

**An Analysis of Spatial and Temporal Changes in Fish and Benthic  
Macroinvertebrate Communities Associated with Zebra Mussel  
(*Dreissena polymorpha*) Abundance in the Huron River,  
Southeastern Michigan**

**Katherine M. Birkett**

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**Committee Members:**

**James Diana**

**Edward Rutherford**

**Gerald Smith**

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## Abstract

This study examines the effects of the introduction of zebra mussels (*Dreissena polymorpha*) on fishes and benthic invertebrates in the middle stretch of the Huron River in southeastern Michigan. Fish community surveys were conducted during the summer of 2008 and compared with data taken in the same area in 1977 and 1993, before the introduction of *Dreissena*. No significant difference was detected in fish species richness and diversity between sites with mussels versus those without. However, several significant changes in fish community composition were detected, with fishes belonging to the families Centrarchidae, Percidae, and Ictaluridae increasing significantly and Cyprinidae and Catostomidae decreasing significantly as *Dreissena* density increased. Historical data showed a significant decline in the abundance of cyprinids and catostomids after the introduction of *Dreissena*. Benthos sampling conducted in 2008 and 2009 showed a dramatic increase in the overall abundance of macroinvertebrates associated with increased mussel density, as well as a significant increase in the numbers of chironomid larvae and amphipods and a decrease in the number of oligochaetes. Results of this study indicate that the introduction of *Dreissena* to the Huron River has not resulted in a loss of fish biodiversity, but communities of fishes and macroinvertebrates have experienced changes in species composition.

## Introduction

First coined in 1994, the term “ecosystem engineer” was used to describe organisms that “directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical changes in biotic or abiotic materials” (Jones *et al.* 1994).

Numerous examples of this phenomenon exist in the natural world, the most commonly cited being the construction of dams by beavers (Naiman *et al.* 1988), the creation of bogs by *Sphagnum* moss (Tansley 1949), and the construction of reefs by hermatypic corals.

Many species of aquatic mollusks are capable of altering their environment by virtue of their own body structures (Jones *et al.* 1994). Their shells add spatial heterogeneity and habitat complexity to an ecosystem, providing living space for other organisms and refuge from predation and stress (Gutiérrez *et al.* 2003). In a study conducted on the coast of Uruguay, colonization of shallow, subtidal areas by mussels belonging to the genera *Mytilus*, *Brachidontes*, and *Perna* resulted in an increase in benthic macroinvertebrate species richness when compared with non-colonized patches (Borthagaray and Carranza 2007). This phenomenon is not restricted to marine ecosystems. A similar relationship was observed between unionid mussels in the upper Mississippi River and midge and caddisfly larvae, in which the abundance of the aquatic insects was directly correlated with the surface area provided by the mussel shells (Beckett *et al.* 1996).

Like the mollusk species cited in the previous examples, zebra mussels (*Dreissena polymorpha*) and quagga mussels (*D. bugensis*) also function as ecosystem engineers in freshwater systems. Native to the Ponto-Caspian region of Eastern Europe, they were unintentionally introduced to the Laurentian Great Lakes via untreated ballast water from trans-

Atlantic ships in the late 1980s. They are considered a nuisance species in North America largely due to their tendency to grow and reproduce rapidly, forming dense, carpet-like colonies over any hard substrate with which they come into contact. Dreissenid mussels are notorious for fouling important infrastructure such as cooling pipes for nuclear power plants, resulting in as much as \$4 billion in annual costs (Britton 1991). *Dreissena* are also responsible for the ecological disturbances in the Great Lakes and other North American freshwater systems, literally choking out native species such as unionid mussels by fouling their shells and preventing them from feeding. A study of native bivalves from Lake St. Clair found that individual unionids can carry thousands of dreissenids on their shells, and that these fouled mussels were starving to death, containing only a portion of the lipid reserves of their unafflicted counterparts (Hebert *et al.* 1991). Because of this, zebra and quagga mussels have become serious threat to the survival of native freshwater mussel species, over 70% of which are already considered threatened or endangered due to human activity and the introduction of other aquatic nuisance species (Williams *et al.* 1993).

