thornapple US, and Thornapple DS) in 1998; however, more chironomids were found in 2011 at the most upstream site (Croton) and most downstream sites (Henning US and Henning DS) (Figure 19a). In the fall, the chironomid densities of the 1998 samples were much higher than the densities found in 2011 (Figure 19b). The 2011 summer Hydropsychidae densities were always higher than the 1998 sample densities (with the exception of the Thornapple US site). However, in the fall, the 1998 samples had higher densities than the 2011 samples with the exception of the Pine and Henning US sites (Figure 20a, b). These data seem to show a shift in production of the Muskegon River from 1998 to 2011. In 1998, most macroinvertebrate production occurred in the mid-river sample sites than in the upper or lower reaches, and in 2011 macroinvertebrate production shifted to the upper-river sample sites nearest to Croton Dam. Many factors could have affected the macroinvertebrate communities since 1998, such as the zebra mussel invasion in the early 2000s, a shift in the way Croton Dam is operated, an increase of riparian landowners, or just a natural change in the river itself. However, examining the common taxa richness found in the Muskegon River samples (Table 6), it seems as though these shifts in the macroinvertebrate production is caused by the numerous rare (<5% relative abundance) macroinvertebrate taxa, instead of the fewer abundant taxa (≥5% relative abundance). There is no way to identify the source of this change in macroinvertebrate communities to any one variable with the data available.

The taxa driving the communities between the upper site (Croton) and the lower site (Henning DS) (Hydropsychidae and *Cheumatopsyche*) did not change between 1998 and 2011 (Appendix B). Since there was not a change in the driving-force taxa from upstream to downstream between the 1998 and 2011 samples, and upon examining the common taxa richness found in the Muskegon River samples (Table 6), it seems as though these shifts in the macroinvertebrate production are caused by the numerous rare (<5% relative abundance) macroinvertebrate taxa, instead of the fewer abundant taxa (≥5% relative abundance).

When the Henning DS site was compared between the years, the taxa that were driving the change at this site were *Protoptila* and Hydropsychidae. There was an almost 720% increase in *Protoptila* at this site from 1998 to 2011. *Protoptila* are facultative scrapers found in lotic-erosional zones, and have a mean tolerance value of 1 in the Midwest region, meaning that most of the species are sensitive to pollution and changes in habitat (Merritt et al., 2008). The inflation of the *Protoptila* densities at the Henning DS site is strange since it is the downstream sample of the Henning Park sample. Henning Park (official name Ed H. Henning County Park) is an 82-

acre Newaygo County-run park that is a campsite and boat launch on the Muskegon River, and thus heavily used and disturbed by human-use (Newaygo County Government, 2013). *Protoptila* is supposed to sensitive to pollution and disturbance, and yet their densities have increased seven-fold since 1998. Zebra mussels invaded the Muskegon River after the 1998 sample (approximately the year 2000) and are known to clarify the water column due to their filter feeding, which allows for algal and macrophyte growth (Strayer et al., 1999). This increase in algal, macrophyte, and diatom growth could be the reason that *Protoptila* densities were so high at the Henning DS site, as those plants and algae provide an ample food-source.

The macroinvertebrate communities of Bigelow Creek between 1998 and 2011 were significantly different (Figure 23). However, during the summer 1998 season, no samples were taken at the Bigelow DS site, which may affect the clarity and implications of the results.

The macroinvertebrate communities have changed from Bigelow US to DS from the 1998 sample to the 2011 sample. The important taxa that were driving the community in the 1998 Bigelow US to Bigelow DS were *Protoptila* and Hydropsychidae, while in 2011 the driving taxa were Baetidae and Simuliidae. Again, there was no sample taken in summer 1998, so caution must be taken when comparing the two years. Nevertheless, examining the data from Godby et al. (2000) in 1998, there were hardly any simulids in the Bigelow US site from the summer and none in the fall sample. In 2011, there were many simulids in both the upstream and downstream sites for both seasons (Appendix A). Baetidae followed a similar trend; there were limited individuals in both the upstream and downstream site for both 1998 seasons, and in 2011, there were numerous individuals at both sites and seasons (Appendix A).

Conclusions

This study has shown through regression, ANOVA, t-test, and NMDS analysis (and subsequent post hoc analyses), that the Muskegon River and Bigelow Creek macroinvertebrate communities differed between the 1998 and the 2011 samples. Between the 1998 and 2011 sample periods, the major macroinvertebrate production on the Muskegon River has moved from mid-reach sample sites to the upper reaches, closer to Croton Dam. This production shift is most likely due to the rare (<5% relative abundance) macroinvertebrate taxa, as a SIMPER test has shown that the main driving macroinvertebrate taxa (Hydropsychidae and *Cheumatopsyche*) stayed the same between the Croton and Henning DS 1998 and the Croton and Henning DS 2011samples. This macroinvertebrate shift from mid- to upper reaches could be caused by many environmental or physical changes to the Muskegon River since 1998 such as the zebra mussel invasion.

Macroinvertebrate communities in Bigelow Creek also changed between the 1998 and 2011 samples. The SIMPER test showed from upstream to downstream between the 1998 and 2011 samples that the taxa driving the change shifted from *Protoptila* and Hydropsychidae (in 1998) to *Baetidae* and *Simuliidae* (in 2011). Much restoration work was done on Bigelow Creek since the 1998 sample was taken, including the addition of flow modifiers, woody habitat structures, and other improvements, which possibly caused this macroinvertebrate shift.

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Table 1. Habitat description and location of strata used in this study on the Muskegon River, MI. Stratum 1 is closest to Croton Dam, Stratum 5 is furthest downstream. (Icthyological Associates, 1991, as used by Godby et al., 2007).

Stratum	*Location (m downstream of Croton Dam)*	*Substrate / Habitat Description of River Segments*
1	305 to 1829	Gravel riffle spawning habitat
2	1829 to 4267	Spawning habitat with run-holding habitat
3A	4267 to 8534	Run/pool with some high banks
4	8534 to 11582	Deep and shallow runs with spawning gravel
3B	11582 to 15240	Run/pool with some high banks
5	18288 to 21031	Higher gradient reach with instream cover provided by man-made log/rock cribs

Table 2. Mean (n=3) physical and chemical characteristics of Muskegon River sample sites during summer and fall, 2011. Measurements were taken at upstream, middle, and downstream locations within a 100 m x 3 m sample site. Measurements include temperature (°C), dissolved oxygen (DO, mg·L^{-1}), conductivity (μS·cm^{-1}), and pH. Sites are listed from upstream to downstream (left to right), Thorn is the Thornapple sample site, US denotes an upstream site, DS denotes a downstream site.

	Croton		*Pine*		*Thorn US*		*Thorn DS*		*Henning US*		*Henning DS*	
Season	Summer	Fall	Summer	Fall	Summer	Fall	Summer	Fall	Summer	Fall	Summer	Fall
Temperature	23.67	16.96	23.36	17.11	22.41	17.49	21.94	17.28	23.78	16.36	23.91	15.43
DO	7.21	10.79	6.94	8.05	7.62	8.60	7.05	8.57	9.17	12.69	9.16	12.14
Conductivity	0.325	0.391	0.322	0.397	0.367	0.399	0.360	0.401	0.364	0.396	0.363	0.397
pH	7.91	7.91	7.84	8.12	8.17	8.11	8.02	8.17	8.34	7.97	9.16	7.95

Table 3. Habitat description of macroinvertebrate sample sites on Bigelow Creek, MI from samples taken in 2011.

Site	*Substrate / Habitat Description*
Bigelow Upstream (58th St)	Sandy substrate, many deep pools, little cobble/gravel, few riffles, substantial woody debris, extensive riparian cover
Bigelow Downstream (Mouth)	Cobble and sand substrate, many riffles, frequent woody debris, adequate riparian cover, extensive stream incision/bank erosion

Table 4. Mean (n=3) physical and chemical characteristics of Bigelow Creek sample sites during summer and fall, 2011. Measurements were taken at upstream, middle, and downstream locations within a 100 m x 3 m sample site. Measurements include temperature (°C), dissolved oxygen (DO, mg·L^{-1}), conductivity (µS·cm^{-1}), and pH. Sites are listed from upstream to downstream (left to right), US denotes an upstream site, DS denotes a downstream site.

	Bigelow US		*Bigelow DS*	
Season	Summer	Fall	Summer	Fall
Temperature	23.43	11.30	17.37	10.25
DO	8.14	11.60	9.27	11.04
Conductivity	0.302	0.327	0.329	0.348
pH	8.15	7.95	8.05	7.84

Table 5. Results of a two-way ANOVA and mean (±SE) macroinvertebrate densities in the Muskegon River by season (summer (S) and fall (F)) , and sample site (Site) (Croton (Cr), Pine (P), Thornapple Upstream (TU), Thornapple Downstream (TD), Henning Upstream (HU), Henning Downstream (HD)), and the interaction between the two terms (Season x Site). Data presented are from 2011 samples. Zebra mussels are not included in this analysis.

Source	*df*	*Mean±SE*	*F*	*p*
Season	1	S: 14804±2386 F: 199534±1918	4.417	0.046
Site	5	Cr: 24887±4440 P: 19541±4123 TU: 14338±3613 TD: 19190±4154 HU: 9679±2580 HD: 16639±1784	2.963	0.032
Season x Site	5	-	2.85	0.037

Table 6. Seasonal Richness (R), Common Taxa Richness (CTR, taxa $\geq$5% relative abundance), Shannon-Wiener Diversity Index (H'), and Evenness (J) values for macroinvertebrates (excluding zebra mussels) samples collected at six sites on the Muskegon River during 2011. Sites are arranged from upstream (US) to downstream (DS).

Site	*R*		*CTR*		*H'*		*J*	
Season	Summer	Fall	Summer	Fall	Summer	Fall	Summer	Fall
Croton	31	36	3	3	1.419	1.821	0.413	0.508
Pine	35	43	5	5	2.172	2.280	0.610	0.606
Thorn US	39	39	6	3	2.334	2.123	0.637	0.579
Thorn DS	40	47	5	2	2.411	2.205	0.653	0.573
Henning US	43	55	4	5	2.460	2.855	0.654	0.712
Henning DS	37	47	5	3	2.355	2.192	0.652	0.569

Table 7. Seasonal EPT Richness and EPT Index at sample sites on the Muskegon River during 2011. Sites are arranged from upstream (US) to downstream (DS).

Site	*EPT Richness*		*EPT Index*	
	Summer	Fall	Summer	Fall
Croton	16	19	0.52	0.53
Pine	20	25	0.57	0.58
Thorn US	21	23	0.54	0.59
Thorn DS	27	30	0.68	0.64
Henning US	23	32	0.53	0.58
Henning DS	22	29	0.59	0.62

Table 8. Results of a two-way ANOVA and mean (±SE) Ephemeropteran, Plecopteran, and Trichopteran richness in the Muskegon River by season (summer (S) and fall (F)), and sample site (Site) (Croton (Cr), Pine (P), Thornapple Upstream (TU), Thornapple Downstream (TD), Henning Upstream (HU), Henning Downstream (HD)), and the interaction between the two terms (Season x Site). Data presented are from samples taken in 2011.

Source	*df*	*Mean±SE*	*F*	*p*
Season	1	S: 14.6±0.9 F: 18.7±1.3	6.400	0.018
Site	5	Cr: 11.7±1.7 P: 16.3±2.0 TU: 15.7±0.8 TD: 18.7±1.1 HU: 18.2±3.6 HD: 19.5±1.5	2.154	0.093
Season x Site	5	-	0.281	0.918

Table 9. Mean zebra mussel densities m^{-2} (±SE) for 2011 summer and fall samples in the Muskegon River. This data includes information from both rock cluster and Hess samples. Sites are arranged from upstream (US) to downstream (DS).

Site	*Summer*	*Fall*
Croton	6303 ± 4186	1688 ± 567
Pine	126 ± 59	498 ± 300
Thorn US	6 ± 6	1 ± 1
Thorn DS	17 ± 13	55 ± 48
Henning US	10 ± 6	1 ± 1
Henning DS	0	37.04 ± 29.39

Table 10. Results of a two-way ANOVA on log-transformed Hydropsychidae densities, and mean (±SE) Hydropsychidae densities in the Muskegon River by season (summer (S) and fall (F)), and sample site (Site) (Croton (Cr), Pine (P), Thornapple Upstream (TU), Thornapple Downstream (TD), Henning Upstream (HU), Henning Downstream (HD)), and the interaction between the two terms (Season x Site). Data presented are from samples taken in 2011.

Source	*df*	*Mean±SE*	*F*	*p*
Season	1	S: 4570±1024 F: 3739±992	0.004	0.949
Site	5	Cr: 8657±1608 P: 8846±2002 TU: 1555±596 TD: 2485±916 HU: 1807±891 HD: 1967±366	3.957	0.009
Season x Site	5	-	1.211	0.336

Table 11. Seasonal Richness (R), Common Taxa Richness (CTR, taxa ≥5% relative abundance), Shannon-Wiener Diversity Index (H'), and Evenness (J) values for macroinvertebrates at sample sites on Bigelow Creek in 2011. Sites are arranged from upstream (US) to downstream (DS).

Site	*R*		*CTR*		*H'*		*J*	
	Summer	Fall	Summer	Fall	Summer	Fall	Summer	Fall
Bigelow US	32	41	2	3	1.722	1.771	0.496	0.477
Bigelow DS	32	42	3	5	1.420	2.326	0.409	0.622

Table 12. Seasonal EPT Richness and EPT Index values at sample sites on Bigelow Creek in 2011. Sites are arranged from upstream (US) to downstream (DS).

Site	*EPT Richness*		*EPT Index*	
	Summer	Fall	Summer	Fall
Bigelow US	16	25	0.50	0.60
Bigelow DS	25	27	0.78	0.66

Table 13. Results of a two-way ANOVA and mean (±SE) on Ephemeroptera, Plecoptera, and Trichoptera richness in Bigelow Creek by season (summer (S) and fall (F)), and sample site (Site) (Bigelow Upstream (BU) and Bigelow Downstream (BD)), and the interaction between the two terms (Season x Site). Data presented are from samples taken in 2011.

Source	*df*	*Mean±SE*	*F*	*p*
Season	1	S: 8.8±0.7 F: 14.8±2.1	6.894	0.030
Site	1	BU: 12.8±2.2 BD: 10.8±1.7	0.766	0.407
Season x Site	1	-	0.532	0.487

Table 15. Unique macroinvertebrate taxa on Bigelow Creek, between the two sample sites. Bigelow US and Bigelow DS. The taxa include both summer and fall sample seasons for 2011.

Site	*Site Specific Taxa*
Bigelow US	*Hydropsyche,* Polycentropodidae, *Hexatoma, Baetisca, Caenis, Stenacron, Perlesta, Agnetina*
Bigelow DS	*Tipula, Seratella, Drunella,* Corydalidae, *Acroneuria,* Perlidae, *Podura*

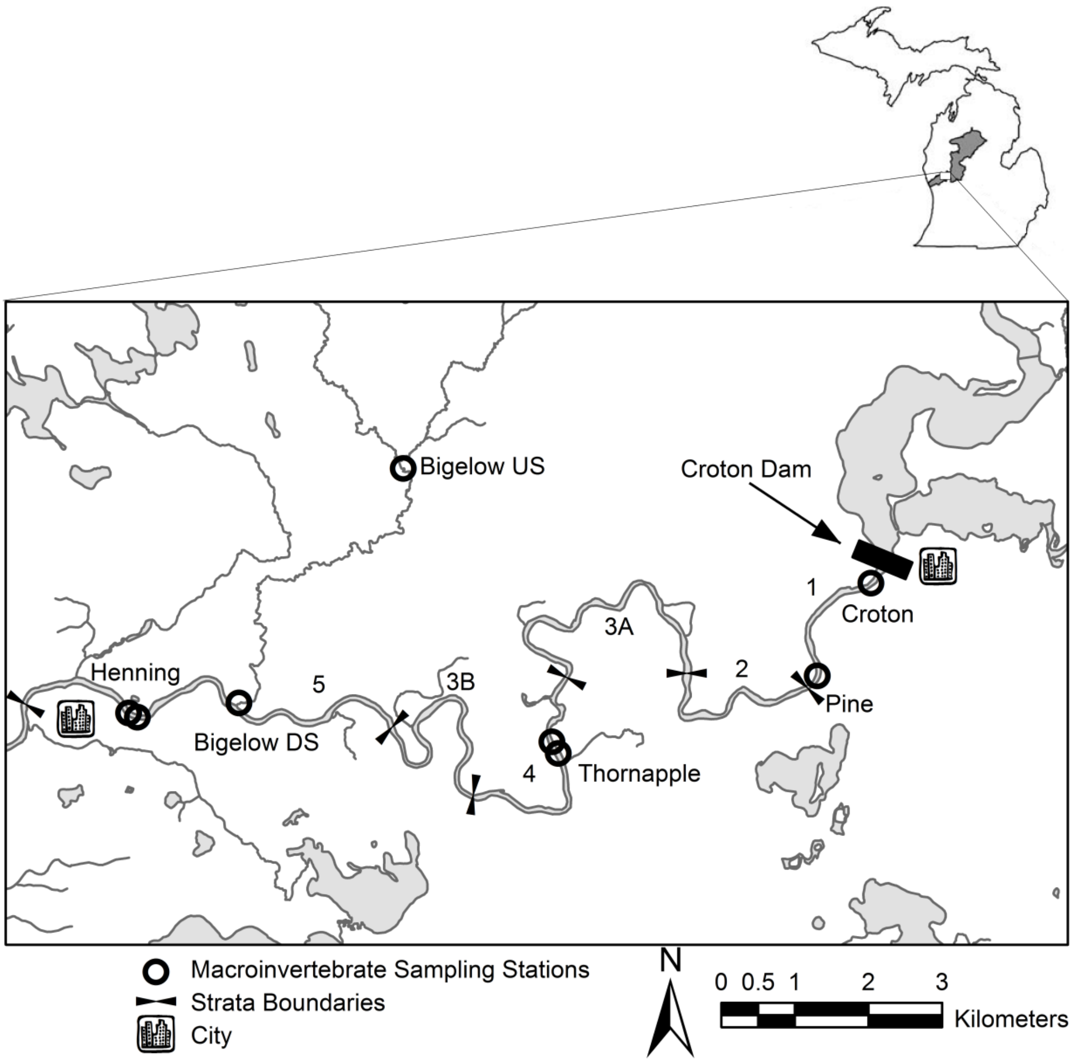

Figure 1. Location of sample sites on the Muskegon River and Bigelow Creek. Macroinvertebrate sampling sites on the Muskegon River and Bigelow Creek are shown and strata boundaries are delineated on the Muskegon River (see Table 1).

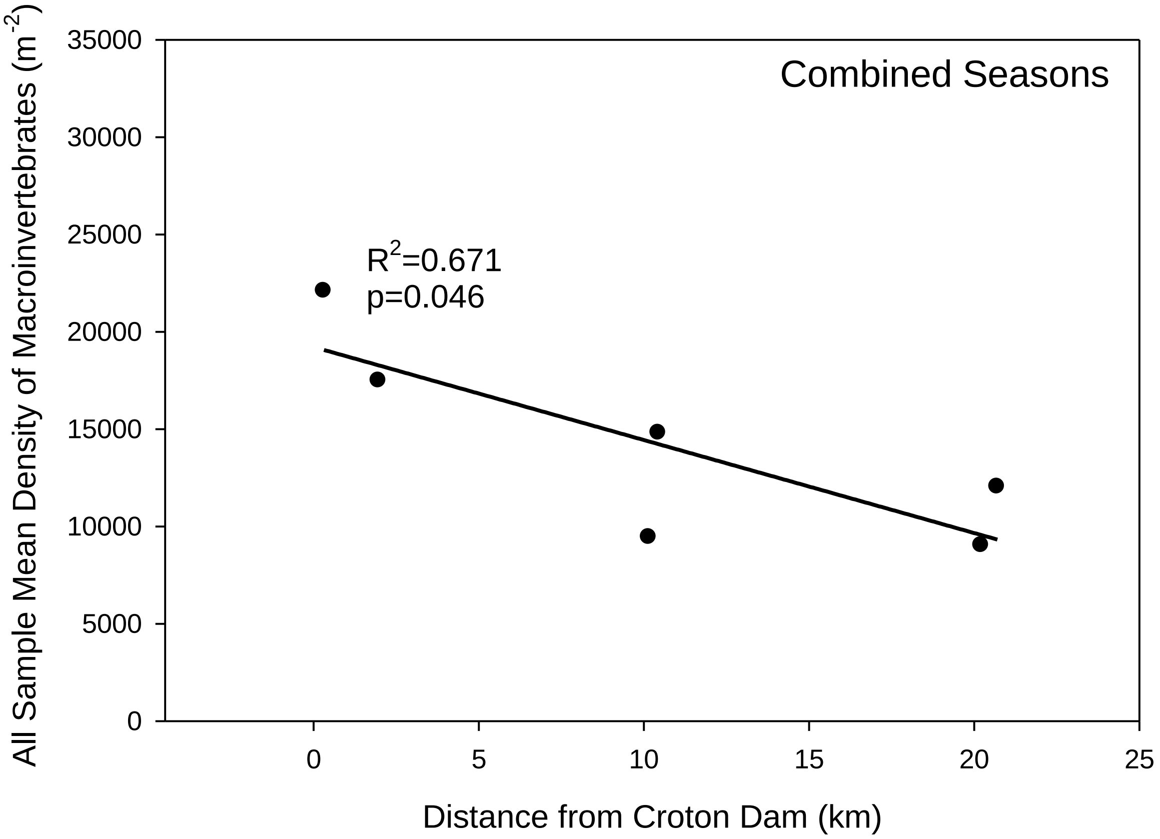

Figure 2. Linear regression of all sample macroinvertebrate mean density and distance from Croton Dam for data collected 2011. Summer and fall samples were combined for this figure.

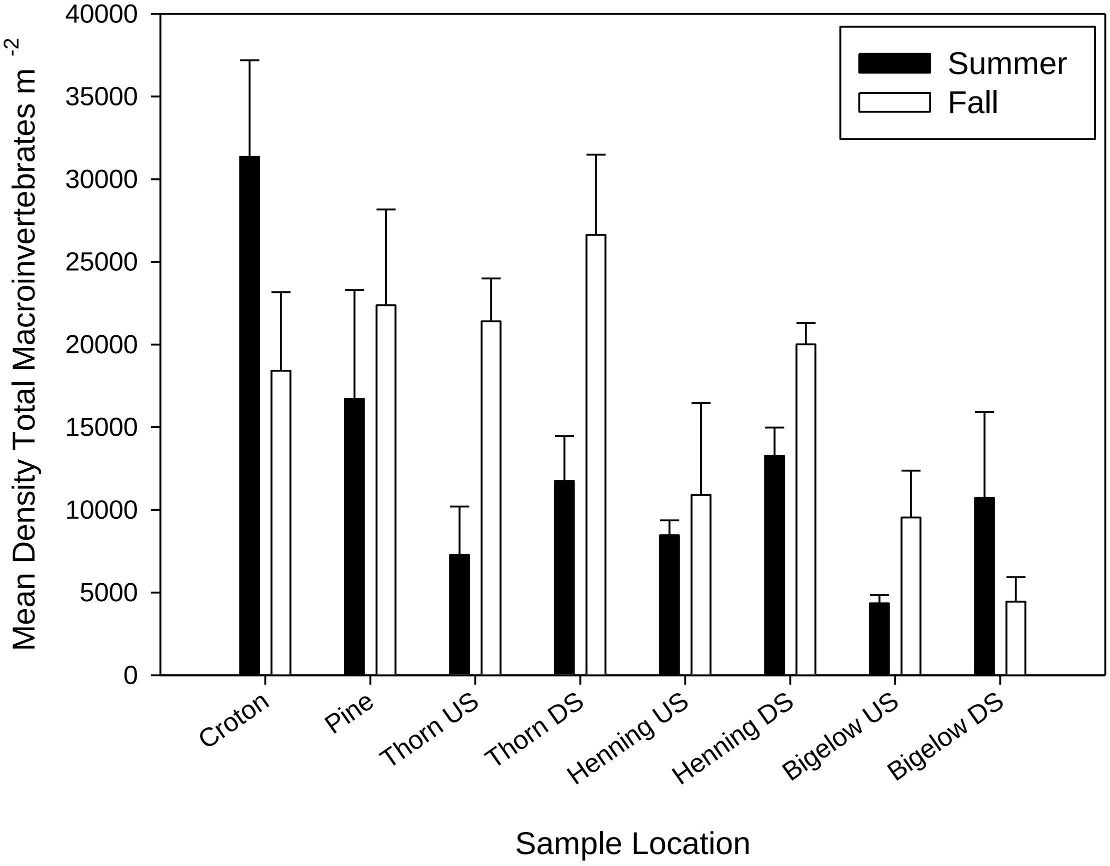

Figure 3. Mean macroinvertebrate densities (± SE, excluding zebra mussels) at Muskegon River and Bigelow Creek sample sites during 2011 sampling events (summer and fall). Sites are arranged from upstream to downstream.

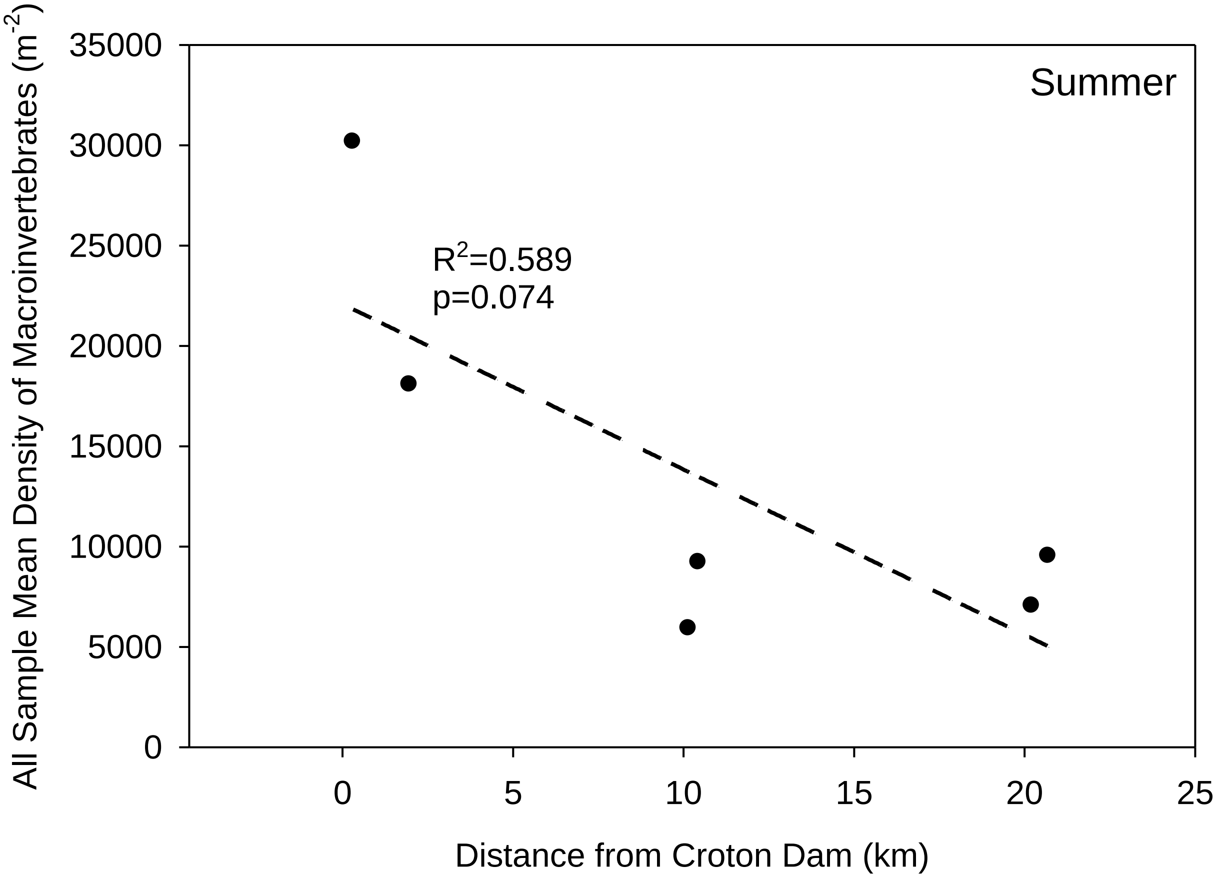

Figure 4. Linear regression of all-sample mean macroinvertebrate density (excluding zebra mussels) and distance from Croton Dam for data collected in summer 2011. This data includes information from both rock cluster and Hess samples.

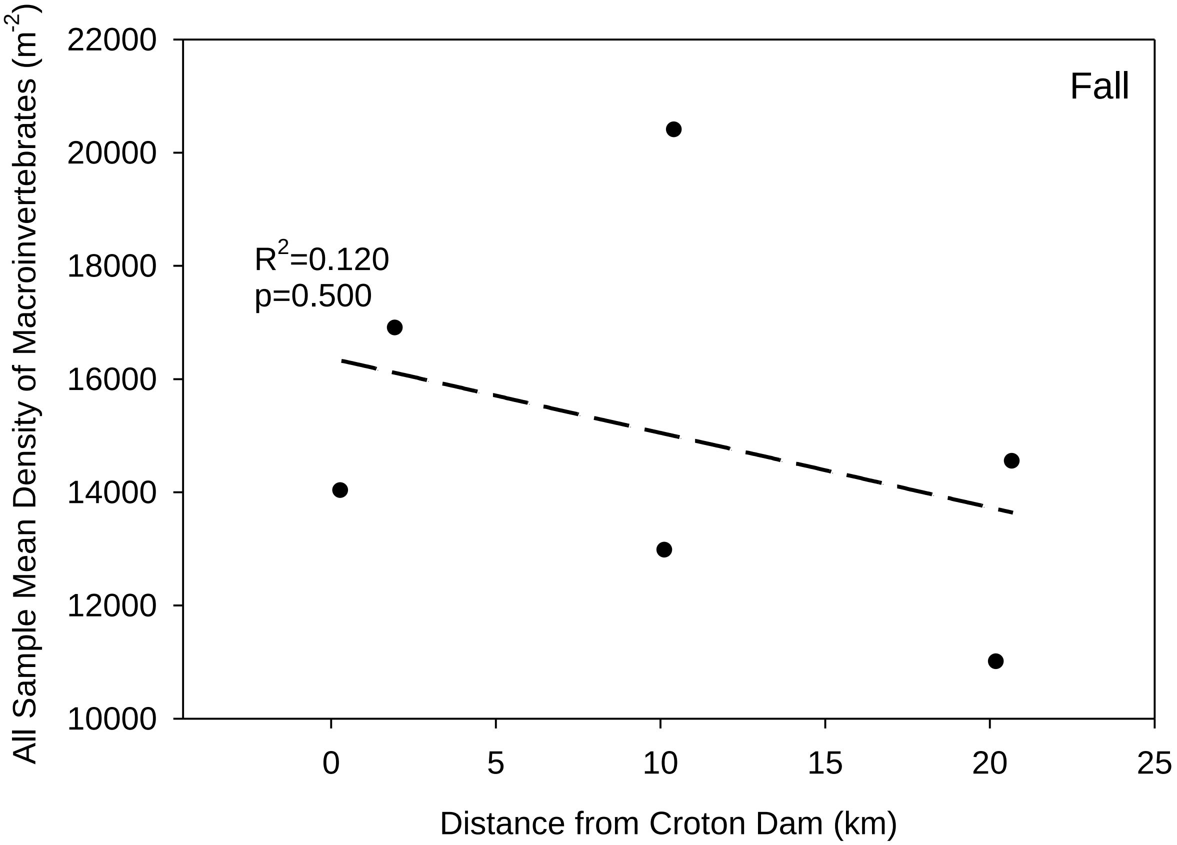

Figure 5. Linear regression of all-sample mean macroinvertebrate density (excluding zebra mussels) and distance from Croton Dam for data collected in fall 2011. This data includes information from both rock cluster and Hess samples.