In addition, *Dreissena* can drastically alter an aquatic ecosystem by virtue of their voracious filter feeding activity. Over the course of just a few years, these mussels were able to transform the once plankton-rich, turbid waters of Lake Erie, filtering approximately 6.4 million tons of phytoplankton in 1990 alone (Madenjian 1995). In less than a decade after their initial introduction, zebra mussels changed a previously turbid, homogeneous Lake St. Clair into a system characterized by clear water, increased macrophyte growth, and dense zebra mussel beds (Griffiths 1993). Even in large, turbid lotic systems such as the Hudson River, *Dreissena* filtered enough phytoplankton to cause a noticeable decline in biomass (Caraco *et al.* 1997). Such drastic changes could lead to a rapid restructuring of the way nutrients are distributed in aquatic



systems, as was observed in the shunting of phosphorus to zebra mussel beds in coastal zones that led to blooms of nuisance algae in western Lake Erie (Hecky *et al.* 2004). Recent studies have demonstrated a link between encroachment of *Dreissena* and the corresponding decline of *Diporeia*, an amphipod that forms the base of the food chain for Great Lakes fish communities, although the exact mechanism behind this development remains uncertain (Nalepa *et al.* 2005).

While much research has been done on the impacts of zebra mussels on large freshwater systems, relatively little attention has been paid to the role that they play in smaller rivers and streams. This may be due to the fact that streams smaller than 30 meters wide have widely been considered unsuitable habitat for *Dreissena* (Martel 1996) because of their fast currents and consequentially high mortality rate for planktonic veligers. However, despite the adverse conditions for colonization, zebra mussels were discovered in the Huron River watershed, a warmwater stream located in southeastern Michigan, in 1994. They were most likely introduced via contaminated watercraft and boating equipment to Portage and Baseline lakes, two lakes located in the upper middle part of the river system. The mussels quickly colonized these bodies of water and began to move into the Huron River. However, since conditions in the first 22 kilometers downstream of these source populations include relatively swift currents and few obstructions, veligers are likely to be swept away before they have a chance to settle. Because of this, the expansion of zebra mussels in the middle Huron River is restricted to the first few kilometers directly downstream from Baseline Lake (Marangelo 1997) in a pattern described by Horvath *et al.* (1996) as the “source-sink” model.

The impact that the colonization of small streams by *Dreissena* has on resident fish and benthic invertebrate communities has not been as well documented. During a fish collecting trip in the spring of 2007, senior faculty from the University of Michigan Museum of Zoology

observed that the river's ichthyofauna appeared to be more depauperate than it had been in previous decades, and that the decline in fish abundance and diversity seemed to coincide with the introduction of zebra mussels (Dr. Gerald Smith, UMMZ Curator Emeritus, personal communication, May 2007).

The primary goal of my research was to determine if zebra mussels influenced the abundance and diversity of benthic macroinvertebrates and fishes in the Huron River ecosystem relative to areas that have not been colonized. I expected to find an increase in the richness of zoobenthos taxa present on riverbeds colonized by zebra mussels, as well as an increase in the total number of benthic macroinvertebrates at these locations. I also hypothesized that fish communities would decline in both species richness and diversity in zebra mussel-colonized areas. Since this species is highly efficient at filter feeding, it contributes to a process known as benthification, in which energy in an aquatic ecosystem is shunted from the water column to the benthic zone. With the system's resources sequestered in the benthos, I expected to see an increase in the number of bottom-dwelling invertivorous fishes that are capable of utilizing this newly available food source. In addition, I expected to see a decrease in the abundance of fish species that are unable to take advantage of this situation, either because their diet does not include benthic invertebrates or because their swimming orientation or body morphology do not allow them to access these resources.

Specific objectives of this study were to 1) analyze current fish community composition for differences in species diversity and representation of individual species, families, and functional guilds throughout the study area; 2) compare recent fish population data to data present in historical records from the 1970s and 1990s; and 3) analyze and compare communities of benthic invertebrates between sampling locations.

## Materials & Methods

Six 50-meter stretches located along the main stem of the Huron River were selected for this study, three exhibiting high densities of *Dreissena* coverage on the riverbed, and three displaying little to no coverage (Figure 1). Aside from the variation described above, all sites displayed similar physical features. The river was relatively shallow at all locations, between 0.29 and 0.82 meters deep on average, and was 28.3 to 48.8 meters wide. The substrate was predominantly gravel or cobble littered with large, partially submerged boulders. The banks at all sampling locations were heavily eroded, lined with large boulders, exposed tree roots, and overhanging branches. Riparian vegetation consisted predominantly of mature deciduous trees (Table 1).