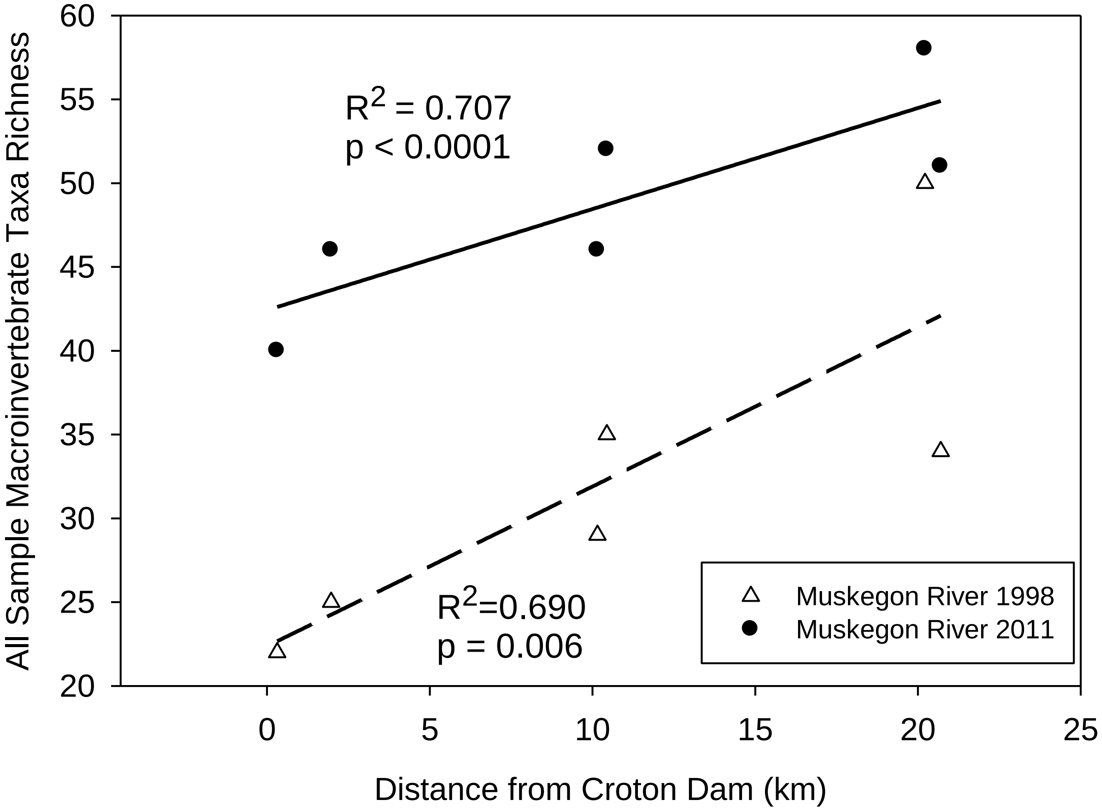

Figure 6. Linear regression of all-sample macroinvertebrate taxa richness and distance from Croton Dam for data collected in 1998 and 2011 macroinvertebrate communities. The 1998 samples are delineated by the open triangles and the dashed regression line, the 2011 samples are the closed circles and solid regression line. This data includes information from both rock cluster and Hess samples. Summer and fall samples were combined for both years in this figure. The 1998 data were used with permission.

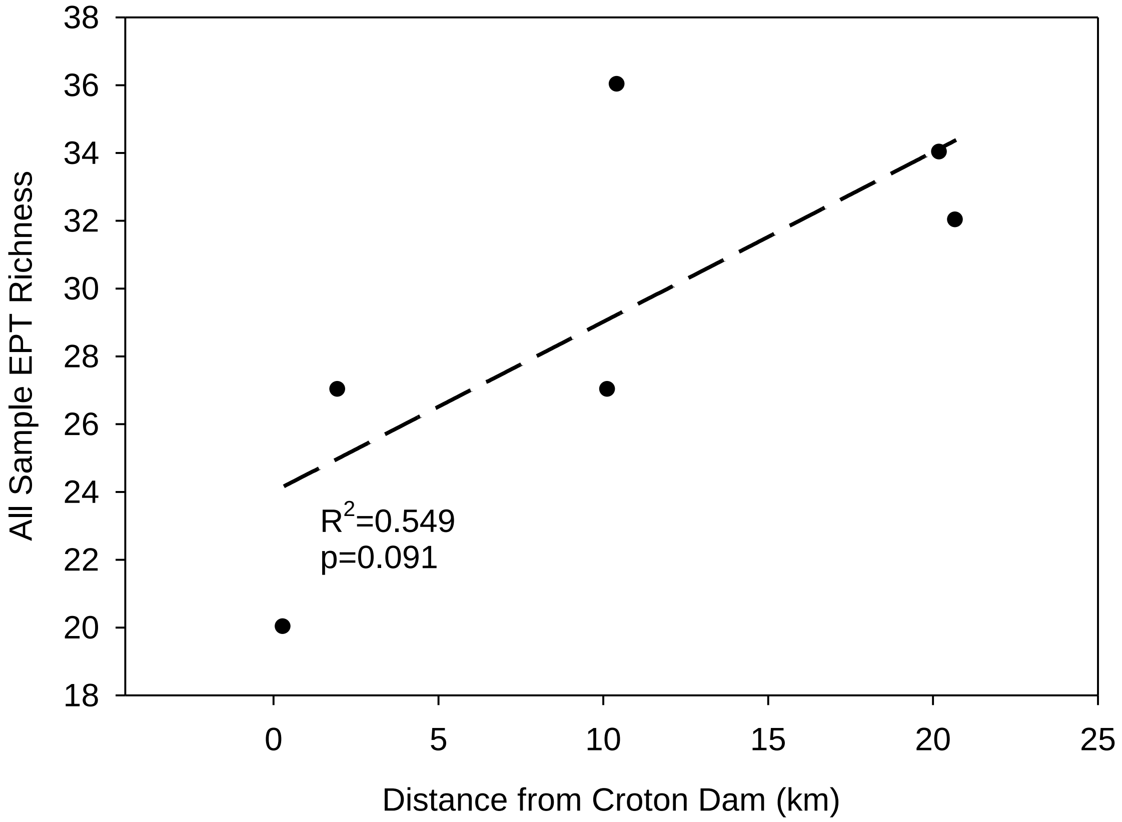

Figure 7. Linear regression of all-sample Ephemeroptera, Plecoptera, and Trichoptera taxa richness and distance from Croton Dam for data collected in 2011. Summer and fall samples were combined for both years. This data includes information from both rock cluster and Hess samples.

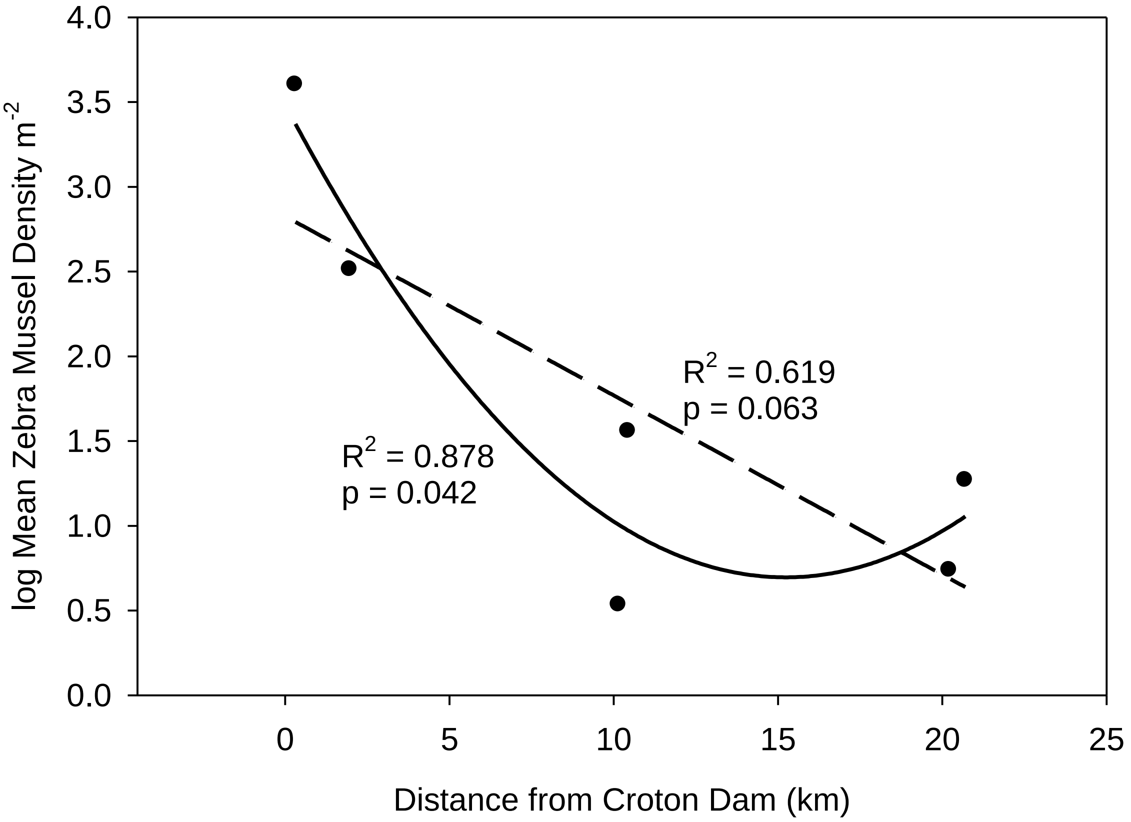

Figure 8. Linear and quadratic regressions of log-transformed mean zebra mussel density and distance downstream of Croton Dam in the Muskegon River during 2011 sampling events (summer and fall).

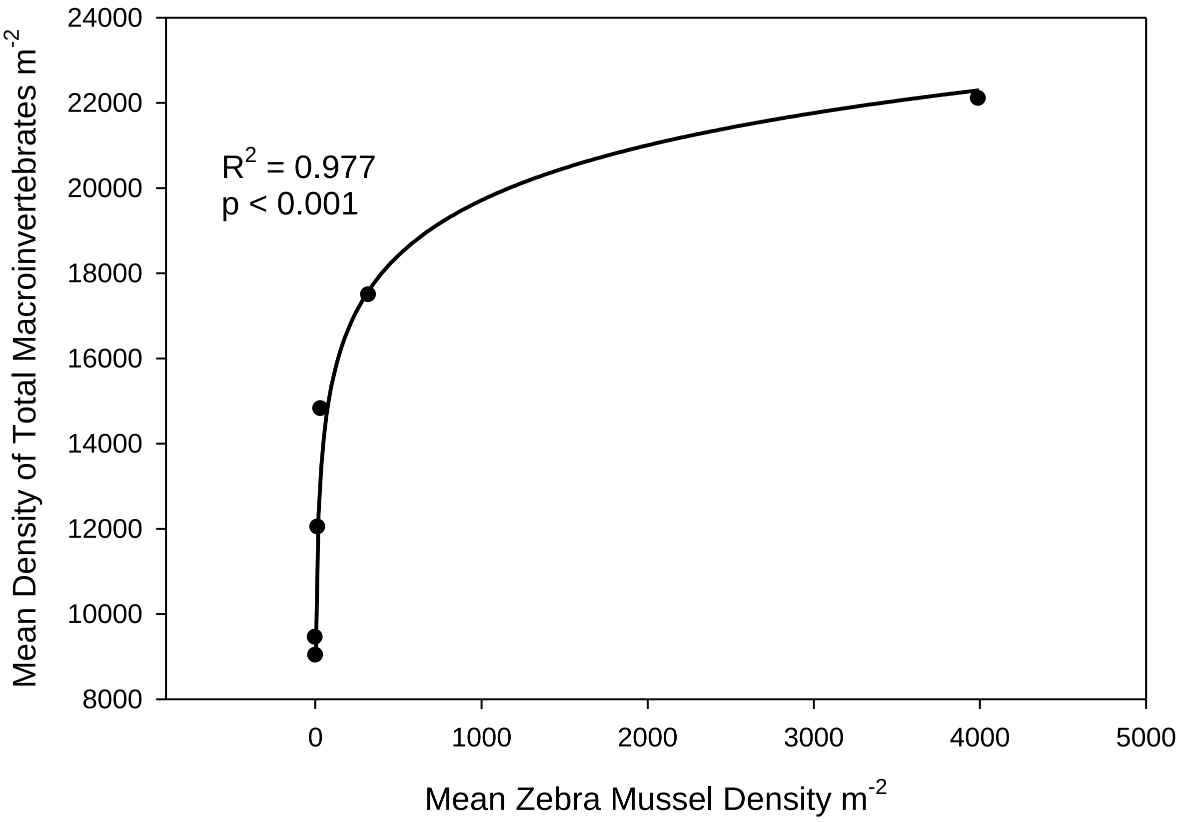

Figure 9. Logarithmic regression of mean total macroinvertebrate density (excluding zebra mussels) and mean zebra mussel density at the six sampling sites in the Muskegon River during 2011 sampling events (summer and fall).

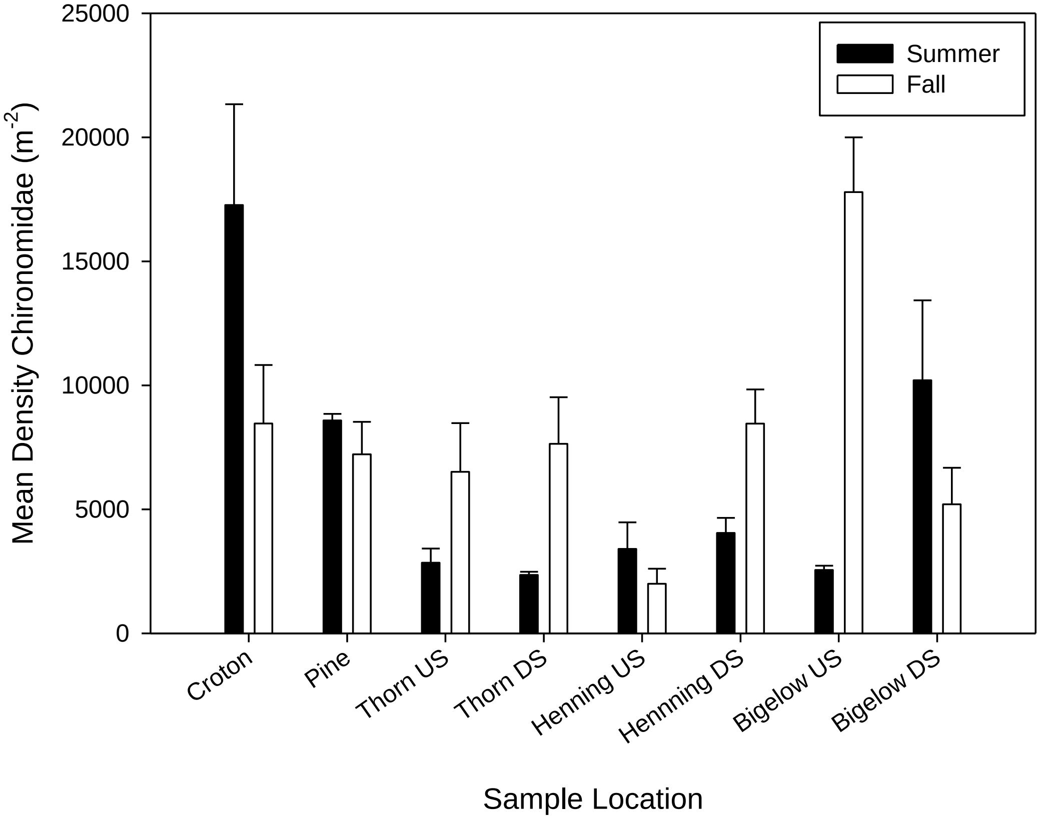

Figure 10. Mean Chironomidae densities (± SE) at Muskegon River and Bigelow Creek sample sites during 2011 sampling events (summer and fall). Sites are arranged from upstream to downstream.