Physical features of each 2008 sampling location were recorded, including width, mean depth, substrate composition, condition of the river banks, and riparian cover. Depth measurements were made every 10 meters along the transect and averaged for each location. Average monthly discharge data for the Huron River at Ann Arbor was obtained from the United States Geological Survey real time water data website for 1977, 1993, and 2008. Average current velocity for each sampling location and year was calculated by dividing discharge by cross-sectional area. Density of *Dreissena* on the riverbed was also assessed. Divers set up square meter plots at each location, one in deeper water and one closer to the bank. All mussels found within the plots were collected, preserved in 10% formalin, and returned to the laboratory for positive species identification and counting. Mean estimates of the number of mussels per square meter were subsequently calculated for each location (Table 1).

Fish were sampled with a pulsed DC electrofisher mounted on a towed-barge that was provided by the Michigan Department of Natural Resources. Stunned fish were temporarily

placed a large recovery tank. Upon completion of each electrofishing session, all animals were counted and identified to species using keys found in Hubbs and Lagler (2004). A small number of voucher specimens belonging to each species were euthanized with an overdose of MS-222 fish tranquilizer, fixed in a 10% formalin solution, and later preserved in ethanol (65%). All voucher specimens were returned to the Division of Fishes at the University of Michigan Museum of Zoology for positive identification and inclusion in the collections. The remaining fish were kept alive and subsequently returned to the river upon completion of sampling.

To determine if there were any significant changes in the Huron River's fish communities over time that might be attributed to the presence of zebra mussels, fish data collected in 2008 were compared with data sets collected at the same or nearby sampling sites in previous decades by researchers at the University of Michigan Museum of Zoology. Species counts were taken from field notes of surveys conducted both before the introduction of *Dreissena* (Humphries & Smith 1977) and during the period of time when *Dreissena* is thought to have been introduced into the watershed (Bailey & Latta 1993). Since the 1977 collections were conducted with a seine while the others used an electrofisher, corrections for gear bias were applied using the adjustment factors detailed by Grossman *et al.* (1990), which utilized statistical comparisons to investigate differences in efficiencies of sampling methods for several different taxonomic classifications of fishes. When the adjustment factor for a particular species could not be found, a number for a closely related species with similar behaviors was substituted, or none was applied (Table 2). All decimals were rounded up to the nearest whole number after adjustment. In this study, fish abundance is measured as the number of fish captured per 50 meters of shoreline.

Species richness and Simpson's index of concentration were used to quantify taxonomic diversity for fish communities for each location and sampling event. Richness measures presence

or absence and is quantified simply as the number of different taxa found during a sampling event. The equation for Simpson's index is

$$D = \frac{\sum_{i=1}^s n_i(n_i - 1)}{N(N - 1)}$$

where  $n_i$  is the number of individuals in a given species, and  $N = \sum n_i$ . SI decreases as the diversity of a community increases, so  $-\ln SI$  was taken in order to convert it into a statistic that increases with diversity and is independent of sample size (Rosenzweig 1995). Comparisons between sites heavily colonized by *Dreissena* and non-colonized sites were made within and between sampling years using a two-sample t-test. Species richness and species diversity were compared between all 2008 sampling locations using a Kruskal-Wallis test. In cases where a two-sample test was required, but the equal variance assumption was not met, a Wilcoxon rank sum test was applied instead. Additionally, each fish species was assigned to categories within four functional guilds, namely trophic guild, substrate preference, current velocity preference, and tolerance to siltation (Poff & Allan 1995). Mean numbers of individuals belonging to each category were calculated by site for all sampling events. Comparisons were made between sampling locations within each year and between years using a Wilcoxon rank sum test. All statistical tests were performed using WaveMetrics Igor software with  $\alpha = 0.05$ .

Benthos samples were also collected throughout the 2008 study period and again in August of 2009. Two 500 ml samples of sediment were collected per sampling period per site at different distances from the bank. All collections were preserved in plastic containers with 10% formalin solution mixed with rose Bengal stain. Each sample was strained using a metal sieve with a 600-micrometer screen and rinsed thoroughly with water. Benthic organisms were removed, counted, sorted into major taxonomic groups, and preserved in 10% formalin. They

were subsequently identified to the lowest reasonable taxonomic level using the keys found in Thorp and Covich (2001) and Wiggins (1977). Mean relative density was calculated for six major taxonomic groups: oligochaetes, chironomids, amphipods, clams, gastropods, and flatworms. Mayflies, caddisflies, and stoneflies were present in the benthos in relatively small abundances, and consequently were not included in the analysis. Taxa densities among sampling locations were compared using a Kruskal-Wallis test. If this test demonstrated a significant difference among sites, a Wilcoxon rank sum test was applied to test for differences in mean relative abundance at sites with high and low *Dreissena* density. Relationships between mussel density and macroinvertebrate functional feeding groups were also examined. Each taxon was assigned to one of five main categories: collector-gatherer/deposit feeder, shredder, filterer-collector/suspension feeder, grazer, and predator using the classification methods found in Allan and Castillo (2007), Ricciardi *et al.* (1997) and Thorp and Covich (2001). These data were analyzed using the methods described above for taxonomic group analysis.

## **Results**

### **Fish Communities in 2008**

During the 2008 electrofishing surveys, 2380 fish were collected representing 38 different species (Table 2). The families Centrarchidae, Percidae, Ictaluridae, Catostomidae, and Cyprinidae comprised approximately 98 percent of the total fish catch at all locations (Figure 1). A Kruskal-Wallis test indicated that there was no significant difference in overall density of fish among sampling locations ( $\alpha=0.05$ ,  $p=0.75$ ). A Wilcoxon rank sum test showed no significant difference in fish species diversity between locations with high and low *Dreissena* density ( $p=0.340$ ) (Table 3). The Fishing Site, which displayed the lowest fish diversity both in terms of species richness (mean=13 species) and the corrected Simpson index (mean=1.22), also

exhibited the highest density of zebra mussels (mean= 774/m<sup>2</sup>), while the location with the highest species richness (mean= 18 species) and corrected Simpson's D (mean= 1.93) had little if any zebra mussel cover (Table 4). However, Wilcoxon tests did indicate significant differences in the representation of certain fish families between high and low-density locations (Table 7). Ictalurids ( $\alpha=0.05$ ,  $p=0.01$ ) and centrarchids ( $p=0.02$ ) were more abundant at high-density sites, while numbers of catostomids ( $p=0.001$ ) and cyprinids ( $p=0.01$ ) were less common at these locations. There was no significant difference in the number of Percids found at either location type.

Differences were detected in the abundance of several fish species between sampling locations with high and low zebra mussel densities (Table 4). During the summer of 2008, logperch (*Percina caprodes*) were particularly abundant in areas with high *Dreissena* density. The mean relative abundance of this species increased with distance upstream from 3.19 per 50 meters of shoreline at the Loch Alpine location to 15.10 at the Fishing Site, where the zebra mussel beds were densest. Rock bass (*Ambloplites rupestris*) were found in large numbers at all sampling locations in 2008, but were particularly abundant at locations with high mussel density. Their mean relative abundance increased from 22.21 per 50 meters of shoreline at Loch Alpine to 49.36 at the Fishing Site. Other species of centrarchids, including smallmouth bass (*Micropterus dolomieu*) and bluegill (*Lepomis macrochirus*) were also more abundant at high-density locations.

The relative abundance of fishes belonging to different trophic guilds also varied between high and low-density locations. A statistically significant increase was detected in the number of general invertivores present at high-density sites (Table 5,  $\alpha=0.05$ , 0.01), as well a decrease in omnivores ( $p=0.01$ ) and herbivores/detritivores ( $p=0.032$ ). There was no significant difference

found between numbers of benthic invertivores, piscivores, and surface/water column invertivores between the two location types. A Wilcoxon two-sample test detected no significant difference between sampling locations for substrate preference. Species that thrive on rubble substrate made up the majority of the fish catch at all sites, followed by substrate generalists. Species preferring sandy or silty bottoms were relatively rare at all sampling locations. Representation of fish species with specific current velocity preferences also did not vary significantly across sites. Fishes that thrive in swift and moderate currents were the most prevalent across all sites, while those that prefer slow current or display no particular preference were less common. The Wilcoxon test found no significant difference in the percentages of sensitive versus tolerant fish species from site to site. The majority of fishes present throughout the study area belonged to low-tolerance species.