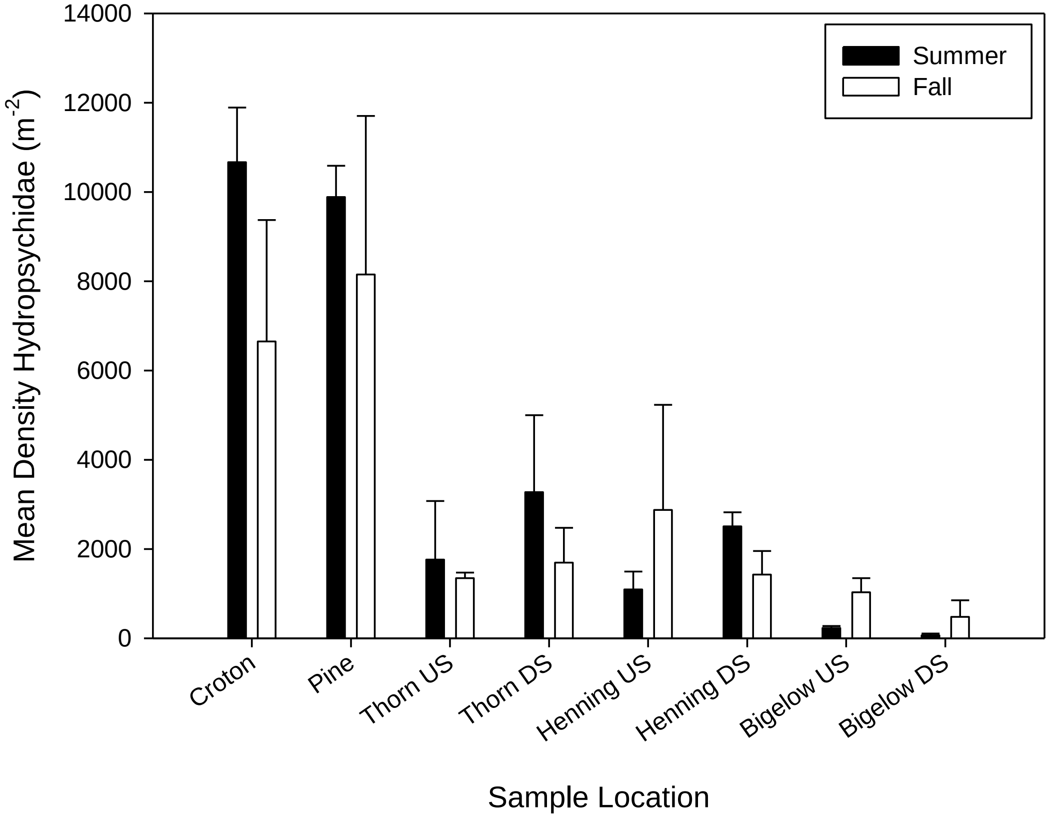

Figure 11. Mean Hydropsychidae densities (± SE) at Muskegon River and Bigelow Creek sample sites during 2011 sampling events (summer and fall). Sites are arranged from upstream to downstream.

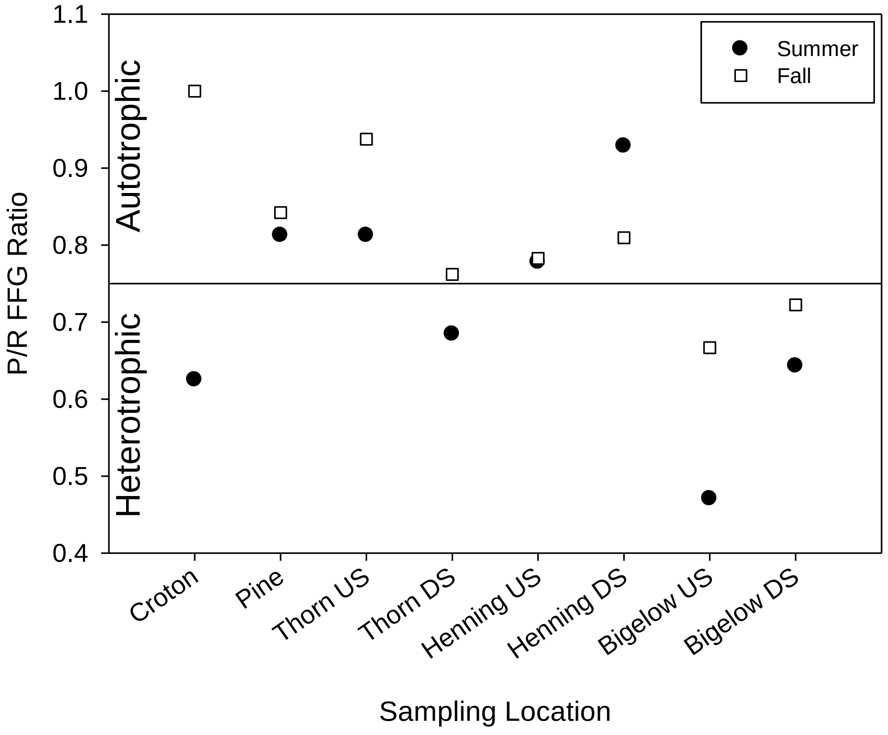

Figure 12. Ratios of functional feeding groups (scrapers/shredders and total collectors) in the Muskegon River and Bigelow Creek, estimating heterotrophic or autotrophic conditions during summer and fall seasons. Sites with values >0.75 (scrapers > shredders and collectors) are considered autotrophic. Sites with values <0.75 are considered heterotrophic.

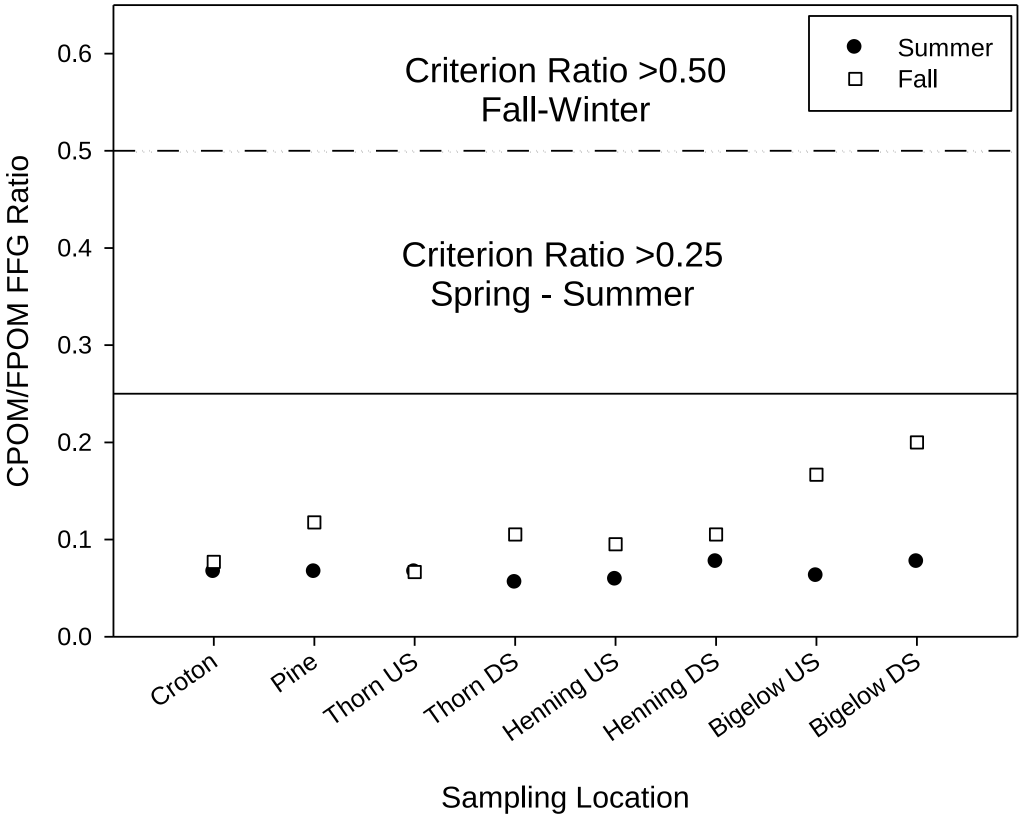

Figure 13. Ratios of functional feeding groups (shredders/total collectors) estimating organic matter size in Muskegon River and Bigelow Creek, were calculated for the summer and fall seasons. The criterion value for spring and summer is >0.25, whereas the criterion value for fall and winter is >0.50.

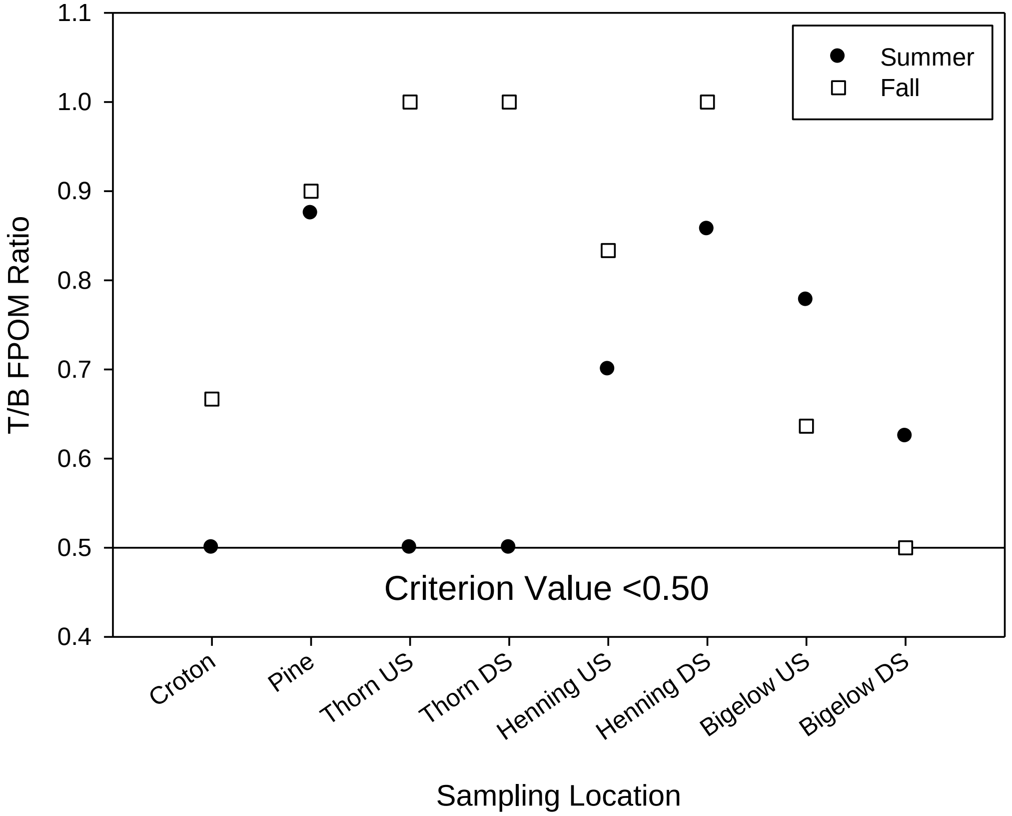

Figure 14. Ratios of functional feeding groups (filtering collectors/gathering collectors) in the Muskegon River and Bigelow Creek during summer and fall 2011. The FPOM in suspension (T) or stored in the benthos (B), has a criterion value that is typically <0.50.

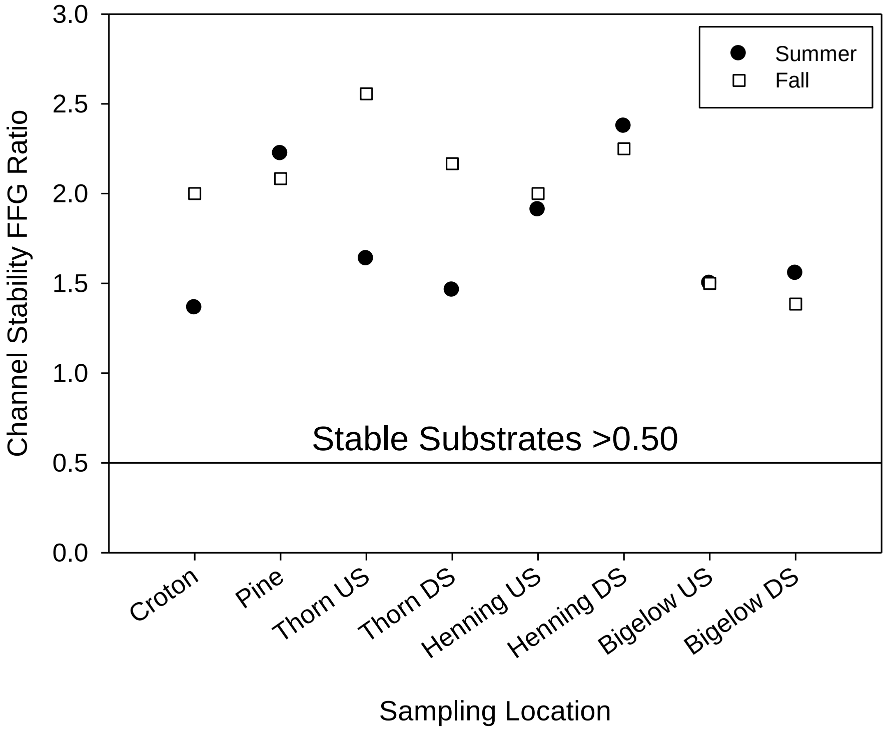

Figure 15. Ratios of functional feeding groups (scrapers and filtering collectors/shredders and gathering collectors) in the Muskegon River and Bigelow Creek, estimating benthic substrate stability were calculated for the summer and fall seasons. A site is considered to have a stable substrate if it has a value >0.50.

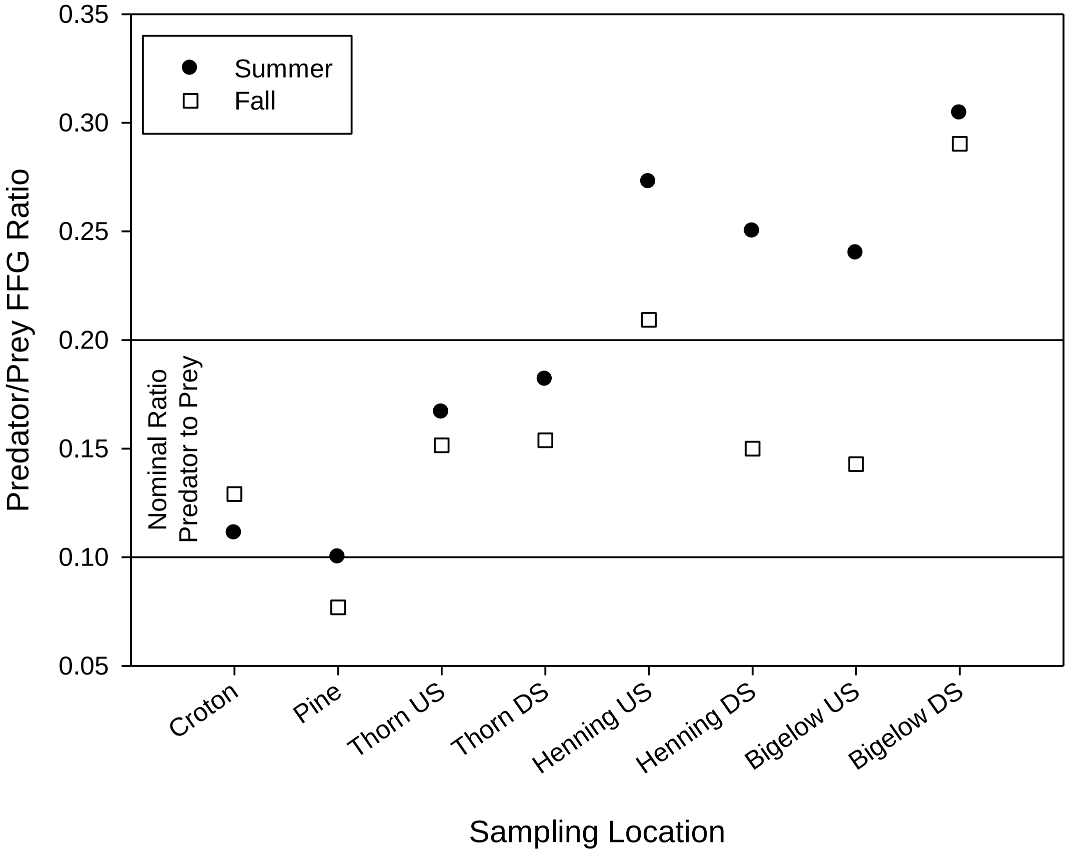

Figure 16. Ratios of functional feeding groups (predators/all other FFGs) in the Muskegon River and Bigelow Creek, estimating predator to prey densities were calculated for the summer and fall seasons. The nominal ratio of macroinvertebrate predators to prey is between 0.10 and 0.20.

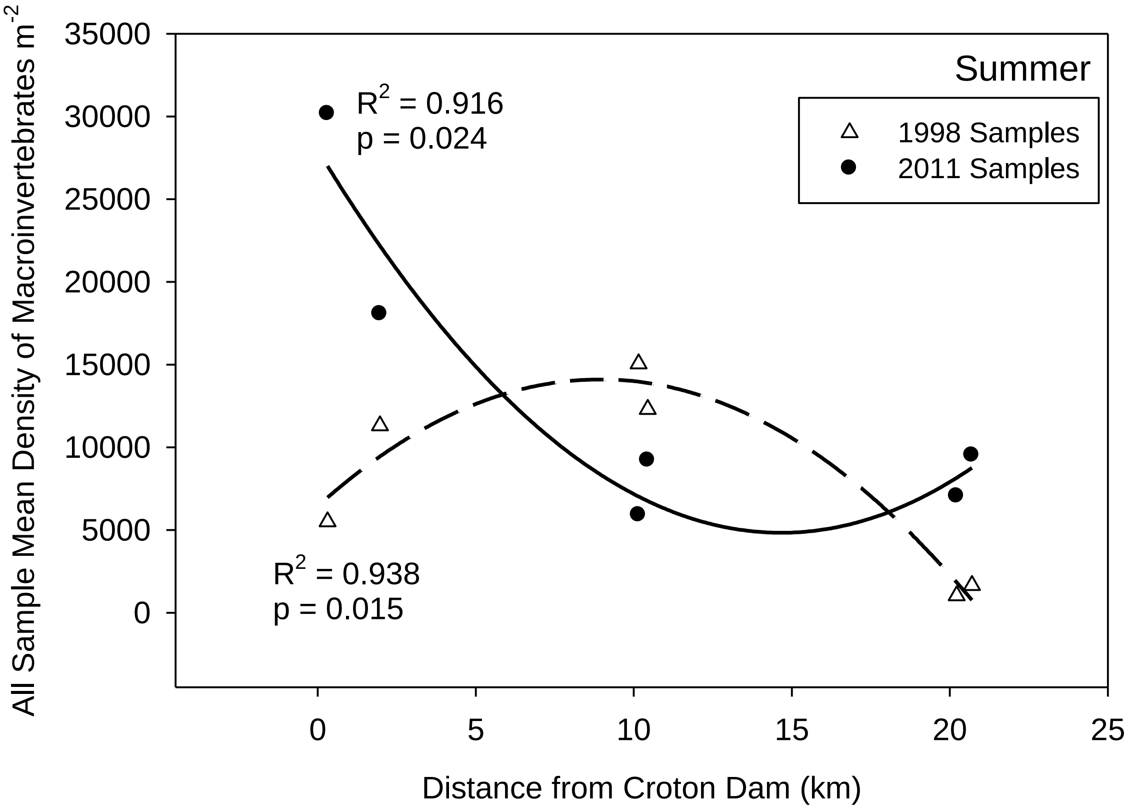

Figure 17. Quadratic regressions of 1998 and 2011 all-sample mean macroinvertebrate density of Muskegon River sites for summersamples. The 1998 samples are delineated by the open triangles and the dashed regression line, the 2011 samples are the closed circles and solid regression line. Data points include invertebrate estimates from both rock cluster and Hess samples. The 1998 data were used with permission.

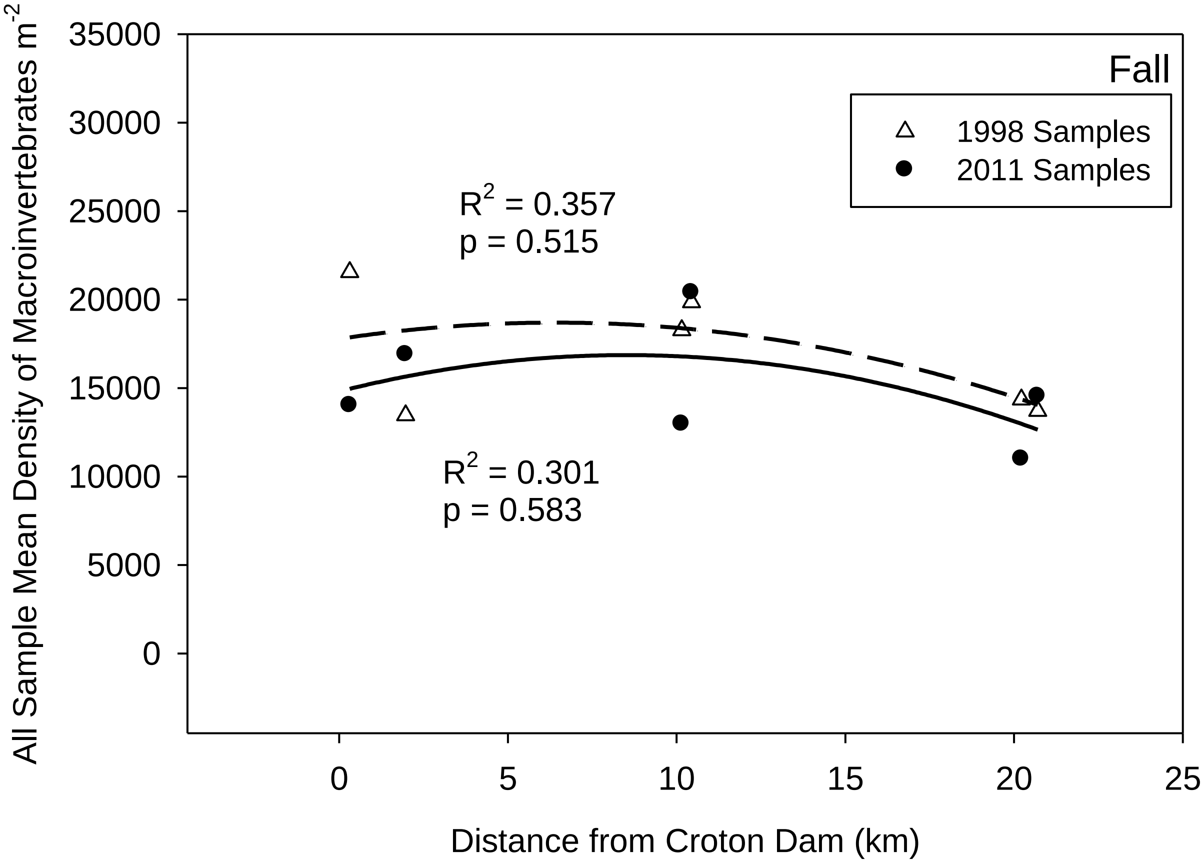

Figure 18. Quadratic regressions of 1998 and 2011 all-sample mean macroinvertebrate density of Muskegon River sites for fall samples. The 1998 samples are delineated by the open triangles and the dashed regression line, the 2011 samples are the closed circles and solid regression line. This data includes invertebrate estimates from both rock cluster and Hess samples. The 1998 data were used with permission.

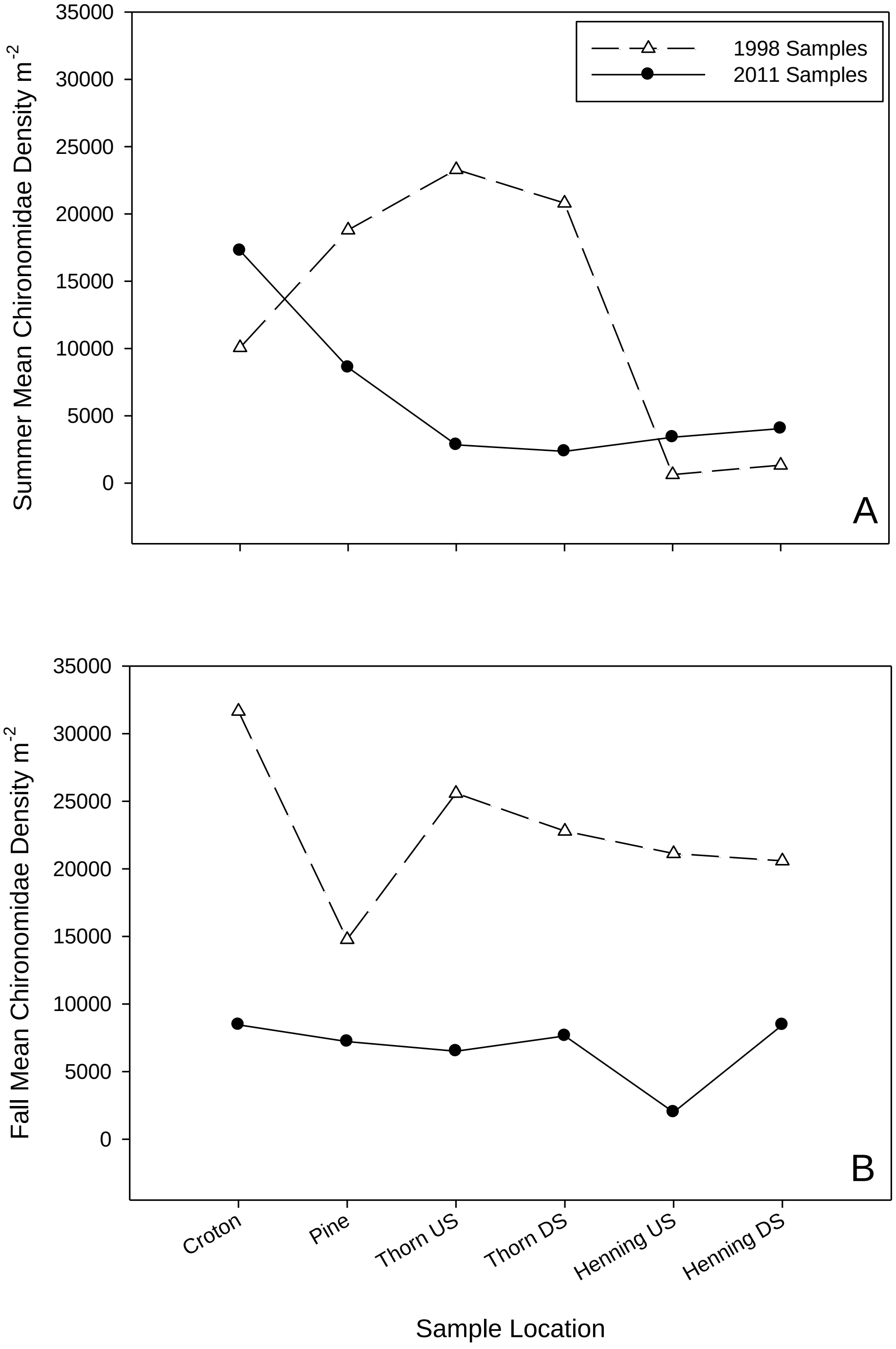

Figure 19. Mean density of Chironomidae in the Muskegon River during summer (A) and fall (B) 1998 and 2011. The 1998 samples are delineated by the open triangles and the dashed line, the 2011 samples are the closed circles and solid line. The 1998 data were used with permission.

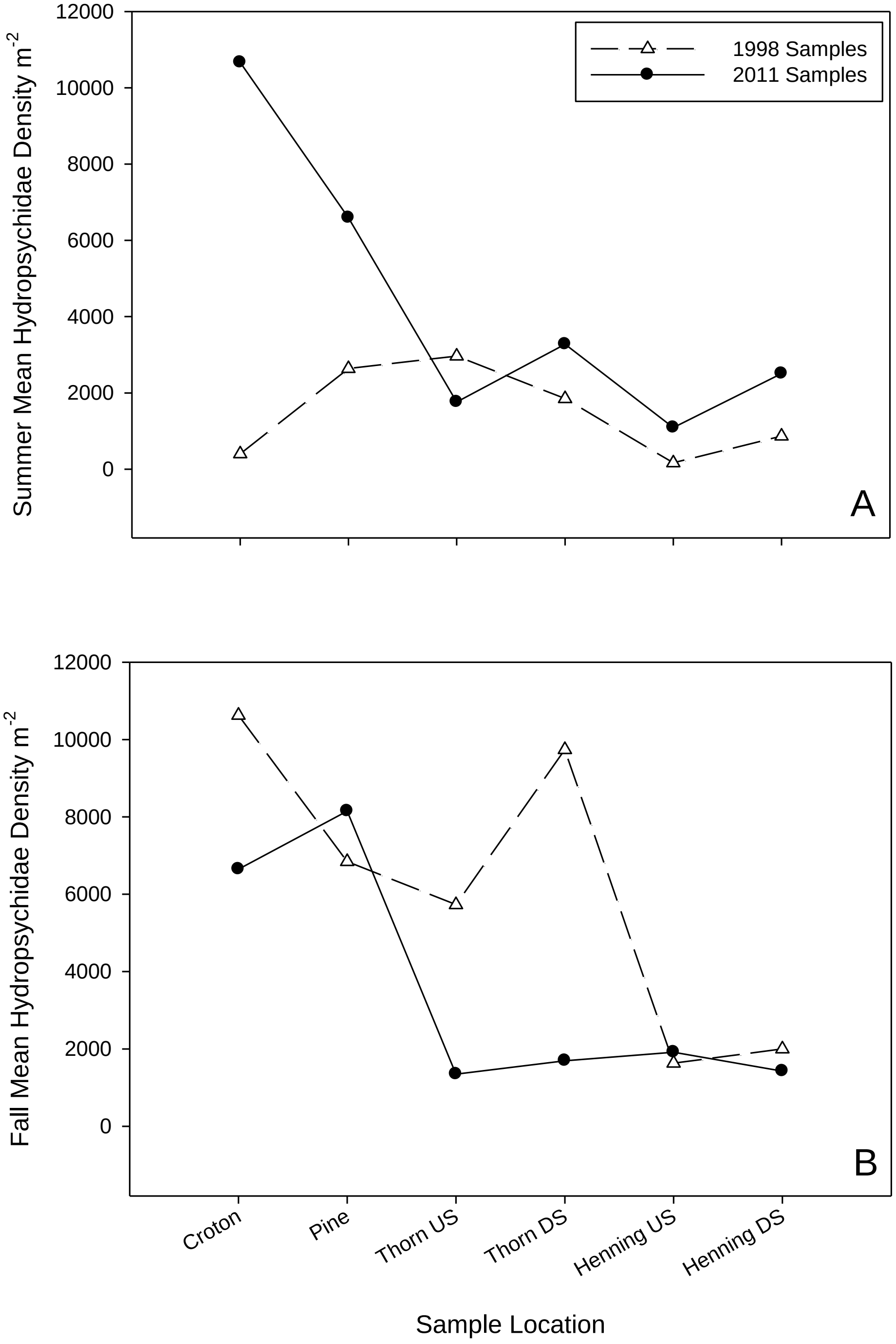

Figure 20. Mean density of Hydropsychidae in the Muskegon River during summer (A) and fall (B) 1998 and 2011. The 1998 samples are delineated by the open triangles and the dashed line, the 2011 samples are the closed circles and solid line. The 1998 data were used with permission.