### **Comparisons to Pre-*Dreissena* Communities**

Several differences were found in presence/absence data for fish species between sampling years (Table 6). Nine species of cyprinids present in this stretch of the river before the introduction of *Dreissena* were not found during the 2008 surveys: the Ohio stoneroller (*Campostoma anomalum*), striped shiner (*Luxilus chrysocephalus*), common shiner (*L. cornutus*), river chub (*Nocomis micropogon*), golden shiner (*Notemigonus crysoleucas*), blacknose shiner (*Notropis heterolepis*), sand shiner (*N. stramineus*), fathead minnow (*Pimephales promelas*), and eastern blacknose dace (*Rhinichthys atratulus*). However, two species of ictalurids were found in 2008 that had not been collected in previous years and are currently endangered in Michigan: the northern madtom (*Noturus stigmosus*) and brindled madtom (*N. miurus*). A complete list of species collected during each sampling year can be found in Table 6. The decline in the number of cyprinid species since 1993 was also



accompanied by a marked decrease in the mean number of individuals belonging to this family across all sampling locations between 1977 and 2008 ( $p=0.0016$ ) (Table 7). These data also showed a statistically significant increase in centrarchids ( $p=0.0259$ ) and percids ( $p=0.0005$ ) throughout this time period. Mean numbers of catostomids and ictalurids showed no significant changes between decades. The mean abundance of several species also changed significantly over these decades. Statistically significant increases were observed in logperch (*Percina caprodes*), rock bass (*Ambloplites rupestris*), bluegill (*Lepomis macrochirus*), greenside darter (*Etheostoma blennioides*), and rainbow darter (*E. caeruleum*) (Table 7). Despite the aforementioned changes in fish community composition, Kruskal-Wallis tests showed no significant differences in mean species richness ( $\alpha=0.05$ ,  $p=0.477$ ) or species diversity ( $p=0.801$ ) between the 1977, 1993, and 2008 datasets (Table 7).

Few statistically significant changes were detected ecological functional groups of fish over time. Distributions of fishes belonging to the six feeding groups remained similar between sampling years. Although there were increases in mean numbers of benthic invertivores, piscivores, and general invertivores, and decreases in surface/water column feeders over time, these changes were not statistically significant. However, there was a significant decrease in the mean abundance of omnivores over time ( $p=0.009$ ). Significant decreases were detected in the average number of fishes with slow ( $p=0.007$ ) and general ( $p=0.013$ ) current preferences, but no such differences were found for fast and medium current preferences. Species preferring silty ( $p=0.038$ ), sandy ( $p=0.009$ ), and general substrata ( $p=0.001$ ) were more abundant in 1977 than in later years, while species with a preference for rubble were abundant throughout the three decades. Fish with medium ( $p=0.022$ ) and high ( $p=0.0006$ ) tolerances to siltation decreased in

average number since 1977, while numbers of fish with low tolerance remained constant (Table 7).

In past sampling years, fish communities were relatively homogeneous throughout the study area. No significant differences in mean total fish catch, species diversity, or species richness were detected between what would become the high and low *Dreissena* density locations in the 1977 dataset. Additionally, there was no statistically significant difference in numbers of fish from any of the main families or functional feeding groups between high and low-density sites (Table 8).

### **Benthic Invertebrates**

There were dramatic spatial changes in zebra mussel cover within the study area. Densities of *Dreissena* in the middle Huron River were highest at the sampling locations closest to the source populations in Baseline and Portage lakes, decreasing exponentially with distance from the source populations (Figure 2). At the Hudson Mills fishing site (FS), zebra mussel colonies formed a thick carpet over the riverbed, reaching an average density of 774 individuals per m<sup>2</sup>. At Loch Alpine (LA), the site furthest downstream, *Dreissena* were present, but in extremely low numbers, occurring in densities of only a few individuals per square meter (Table 1).