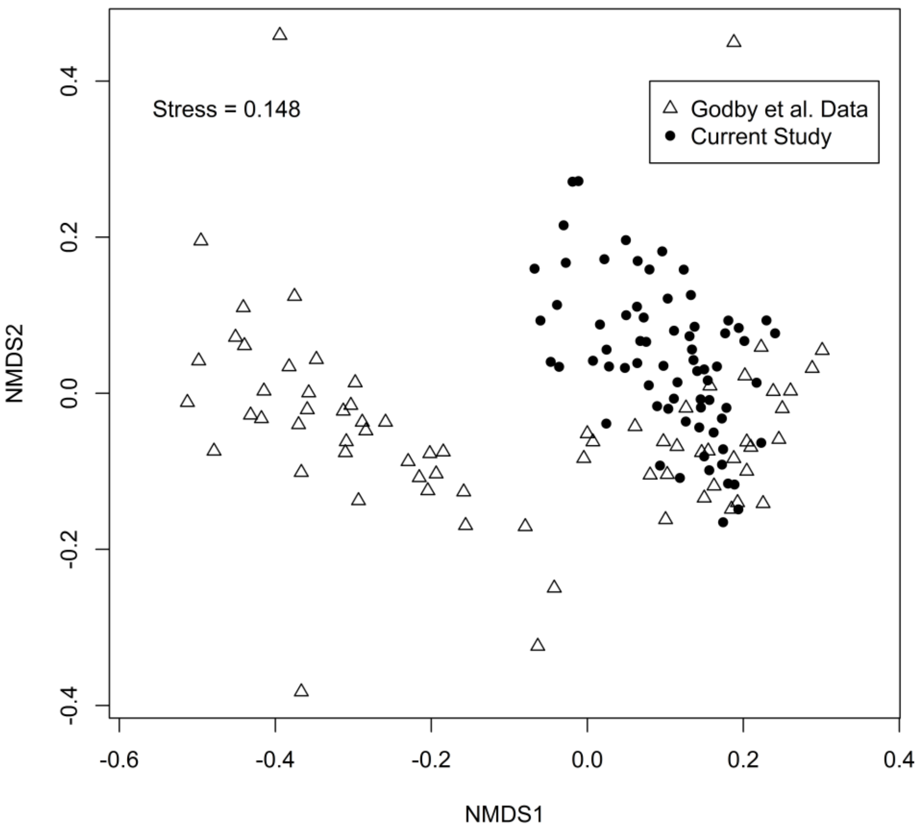

Figure 21. Nonmetric multidimensional scaling (NMDS) ordination plot of macroinvertebrate taxa density collected at sites located on the Muskegon River during the summer and fall of 1998 and 2011. All macroinvertebrate taxa collected were used with the exception of Chironomidae and zebra mussels. The 1998 data were used with permission.

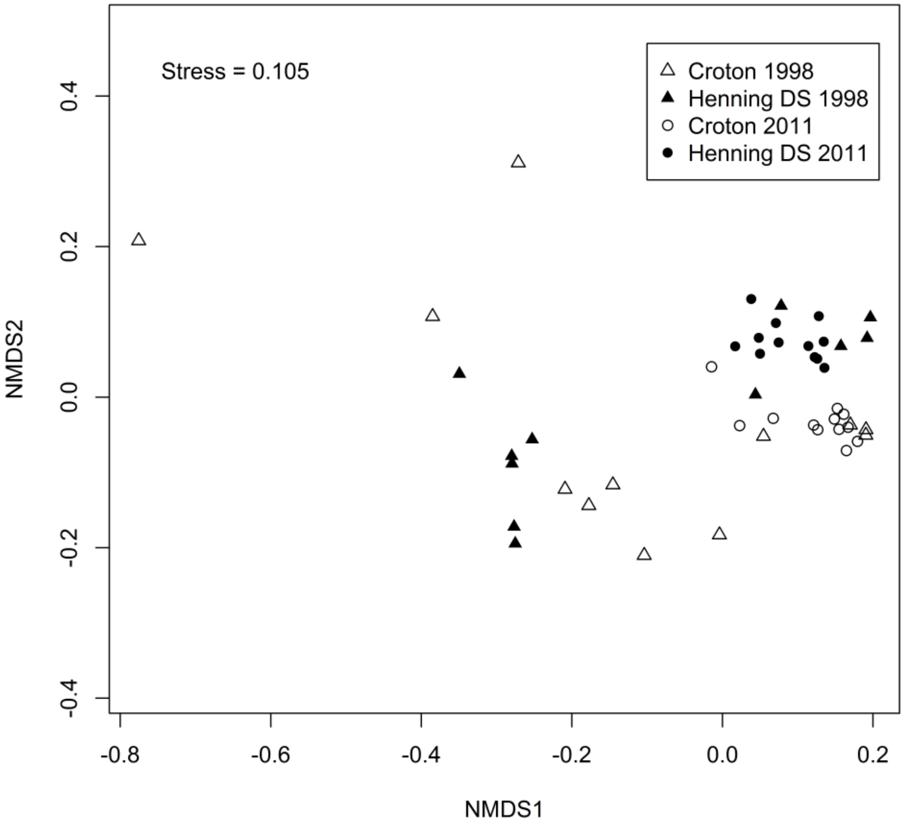

Figure 22. Nonmetric multidimensional scaling (NMDS) ordination plot of macroinvertebrate taxa density at the upstream (Croton) and downstream site (Henning DS) of the Muskegon River collected during summer and fall of 1998 and 2011. All macroinvertebrate taxa were used with the exception of Chironomidae and zebra mussels. The 1998 data were used with permission.

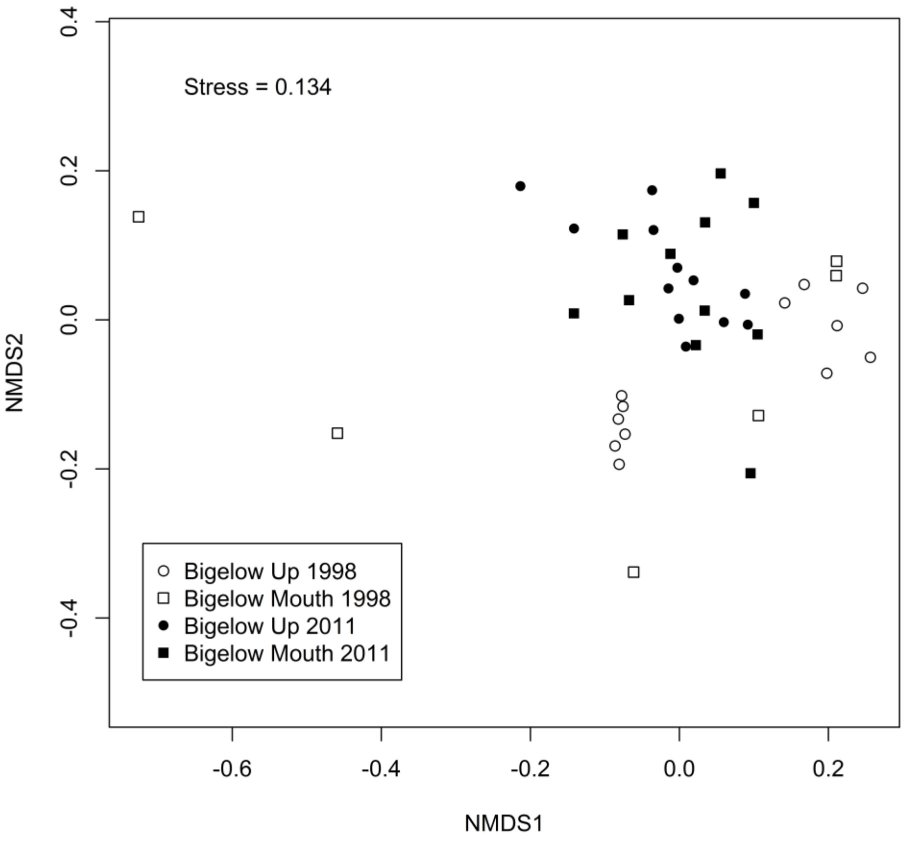

Figure 23. Nonmetric multidimensional scaling (NMDS) ordination plot of macroinvertebrate taxa density at the upstream (Bigelow Up) and downstream site (Bigelow Mouth) of Bigelow Creek collected during summer and fall of 1998 and 2011. All macroinvertebrate taxa were used with the exception of Chironomidae and zebra mussels. The 1998 data were used with permission.

APPENDIX A

Densities of each macroinvertebrate taxon were estimated for both the Hess samples (n=3) and rock cluster samples (n=3) for both Muskegon River and Bigelow Creek. The sample method (either Hess or rock cluster) that generated the highest density estimate for a given taxon was used for that particular sample's replicates. The highest density estimate samples for each taxon are presented below; summer samples are denoted with (S), fall samples are denoted with (F). A density of zero is represented with (-), and (n) is given if there is no data for a sample. Upstream samples are indicated by (US), downstream sites are (DS).

Taxon	***Croton***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Aeshnidae	-	-	-	-	-	-
Coenagrionidae	-	-	-	-	-	-
Gomphidae	-	-	-	-	-	-
Odonata	-	-	-	-	-	-
Corixidae	-	-	-	-	-	-
Hemiptera	-	-	-	-	-	-
Saldidae	-	-	-	-	-	-
Amphipoda	1576.955	1474.850	828.185	215.555	578.595	238.245
Isopoda	714.735	317.660	204.210	-	11.345	56.725
Agraylea	-	471.466	-	-	7.461	-
Brachycentrus	-	22.690	-	-	-	-
Ceratopsyche	67.293	62.035	203.000	195.720	499.887	1313.808
Cheumatopsyche	6330.510	3879.990	2824.905	668.710	4051.323	3147.936
Chimarra	-	-	-	-	-	-
Glossosoma	-	12.407	-	8.155	14.922	-

Taxon	***Croton***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Helicopsyche	-	-	-	8.155	-	13.008
Hydropsyche	-	-	-	8.155	-	-
Hydropsychidae	1839.342	7692.340	9097.731	668.710	3044.088	6354.408
Hydroptilidae	22.690	-	-	8.155	253.674	247.152
Leuchotrichia	29.908	-	-	48.930	29.844	84.552
Macrostemum	-	-	-	-	-	-
Micrasema	-	372.210	40.797	8.155	7.461	19.512
Neophylax	-	22.690	-	16.310	22.383	-
Nyctiophylax	-	-	-	-	-	-
Philopotomidae	-	-	-	1508.885	68.070	-
Protoptila	-	-	-	-	-	-
Psychomyia	-	56.725	34.035	122.325	373.050	526.824
Antocha	89.724	186.105	108.792	163.100	611.802	351.216
Atherix	-	-	-	-	-	-
Ceratopogonidae	13.599	-	-	-	-	-
Chironomidae	12516.498	25359.908	13925.376	3912.665	9676.917	11791.752
Diptera	-	-	-	-	-	-
Empididae	-	24.814	-	22.690	11.345	22.690
Simuliidae	-	37.221	27.198	-	-	91.056
Anthopotamus	-	-	-	-	-	-
Baetidae	-	11.345	-	11.345	-	-
Baetisca	-	-	-	-	-	-
Caenis	22.690	34.035	68.070	11.345	22.690	-
Drunella	-	-	-	-	-	-
Ephemerella	-	-	-	-	-	-
Ephemerellidae	-	-	-	-	-	-

Taxon	***Croton***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Ephemeridae	-	-	-	-	-	-
Ephemeroptera	-	22.690	-	34.035	-	-
Heptageniidae	-	-	-	8.155	89.532	32.520
Isonychia	-	-	-	-	-	-
Maccaffertium	-	-	-	-	-	-
Rhithrogena	-	-	-	-	-	-
Seratella	-	-	-	-	-	-
Stenacron	-	-	-	-	-	-
Stenonema	-	11.345	-	8.155	-	6.504
Tricorythodes	-	-	11.345	40.775	7.461	6.504
Chauliodes	-	-	-	-	-	-
Corydalidae	-	-	-	8.155	7.461	6.504
Nigronia	-	-	-	8.155	-	-
Coleoptera	-	-	-	-	-	-
Dubiraphia	-	-	-	-	-	-
Elmidae	-	-	-	-	-	-
Optioservus	-	-	-	-	-	11.345
Psephenus	-	-	-	-	-	11.345
Stenelmis	-	11.345	-	-	-	-
Petrophila	-	-	-	-	7.461	6.504
Acroneuria	-	-	-	-	-	-
Perlesta	-	-	-	-	-	-
Perlidae	-	-	-	-	-	-
Perlodidae	-	-	-	-	-	-
Plecoptera	-	-	-	-	-	-
Taeniopteryx	-	-	-	-	-	-

Taxon	***Croton***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Gastropoda	34.035	623.975	-	90.760	419.765	56.725
Hydrachnidia	-	136.140	34.035	-	141.759	143.088
Limpets	-	136.140	-	-	193.986	-
Nematoda	-	136.140	306.315	-	22.383	-
Oligochaeta	-	828.185	340.315	918.945	192.865	601.285
Platyhelminthes	-	737.425	13.599	587.160	246.213	175.608
Podura	-	-	13.599	-	-	-
Zebra Mussel	1043.740	26706.130	181.520	1231.405	3335.067	3011.352

Taxon	***Pine***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Aeshnidae	-	-	-	-	-	-
Coenagrionidae	-	-	-	-	-	11.345
Gomphidae	-	-	-	-	-	-
Odonata	-	-	-	-	-	-
Corixidae	-	-	-	-	-	-
Hemiptera	-	-	-	-	-	-
Saldidae	-	-	-	-	-	-
Amphipoda	n	453.800	453.800	1293.330	487.835	612.630
Isopoda	-	-	-	11.345	11.345	11.345
Agraylea	-	-	127.820	-	-	-
Brachycentrus	n	34.035	11.345	22.206	95.051	40.565
Ceratopsyche	n	1486.195	1792.510	481.130	1849.174	1533.357
Cheumatopsyche	n	3165.255	3142.565	2030.755	113.450	3641.745
Chimarra	-	-	-	-	-	11.345
Glossosoma	-	-	-	-	17.282	32.452
Helicopsyche	-	-	-	207.256	146.897	137.921
Hydropsyche	12.303	-	-	29.608	155.538	97.356
Hydropsychidae	n	4538.000	5649.810	4447.240	726.080	9631.905
Hydroptilidae	553.635	353.848	127.820	133.236	-	576.023
Leuchotrichia	1500.966	1141.964	1035.342	703.190	1175.176	567.910
Macrostemum	n	-	45.380	-	-	-
Micrasema	n	158.830	181.520	59.216	-	170.373
Neophylax	319.878	112.588	12.782	-	-	8.113
Nyctiophylax	-	-	-	11.345	-	-
Philopotomidae	-	-	-	-	136.140	-
Protoptila	n	465.145	181.520	90.760	22.690	4696.830

Taxon	***Pine***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Psychomyia	233.757	434.268	76.692	59.216	-	48.678
Antocha	n	215.555	170.175	325.688	69.128	227.164
Atherix	-	-	-	-	-	-
Ceratopogonidae	-	-	-	-	-	-
Chironomidae	n	8315.885	8849.100	9699.975	5241.390	6704.895
Diptera	-	60.487	-	-	-	-
Empididae	n	1363.140	-	363.040	329.005	147.485
Simuliidae	184.545	209.092	242.858	11.345	-	79.415
Anthopotamus	-	-	-	-	-	-
Baetidae	n	669.355	260.935	102.105	11.345	226.900
Baetisca	-	-	-	-	-	-
Caenis	n	442.455	465.145	45.380	22.690	-
Drunella	-	-	-	-	-	-
Ephemerella	-	-	-	-	-	-
Ephemerellidae	-	-	-	-	-	-
Ephemeridae	-	-	-	-	-	-
Ephemeroptera	86.121	80.420	51.128	14.804	8.641	16.226
Heptageniidae	24.606	16.084	-	397.075	113.450	136.140
Isonychia	-	-	-	-	-	-
Maccaffertium	12.303	-	-	90.760	22.690	45.380
Rhithrogena	-	-	-	-	-	-
Seratella	-	-	-	-	-	-
Stenacron	-	-	-	29.608	-	81.130
Stenonema	-	16.084	-	34.035	22.690	11.345
Tricorythodes	n	11.345	-	238.245	7.461	6.504
Chauliodes	-	-	-	-	-	-