Benthos surveys conducted in 2008 and 2009 revealed dramatic spatial changes in macroinvertebrate communities. Over the course of this study, 26 major benthic macroinvertebrate taxa were collected. The most abundant groups included midge larvae (Chironomidae), scuds (Amphipoda: Gammaridae), worms (Oligochaeta), riffle beetles (Coleoptera: Elmidae), fingernail clams (Sphaeriidae), and snails (Gastropoda) (Table 10 and Figure 4). Major differences in overall abundance of zoobenthos were also detected among sites

( $\alpha=0.05$ ,  $p=0.002$ ), with a marked increase in total macroinvertebrate density over zebra mussel beds (Table 9). There were dramatic differences among sampling locations in the number of midge larvae collected (Kruskal-Wallis test,  $p=0.0001$ ), with their larval density higher at sites where zebra mussels were present in high densities. In addition, there were statistically significant differences in numbers of scuds ( $p=0.009$ ) and snails ( $p=0.0051$ ) among sites. There were no statistically significant differences among sites in the number of oligochaete worms ( $p=0.205$ ), fingernail clams ( $p=0.4872$ ), or flatworms ( $p=0.235$ ). Differences in benthos taxa density among sites were related to the density of *Dreissena*. Wilcoxon two-sample tests demonstrated highly significant differences for all of these groups between sites with high and low zebra mussel densities (Table 9).

Variability in the distributions of macroinvertebrates belonging to different functional feeding groups was also observed throughout the study area. Although the mean relative abundance of the benthos classified as collector-gather/deposit feeders was high across all sites, it increased significantly when zebra mussels were present in high densities, from a low of 72.41% at the Dexter-Huron site to high of 93.5% at the Fishing Site (Table 10). Grazers experienced a decline associated with increased zebra mussel density, dropping from 5-6% at low-density sites to less than 1% at the highest density location. Filter-collectors/suspension feeders and predators were more numerous at the low zebra mussel density locations. The relative abundance of scrapers was low across sites and declined slightly with increasing mussel density (Table 10).

## Discussion

I found no significant differences in fish species richness and evenness between sites with low and high *Dreissena* densities. These results are surprising considering the widely-accepted

hypothesis that biodiversity tends to decline in places where invasive species become abundant. This hypothesis has been supported by numerous prior studies; for example, it is estimated that of the nearly 30 species of North American fishes that were forced into extinction throughout the twentieth century, introduced species played pivotal roles in their disappearance (Miller *et al.* 1989).

However, there were significant spatial and temporal differences in relative abundance of fishes at the family level. The mean density of individuals belonging to the five primary fish families varied among sites in the 2008 dataset and was characterized by a steep decline in mean density of cyprinids and catostomids and an increase in numbers of centrarchids and percids. This data is complemented by an identical temporal trend throughout the sampling area since the introduction of *Dreissena* to the watershed in the early 1990s. These trends may be attributed to changes in food availability initiated by the introduction of zebra mussels. *Dreissena* are voracious filter feeders and may drastically reduce the amount of food available for some planktivorous cyprinid species. In addition, some species of fishes (particularly suckers) are better suited for foraging in gravel than on mussel beds. However, this increased structural complexity may benefit darters – small, bottom-dwellers that would have little difficulty picking small benthic invertebrates out of the many nooks and crevices found on *Dreissena* beds.

There is also evidence that the spatial and temporal changes observed in the abundances of individual fish species could be attributed to the presence of *Dreissena*. Logperch in particular seemed to thrive in areas where zebra mussels were present in high densities. This may be due in part to the pointed shape of their rostrum, which could allow them to access invertebrate prey hiding in the small spaces between zebra mussel shells via “picking”. Prior studies of logperch diets indicate a strong preference for both micro-crustaceans and aquatic insect larvae,

particularly chironomids (Dobie 1959, Mullan *et al.* 1968), both of which were significantly more abundant in zebra mussel beds. Several predatory centrarchid species, including rockbass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieu*) were also present in higher numbers in areas heavily colonized by zebra mussels. Once again, this is most likely due to an increase in prey organisms that have been drawn in by the abundant resources found within the mussel beds, rather than the mussels themselves. In rivers and streams, juvenile rockbass and smallmouth bass feed on chironomid larvae, amphipods, and small fishes (George & Hadley 1979, Probst *et al.* 1984), all of which are more abundant at locations with high zebra mussel densities. As adults, both species tend to prefer habitats with plenty of cover and spatial complexity, and both display similar feeding preferences, with smaller fish and crayfish (which thrive in the presence of *Dreissena*, according to Martin and Corkum 1994) comprising the bulk of their diet (Probst *et al.* 1984). Small ictalurid catfishes, including stonecats (*Noturus flavus*) and northern madtoms (*N. stigmosus*), were also present in higher densities over *Dreissena* beds. By contrast, brindled madtoms (*N. miurus*) tended to be more abundant in areas without zebra mussels, and absent entirely at locations with high mussel density. It is also interesting to note that the latter two species were not collected in either the 1977 or the 1993 sampling events, but were frequently captured throughout the summer of 2008. Northern and brindled madtoms are of special interest because of their relative rarity in Michigan. Northern madtoms are only found in the southeastern corner of the state, confined to Lake St. Clair and the tributaries of Lake Erie, including the Huron River, while southern Michigan is the northern extent of the brindled madtom's range (Hubbs and Lagler 2004).