Taxon	***Pine***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Corydalidae	-	-	-	-	-	-
Nigronia	n	22.690	-	-	-	-
Coleoptera	-	-	-	-	-	-
Dubiraphia	-	-	-	-	-	-
Elmidae	-	-	-	-	-	-
Optioservus	n	11.345	22.690	56.725	-	-
Psephenus	n	22.690	-	11.345	34.035	34.035
Stenelmis	n	22.690	79.415	-	-	22.690
Petrophila	-	-	-	44.412	-	24.339
Acroneuria	-	-	-	-	-	-
Perlesta	-	-	-	-	-	-
Perlidae	-	-	-	-	-	-
Perlodidae	-	-	-	-	-	-
Plecoptera	-	-	-	-	-	-
Taeniopteryx	-	-	-	-	-	11.345
Gastropoda	49.212	-	-	987.015	181.520	805.495
Hydrachnidia	295.272	273.428	25.564	476.490	238.245	623.975
Limpets	-	-	-	-	-	-
Nematode	n	68.070	11.345	68.070	-	102.105
Oligochaeta	n	521.870	147.485	113.450	34.035	11.345
Platyhelminthes	270.666	16.084	12.782	760.115	419.765	102.105
Podura	-	-	-	11.345	-	-
Zebra Mussel	282.969	176.924	-	1917.305	680.700	158.830

Taxon	***Thornapple US***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Aeshnidae	-	-	-	-	-	-
Coenagrionidae	-	-	-	-	-	-
Gomphidae	-	-	-	-	-	-
Odonata	-	-	-	-	-	13.918
Corixidae	-	-	-	-	-	-
Hemiptera	-	-	-	-	-	-
Saldidae	-	-	-	-	-	-
Amphipoda	34.035	79.415	11.345	90.760	181.520	226.900
Isopoda	-	-	-	-	-	-
Agraylea	-	-	-	-	-	-
Brachycentrus	-	-	-	-	60.472	34.795
Ceratopsyche	283.625	34.035	1531.575	121.770	158.739	125.262
Cheumatopsyche	45.380	22.690	1747.130	73.062	226.770	361.868
Chimarra	-	-	-	-	22.690	56.725
Glossosoma	20.283	-	-	-	-	-
Helicopsyche	-	-	6.761	-	52.913	48.713
Hydropsyche	124.795	11.345	124.795	474.903	748.341	389.704
Hydropsychidae	241.087	280.876	1102.043	949.806	944.875	1078.645
Hydroptilidae	-	-	68.070	-	400.627	-
Leuchotrichia	7.777	19.596	527.358	840.213	393.068	1530.980
Macrostemum	-	-	-	-	-	-
Micrasema	101.101	39.192	-	124.795	158.830	-
Neophylax	-	-	-	-	-	6.959
Nyctiophylax	-	-	-	-	-	-
Philopotomidae	-	-	-	-	-	-
Protoptila	90.760	11.345	45.380	4249.773	7657.267	9081.495

Taxon	***Thornapple US***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Psychomyia	23.331	71.852	67.610	170.478	393.068	626.310
Antocha	93.324	300.472	54.088	669.335	329.005	22.690
Atherix	45.380	-	136.140	-	-	13.918
Ceratopogonidae	-	-	-	-	-	-
Chironomidae	1974.030	2632.040	3925.370	4742.210	10426.055	4367.825
Diptera	-	-	-	-	-	-
Empididae	-	-	-	192.865	329.005	170.175
Simuliidae	46.662	13.064	365.094	36.531	30.236	34.795
Anthopotamus	-	-	-	-	-	-
Baetidae	192.865	204.210	952.980	680.700	363.040	-
Baetisca	-	-	-	-	-	-
Caenis	34.035	181.520	113.450	73.062	-	-
Drunella	-	-	-	-	-	-
Ephemerella	-	-	-	-	-	-
Ephemerellidae	-	65.320	-	1690.405	1531.575	703.390
Ephemeridae	-	-	-	-	-	-
Ephemeroptera	79.415	-	-	-	-	-
Heptageniidae	-	45.380	79.415	964.325	260.935	397.075
Isonychia	-	-	-	-	-	6.959
Maccaffertium	-	11.345	-	328.779	347.714	13.918
Rhithrogena	-	-	-	-	-	-
Seratella	11.345	-	11.345	12.177	-	13.918
Stenacron	-	-	-	-	-	-
Stenonema	11.345	-	-	36.531	45.354	-
Tricorythodes	-	-	-	207.009	128.503	20.877
Chauliodes	-	-	-	-	-	-

Taxon	***Thornapple US***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Corydalidae	-	-	-	-	-	-
Nigronia	-	-	-	-	-	-
Coleoptera	-	-	11.345	-	-	-
Dubiraphia	-	11.345	11.345	-	-	-
Elmidae	-	-	-	-	-	-
Optioservus	22.690	-	249.590	56.725	-	-
Psephenus	-	22.690	-	-	22.690	-
Stenelmis	-	-	113.450	-	22.690	-
Petrophila	-	-	-	-	-	6.959
Acroneuria	-	-	-	-	-	-
Perlesta	11.345	-	-	-	-	-
Perlidae	-	-	-	-	-	-
Perlodidae	-	-	-	-	-	-
Plecoptera	-	-	-	-	-	13.918
Taeniopteryx	-	-	-	-	-	-
Gastropoda	-	249.590	-	-	124.795	22.690
Hydrachnidia	260.935	79.415	1361.400	1077.775	703.390	113.450
Limpets	-	-	-	-	-	-
Nematode	34.035	340.350	-	-	68.070	-
Oligochaeta	45.380	136.140	465.145	136.140	294.970	215.555
Platyhelminthes	-	-	22.690	-	22.690	11.345
Podura	-	-	-	-	-	-
Zebra Mussel	-	34.035	-	-	-	6.959

Taxon	***Thornapple DS***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Aeshnidae	-	-	-	-	-	-
Coenagrionidae	-	-	-	-	26.055	-
Gomphidae	-	-	-	-	-	-
Odonata	-	-	-	-	-	-
Corixidae	-	-	-	-	-	-
Hemiptera	-	-	-	-	-	-
Saldidae	-	-	-	-	-	-
Amphipoda	34.035	11.345	11.345	124.795	95.535	201.852
Isopoda	-	-	-	-	-	-
Agraylea	-	-	-	-	-	-
Brachycentrus	45.380	22.690	34.035	419.765	34.035	-
Ceratopsyche	1281.985	90.760	181.520	283.136	43.425	661.626
Cheumatopsyche	726.080	873.565	45.380	73.062	226.770	361.868
Chimarra	-	-	-	-	-	44.856
Glossosoma	748.770	-	-	-	-	-
Helicopsyche	-	11.345	-	10.112	130.275	89.712
Hydropsyche	317.660	204.210	34.035	485.376	8.685	470.988
Hydropsychidae	4538.000	1610.990	476.490	1820.160	34.740	1244.754
Hydroptilidae	-	-	-	485.376	-	201.852
Leuchotrichia	113.450	22.690	-	1688.704	8.685	1715.742
Macrostemum	-	-	-	10.112	-	-
Micrasema	-	193.292	148.475	-	26.055	100.926
Neophylax	12.017	43.930	89.085	-	138.960	-
Nyctiophylax	-	-	-	-	8.685	-
Philopotomidae	-	-	-	-	-	-
Protoptila	3596.365	2473.210	1213.915	10263.680	-	17202.276

Taxon	***Thornapple DS***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Psychomyia	45.380	-	-	170.478	393.068	626.310
Antocha	84.119	114.218	41.573	131.456	816.390	381.276
Atherix	158.830	56.725	22.690	34.035	-	-
Ceratopogonidae	-	-	-	-	-	-
Chironomidae	2541.280	2110.170	2405.140	8883.135	10085.705	3959.405
Diptera	-	-	-	-	-	-
Empididae	-	11.345	-	10.112	972.720	100.926
Simuliidae	79.415	56.725	2098.825	202.240	8.685	302.778
Anthopotamus	-	-	-	-	11.345	-
Baetidae	997.411	966.460	314.767	717.952	69.480	706.482
Baetisca	11.345	-	-	-	-	-
Caenis	385.730	170.175	79.415	-	8.685	56.070
Drunella	-	-	-	-	-	-
Ephemerella	-	-	5.939	-	-	-
Ephemerellidae	-	11.345	-	1939.995	34.035	11.345
Ephemeridae	11.345	-	-	-	-	-
Ephemeroptera	181.520	56.725	147.485	-	-	22.428
Heptageniidae	34.035	11.345	22.690	2178.240	-	45.380
Isonychia	-	-	-	-	-	-
Maccaffertium	-	-	11.345	1293.330	-	11.345
Rhithrogena	11.345	-	-	34.035	-	-
Seratella	-	26.358	-	34.035	11.345	-
Stenacron	-	-	-	-	-	-
Stenonema	11.345	11.345	-	20.224	17.370	179.424
Tricorythodes	11.345	-	-	329.005	56.725	22.690
Chauliodes	-	-	-	-	-	-

Taxon	***Thornapple DS***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Corydalidae	-	-	-	-	-	-
Nigronia	-	-	-	-	-	-
Coleoptera	-	-	-	-	-	-
Dubiraphia	-	-	-	-	-	-
Elmidae	-	-	-	-	-	-
Optioservus	113.450	22.690	68.070	294.970	-	-
Psephenus	-	-	-	-	8.685	-
Stenelmis	-	22.690	34.035	158.830	-	-
Petrophila	-	-	-	-	34.740	11.214
Acroneuria	-	8.786	-	-	-	-
Perlesta	11.345	-	-	-	-	-
Perlidae	-	-	-	-	-	-
Perlodidae	-	-	-	-	-	22.428
Plecoptera	-	-	-	79.415	-	-
Taeniopteryx	-	-	-	-	-	11.214
Gastropoda	-	-	306.315	11.345	192.865	374.385
Hydrachnidia	748.770	294.970	136.140	323.584	2240.730	347.634
Limpets	-	-	-	-	-	-
Nematode	56.725	34.035	34.035	30.336	52.110	11.214
Oligochaeta	192.865	294.970	294.970	80.896	1702.260	392.490
Platyhelminthes	-	22.690	11.345	11.345	-	-
Podura	-	-	-	-	-	-
Zebra Mussel	-	79.074	-	-	294.970	-

Taxon	***Henning US***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Aeshnidae	-	-	-	-	-	-
Coenagrionidae	-	-	-	-	5.913	-
Gomphidae	-	-	-	-	-	-
Odonata	-	-	7.948	n	-	22.690
Corixidae	-	-	-	n	11.345	-
Hemiptera	-	-	7.948	-	-	-
Saldidae	12.450	-		n	-	11.345
Amphipoda	-	-	22.690	n	22.690	22.690
Isopoda	-	-	-	-	-	-
Agraylea	-	-	-	-	5.913	-
Brachycentrus	11.345	22.690	34.305	n	79.415	294.970
Ceratopsyche	12.450	400.775	325.868	n	192.865	930.290
Cheumatopsyche	1.345	260.935	499.180	n	113.450	918.945
Chimarra	-	-	-	n	5.913	32.664
Glossosoma	-	-	278.180	n	-	11.345
Helicopsyche	-	-	11.345	31.000	35.478	-
Hydropsyche	-	11.345	56.725	n	374.385	703.390
Hydropsychidae	363.040	476.490	941.635	n	215.555	3380.810
Hydroptilidae	181.520	90.760	136.140	n	612.630	2938.355
Leuchotrichia	149.400	185.725	143.064	2503.250	1182.600	5.444
Macrostemum	-	-	7.948	n	11.345	226.900
Micrasema	124.500	166.175	63.584	n	113.450	272.280
Neophylax	24.900	9.775	65.584	15.500	11.826	-
Nyctiophylax	-	-	-	-	-	-
Philopotomidae	-	-	-	-	-	-
Protoptila	34.035	124.795	850.875	-	-	-

Taxon	***Henning US***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Psychomyia	796.800	322.575	373.556	n	113.450	941.635
Antocha	298.800	146.625	95.376	54.250	230.607	506.292
Atherix	-	45.380	22.690	-	-	-
Ceratopogonidae	-	-	-	-	-	-
Chironomidae	5502.900	2746.775	1955.208	891.250	2093.202	2999.644
Diptera	-	-	-	-	-	-
Empididae	-	-	34.035	46.500	189.216	146.988
Simuliidae	181.520	22.690	79.415	46.500	-	10.888
Anthopotamus	-	-	-	n	34.035	-
Baetidae	771.460	476.490	646.665	n	79.415	306.315
Baetisca	-	-	-	-	-	-
Caenis	408.420	408.420	215.555	n	-	34.035
Drunella	-	-	-	-	-	-
Ephemerella	-	-	-	-	-	-
Ephemerellidae	22.690	-	11.345	n	204.210	113.450
Ephemeridae	-	5.913	-	-	-	-
Ephemeroptera	-	107.525	39.740	n	56.725	215.555
Heptageniidae	238.245	158.830	170.175	n	204.210	2666.075
Isonychia	-	-	-	n	-	68.070
Maccaffertium	34.035	45.380	-	n	56.725	737.425
Rhithrogena	-	-	-	n	11.345	90.760
Seratella	-	19.550	-	n	11.345	204.210
Stenacron	-	11.826	-	-	-	-
Stenonema	-	11.345	-	n	-	192.865
Tricorythodes	-	-	-	n	11.345	68.070
Chauliodes	-	-	-	-	-	-

Taxon	***Henning US***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Corydalidae	-	-	-	-	-	-
Nigronia	-	11.345	-	-	-	-
Coleoptera	34.035	-	-	-	-	10.888
Dubiraphia	-	-	-	-	-	-
Elmidae	-	11.345	-	n	-	11.345
Optioservus	204.210	238.245	283.625	n	147.485	1247.950
Psephenus	45.380	11.345	11.345	15.500	118.260	97.992
Stenelmis	22.690	34.035	22.690	n	-	68.070
Petrophila	-	-	-	-	47.304	38.108
Acroneuria	-	-	-	-	-	-
Perlesta	-	11.345	-	-	-	-
Perlidae	-	-	-	n	-	22.690
Perlodidae	-	-	-	-	-	-
Plecoptera	-	-	-	n	22.690	22.690
Taeniopteryx	-	-	-	n	34.035	22.690
Gastropoda	99.600	68.425	-	54.250	153.738	179.652
Hydrachnidia	136.140	204.210	385.730	n	68.070	987.015
Limpets	-	-	-	-	-	-
Nematode	68.070	-	45.380	n	158.830	-
Oligochaeta	283.625	158.830	340.350	-	100.521	-
Platyhelminthes	62.250	29.325	39.740	-	23.652	-
Podura	-	-	-	n	-	56.725
Zebra Mussel	37.350	9.775	-	-	5.913	-

Taxon	***Henning DS***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Aeshnidae	-	-	-	-	-	6.509
Coenagrionidae	-	-	-	-	-	-
Gomphidae	-	-	-	-	11.345	-
Odonata	-	-	-	-	-	-
Corixidae	-	-	-	-	-	-
Hemiptera	-	-	-	-	-	-
Saldidae	-	-	-	-	-	-
Amphipoda	-	-	-	34.035	45.380	68.070
Isopoda	-	-	-	-	-	-
Agraylea	-	57.228	8.562	27.262	26.812	-
Brachycentrus	34.035	-	22.690	22.690	170.175	11.345
Ceratopsyche	347.152	314.754	188.364	218.096	475.913	117.162
Cheumatopsyche	106.816	143.070	51.372	54.524	375.368	247.342
Chimarra	-	-	-	-	22.690	34.035
Glossosoma	-	-	-	-	136.140	-
Helicopsyche	-	-	-	313.513	60.327	-
Hydropsyche	253.688	457.824	359.604	258.989	221.199	670.427
Hydropsychidae	1882.632	2661.102	1823.706	926.908	1581.908	286.396
Hydroptilidae	400.560	71.535	-	2126.436	2553.843	839.661
Leuchotrichia	22.690	-	748.770	1549.876	1072.480	221.306
Macrostemum	-	-	-	-	13.406	78.108
Micrasema	200.280	200.298	136.992	95.417	100.545	52.072
Neophylax	11.345	56.725	-	-	-	-
Nyctiophylax	-	-	-	-	-	-
Philopotomidae	-	-	-	-	-	-
Protoptila	2163.024	1745.454	1164.432	4934.422	3820.710	1314.818

Taxon	***Henning DS***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Psychomyia	413.912	114.456	102.744	354.406	415.586	117.162
Antocha	120.168	1573.770	59.934	313.513	636.785	273.378
Atherix	34.035	-	11.345	-	-	22.690
Ceratopogonidae	-	-	-	-	-	-
Chironomidae	3671.800	5236.362	3227.874	6126.300	8361.265	10879.855
Diptera	-	-	-	-	-	-
Empididae	11.345	57.228	-	794.415	79.415	397.075
Simuliidae	373.856	1573.770	2097.690	218.096	100.545	39.054
Anthopotamus	-	-	-	-	-	79.415
Baetidae	192.865	805.495	1100.465	34.035	385.730	34.035
Baetisca	-	-	-	-	-	-
Caenis	136.140	113.450	226.900	-	22.690	11.345
Drunella	-	14.307	-	-	-	-
Ephemerella	-	-	-	-	-	-
Ephemerellidae	-	-	-	204.210	226.900	204.210
Ephemeridae	-	-	-	-	-	-
Ephemeroptera	-	-	68.496	-	-	91.126
Heptageniidae	13.352	14.307	8.562	245.358	241.308	52.072
Isonychia	-	-	-	13.631	20.109	-
Maccaffertium	-	-	22.690	90.760	102.105	-
Rhithrogena	13.352	14.307	8.562	-	22.690	-
Seratella	-	-	34.035	-	6.703	6.509
Stenacron	-	-	-	-	-	-
Stenonema	-	-	-	13.631	33.515	6.509
Tricorythodes	-	-	-	-	22.690	-
Chauliodes	-	-	8.562	-	-	-

Taxon	***Henning DS***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Corydalidae	-	-	-	-	-	-
Nigronia	-	-	-	-	-	-
Coleoptera	-	-	-	-	-	-
Dubiraphia	-	-	-	-	-	-
Elmidae	-	-	-	-	-	-
Optioservus	124.795	226.900	170.175	-	544.560	351.695
Psephenus	-	-	11.345	-	68.070	22.690
Stenelmis	11.345	56.725	45.380	-	90.760	-
Petrophila	-	-	-	13.631	-	-
Acroneuria	-	-	-	-	-	-
Perlesta	-	28.614	8.562	-	-	-
Perlidae	-	-	-	-	-	-
Perlodidae	-	-	-	-	-	-
Plecoptera	-	11.345	133.035	-	6.703	-
Taeniopteryx	-	-	-	11.345	-	11.345
Gastropoda	53.408	71.535	25.686	45.380	68.070	45.380
Hydrachnidia	90.760	294.970	238.245	477.085	241.308	299.414
Limpets	-	-	-	-	-	-
Nematode	-	22.690	-	113.450	-	45.380
Oligochaeta	11.345	521.870	408.420	-	22.690	930.290
Platyhelminthes	80.112	71.535	-	27.262	-	58.581
Podura	-	-	-	-	-	11.345
Zebra Mussel	-	-	-	34.035	-	181.520

Taxon	***Bigelow US***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Corixidae	50.348	56.496	22.116	22.690	34.035	11.345
Hemiptera	11.345	-	-	-	-	-
Saldidae	181.520	-	-	241.098	29.604	73.469
Amphipoda	-	71.904	73.720	-	1372.745	215.555
Brachycentrus	-	-	-	-	-	13.358
Ceratopsyche	-	22.690	-	27.819	-	93.506
Cheumatopsyche	37.761	238.240	84.168	287.463	207.228	661.221
Helicopsyche	-	11.345	-	-	-	53.432
Hydropsyche	37.761	-	-	-	-	-
Hydroptilidae	-	-	7.372	9.273	19.736	6.679
Leuchotrichia	-	-	-	-	-	11.345
Macrostemum	-	-	-	-	45.380	11.345
Micrasema	-	-	-	-	-	6.679
Nyctiophylax	25.174	339.849	25.174	157.641	9.868	86.827
Paranyctiophylax	-	-	14.744	-	-	-
Philopotomidae	-	-	-	79.415	22.690	-
Polycentropodidae	2706.205	2218.752	2742.384	3732.505	10346.640	3709.815
Protoptila	-	11.345	-	-	34.035	-
Psychomyia	-	-	-	-	-	53.432
Rhyacophila	-	5.136	-	-	-	-
Trichoptera	-	-	81.092	111.276	404.588	514.283
Antocha	22.690	-	-	-	-	-
Atherix	-	-	-	56.725	-	11.345
Chironomidae	12.587	46.224	250.648	111.276	611.816	768.085
Chrysops	11.345	-	-	79.415	-	68.070
Empididae	-	-	-	-	-	-

Taxon	***Bigelow US***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Pilaria	-	-	-	-	9.868	33.395
Simuliidae	22.690	-	-	22.690	340.350	340.350
Tipulidae	873.565	374.385	22.690	22.690	90.760	113.450
Anthopotamus	-	-	-	-	-	-
Baetidae	12.587	-	14.744	18.546	39.472	13.358
Ephemera	-	-	-	-	69.076	6.679
Ephemerella	-	22.690	-	-	56.725	90.760
Ephemerellidae	-	-	-	56.725	-	-
Ephemeroptera	-	-	-	-	-	11.345
Heptageniidae	-	-	-	45.380	113.450	-
Isonychia	-	-	-	-	-	-
Maccaffertium	-	-	-	-	-	-
Rhithrogena	37.761	-	14.744	-	9.868	-
Seratella	440.545	-	95.836	9.273	118.416	26.716
Tricorythodes	12.587	-	-	-	-	-
Chauliodes	34.035	-	-	-	-	306.315
Corydalidae	-	-	-	-	-	-
Coleoptera	22.690	-	-	-	294.970	204.210
Elmidae	-	-	-	-	-	11.345
Stenelmis	-	-	-	-	-	-
Petrophila	-	11.345	-	-	-	-
Acroneuria	-	-	7.372	-	-	-
Agnetina	-	-	-	-	-	79.415
Nemouridae	-	-	-	-	-	-
Paragnetina	-	-	-	-	9.868	46.753
Perlesta	-	-	-	-	-	-

Taxon	***Bigelow US***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Perlidae	-	-	-	-	113.450	-
Perlodidae	294.970	11.345	283.625	90.760	170.175	340.350
Plecoptera	-	-	-	-	-	-
Gastropoda	5313.311	3963.616	3774.464	5364.180	14947.250	8289.202
Hydrachnidia	-	-	-	-	88.812	-
Limpets	20.000	16.000	16.000	21.000	27.000	34.000
Oligochaeta	465.145	521.870	34.035	181.520	283.625	294.970
Zebra Mussel	-	-	-	-	-	11.345

Taxon	***Bigelow DS***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Corixidae	68.070	90.760	68.070	124.795	-	45.380
Hemiptera	11.345	-	-	-	-	-
Saldidae	24.744	n	-	-	-	68.070
Amphipoda	68.070	-	-	56.725	22.690	1077.775
Brachycentrus	-	-	-	-	7.436	-
Ceratopsyche	-	-	-	-	-	-
Cheumatopsyche	43.302	n	63.126	9.314	126.412	74.187
Helicopsyche	-	-	-	-	104.104	34.035
Hydropsyche	185.580	n	70.140	-	-	-
Hydroptilidae	34.035	45.380	11.345	34.035	-	102.105
Leuchotrichia	-	-	-	-	-	-
Macrostemum	11.345	45.380	-	124.795	-	623.975
Micrasema	22.690	147.485	-	102.454	118.976	362.692
Nyctiophylax	736.134	n	2511.012	-	44.616	131.888
Paranyctiophylax	11.345	-	11.345	-	-	-
Philopotomidae	-	-	-	11.345	-	-
Polycentropodidae	13423.620	n	6985.944	74.512	4662.372	469.851
Protoptila	-	34.035	-	-	-	-
Psychomyia	-	-	-	-	-	8.243
Rhyacophila	-	-	-	-	-	-
Trichoptera	-	-	-	-	7.436	90.673
Antocha	11.345	-	-	-	-	22.690
Atherix	-	-	-	-	-	-
Chironomidae	971.202	n	-	9.314	104.104	8.243
Chrysops	-	-	-	-	-	-

Taxon	***Bigelow DS***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Empididae	-	-	11.345	-	-	-
Pilaria	-	-	-	-	44.616	8.243
Simuliidae	-	-	11.345	-	-	-
Tipulidae	2876.490	n	757.512	-	208.208	41.215
Anthopotamus	12.372	n	7.014	-	-	22.690
Baetidae	-	-	-	-	-	56.725
Ephemera	-	-	-	-	-	22.690
Ephemerella	-	-	-	-	-	-
Ephemerellidae	-	-	11.345	-	-	-
Ephemeroptera	-	-	-	-	-	11.345
Heptageniidae	11.345	22.690	-	68.070	-	771.460
Isonychia	-	-	-	34.035	-	34.035
Maccaffertium	-	-	11.345	-	-	-
Rhithrogena	-	-	-	-	-	-
Seratella	11.345	-	-	-	-	45.380
Tricorythodes	-	-	-	-	11.345	22.690
Chauliodes	11.345	-	11.345	11.345	56.725	45.380
Corydalidae	-	-	-	-	11.345	-
Coleoptera	192.865	249.590	363.040	113.450	170.175	1497.540
Elmidae	-	68.070	11.345	-	-	68.070
Stenelmis	-	-	-	-	-	11.345
Petrophila	-	-	-	-	-	-
Acroneuria	-	-	-	-	-	-
Agnetina	-	-	-	-	22.690	-
Nemouridae	-	-	-	-	11.345	-

Taxon	***Bigelow DS***					
	S1	*S2*	*S3*	*F1*	*F2*	*F3*
Paragnetina	-	215.555	56.725	476.490	124.795	-
Perlesta	-	-	11.345	-	7.436	-
Perlidae	-	-	-	-	11.345	-
Perlodidae	45.380	-	45.380	56.725	-	-
Plecoptera	-	-	-	-	11.345	-
Gastropoda	19203.734	1281.985	11699.423	1500.269	5946.241	5903.410
Hydrachnidia	-	-	-	22.690	-	34.035
Limpets	22.000	11.000	21.000	18.000	23.000	30.000
Oligochaeta	419.765	363.040	669.355	170.175	56.725	90.760
Zebra Mussel	-	-	-	-	11.345	-

APPENDIX B

Similarity of percentage (SIMPER) test results for the upstream sample site (Croton) and the downstream sample site (Henning DS) on the Muskegon River, and the two sites on Bigelow Creek for the 1998 data and 2011 data. A SIMPER test evaluates the percent contribution of dissimilar taxa to the percent contribution of similar taxa between samples, and calculates an average. Taxa with the largest average to dissimilarity ratios are responsible for the observed differences between samples (Quinn and Keough, 2002). Upstream sites are indicated by (US), and downstream sites are (DS). Chironomidae and zebra mussels were excluded from this test.

Taxon	*Croton 1998 Avg*	*Henning DS 1998 Avg*	*Cum. Contribution*
Hydropsychidae	1774.7283	723.8954	23.51%
Cheumatopsyche	656.6375	545.9400	45.43%
Ceratopsyche	311.5117	105.6788	54.25%
Antocha	92.3075	359.1375	60.83%
Corixidae	18.5717	0.2383	66.41%
Stenonema	9.5600	13.3883	71.15%
Protoptila	0.0000	229.7950	75.59%
Amphipoda	55.8600	132.3663	79.90%
Micrasema	0.0000	203.9100	82.72%

Taxon	*Croton 1998 Avg*	*Croton 2011 Avg*	*Cum. Contribution*
Hydropsychidae	1774.7283	3495.6316	37.65%
Cheumatopsyche	656.6375	2231.6537	60.28%
Amphipoda	55.8600	367.7231	66.55%
Oligochaeta	0.0000	275.7282	71.82%
Platyhelminthes	0.0000	252.4656	75.85%
Ceratopsyche	311.5117	212.2448	79.48%
Gastropoda	0.0000	144.9262	82.52%

Taxon	*Henning DS 1998 Avg*	*Henning DS 2011 Avg*	*Cum. Contribution*
Protoptila	229.7950	1765.4477	18.73%
Hydropsychidae	723.8954	1083.5897	31.66%
Hydroptilidae	22.6308	686.0273	39.22%
Leuchotrichia	143.7133	480.0498	44.74%
Simuliidae	20.7400	427.0892	50.17%
Baetidae	49.9767	323.2030	55.10%
Cheumatopsyche	545.9400	125.0515	59.87%
Antocha	359.1375	190.6665	64.43%
Oligochaeta	0.0000	200.5900	68.50%
Hydrachnidia	0.0000	252.0931	71.93%
Hydropsyche	57.8633	232.1381	74.87%
Ceratopsyche	105.6788	221.1728	77.80%
Empididae	30.5450	140.6772	80.72%

Taxon	*Croton 2011 Avg*	*Henning DS 2011 Avg*	*Cum. Contribution*
Hydropsychidae	3495.6316	1083.5897	21.50%
Cheumatopsyche	2231.6537	125.0515	37.55%
Protoptila	34.9804	1765.4477	52.19%
Hydroptilidae	53.7601	686.0273	57.67%
Simuliidae	18.6288	427.0892	61.58%
Leuchotrichia	28.3933	480.0498	65.41%
Oligochaeta	275.7282	200.5900	68.71%
Baetidae	18.5049	323.2030	72.00%
Amphipoda	367.7231	26.5039	75.16%
Ceratopsyche	212.2448	221.1728	77.37%
Platyhelminthes	252.4656	21.5900	79.53%
Hydropsyche	9.1883	232.1381	81.64%

Taxon	*Bigelow US 1998 Avg*	*Bigelow DS 1998 Avg*	*Cum. Contribution*
Protoptila	1255.8600	844.5833	19.66%
Hydropsychidae	1231.0625	255.8850	32.91%
Ceratopsyche	465.4792	73.6700	44.01%
Hydropsyche	430.5375	24.5567	54.54%
Cheumatopsyche	361.8083	24.5567	63.42%
Glossosoma	132.5350	466.3667	71.26%
Antocha	571.9650	98.9833	77.22%
Elmidae	362.8590	0.0000	80.55%

Taxon	*Bigelow US 1998 Avg*	*Bigelow US 2011 Avg*	*Cum. Contribution*
Hydropsychidae	1231.0625	215.0824	15.33%
Protoptila	1255.8600	7.7262	27.13%
Antocha	571.9650	204.8872	36.29%
Ceratopsyche	465.4792	214.5617	44.15%
Baetidae	138.2117	170.1857	51.32%
Hydropsyche	430.5375	16.2109	56.83%
Cheumatopsyche	361.8083	52.4561	61.64%
Oligochaeta	2.6192	101.6659	66.00%
Hydrachnidia	0.0000	124.4787	69.56%
Elmidae	362.8592	28.3625	72.95%
Psychomyia	0.0000	127.5837	76.17%
Heptageniidae	0.0000	57.5655	79.00%
Nematoda	0.0000	57.6704	81.59%

Taxon	*Bigelow DS 1998 Avg*	*Bigelow DS 2011 Avg*	*Cum. Contribution*
Protoptila	844.5833	88.1057	14.28%
Baetidae	49.4900	635.6323	28.54%
Glossoma	466.3667	85.8060	40.18%
Simuliidae	0.0000	491.7295	51.43%
Optioservus	0.4767	237.0653	57.97%
Ceratopsyche	73.6700	155.5893	63.80%
Hydropsychidae	255.8850	55.5737	68.99%
Plecoptera	0.0000	91.3472	73.44%
Hyrachnidia	0.0000	130.9835	77.84%
Antocha	98.9833	110.6962	81.33%

Taxon	*Bigelow US 2011 Avg*	*Bigelow DS 2011 Avg*	*Cum. Contribution*
Baetidae	170.1857	635.6323	16.32%
Simuliidae	44.5859	491.7295	28.29%
Ceratopsyche	214.5617	155.5893	35.45%
Antocha	204.8872	110.6962	42.32%
Optioservus	50.6746	237.0653	48.68%
Hydropsychidae	215.0824	55.5737	54.40%
Hydrachnidia	124.4787	130.9835	59.33%
Oligochaeta	1010.6659	14.0454	63.28%
Glossosoma	0.5566	85.8060	67.16%
Plecoptera	8.5001	91.3472	70.95%
Psychomyia	127.5837	15.1072	74.58%
Nematoda	57.6704	41.7219	77.81%
Heptageniidae	57.5655	6.0035	80.49%