The data also indicate that there may be a relationship between the ecological roles of fish species and the presence of *Dreissena*. Although no significant temporal differences were

found in the abundance of piscivores, benthic invertivores, general invertivores, surface/water column feeders, and herbivores/detritivores, there were spatial differences detected in the mean abundance of individuals belonging to these trophic guilds across sampling locations in the 2008 dataset. A dramatic increase was observed in the number of piscivorous fish species such as rock bass present at the sites with high *Dreissena* density. One explanation for this may be the tendency of zebra mussels to increase water clarity, which could aid predatory fishes in their ability to visualize prey. Previous research compliments the decline in abundance of benthic invertivores in association with zebra mussels observed in this study. One study investigating the feeding efficiency of several different benthic invertivorous fishes noted a decline in the number of successful foraging attempts amongst bullheads (*Ameiurus* spp.), logperch, and mottled sculpin (*Cottus bairdii*) in areas where zebra mussels were present, suggesting that prey organisms were better able to hide in the more complex habitat structure created by the mussel shells (Beeky *et al.* 2004). While dense clusters of zebra mussels may impede some fishes in foraging successfully, this effect may be offset by the increased abundance of prey organisms associated with mussel beds. Although some fish would not be able to access the newly abundant food resources due to body morphology or other constraints, those species that were able to circumvent these obstacles and obtain prey would become the dominant species in high mussel density areas. The hypothesis that foraging success in zebra mussel beds is dependent upon the species of predator was tested in a laboratory setting by González and Downing (1999), who found that bluegill (*Lepomis macrochirus*) were less adept than yellow perch at capturing amphipods on substrate with zebra mussels. Similarly, differential ability to utilize food resources between fish species may account for many of the changes in fish community structure observed throughout the study area.

Another ecological variable that frequently changes in the presence of *Dreissena* is the physical structure due to ecosystem engineering. Macrophyte growth due to increased water clarity associated with zebra mussels and the increased spatial complexity provided by the mussel beds themselves may provide additional habitat for some fish species. Probst *et al.* (1984) found that rock bass in particular prefer habitats with more vegetative coverage. Mittelbach (1981) demonstrated that small to medium-sized bluegill remained near areas with denser vegetation due to decreased risk of predation, despite the higher abundance of potential prey items in pelagic areas. Consequently, the potential increase in cover provided both directly and indirectly by zebra mussels may affect habitat selection in a variety of different fish species.

Some species of native fishes in the middle Huron River study area may benefit more directly from the increased presence of zebra mussels by utilizing them as a food source. Several studies conducted in the Great Lakes have shown that some native fish species have been able to include zebra mussels as a significant part of their diet in the absence of their usual prey. Lake whitefish (*Coregonus clupeaformis*) have been shown to consume zebra and quagga mussels in the absence of their usual prey, the amphipod *Diporeia*. Madenjian *et al.* (2010) found that lake whitefish has become an important predator for quagga mussels in Lake Huron, consuming approximately 820 kt annually. However, *Dreissena* have poor nutritional value, and the body condition of these fish has decreased overall as a result of this diet switch (Pothoven *et al.* 2001). Morrison *et al.* (1997) showed that both freshwater drum (*Aplodinotus grunniens*) and yellow perch frequently preyed upon *Dreissena* once they attained sufficient size to crush them. The round goby (*Neogobius melanostomus*), another invasive species from the Ponto-Caspian region, is a voracious predator on smaller zebra mussels, which make up over half of their diet in Detroit River populations (Ray and Corkum 1997). Molloy and Karatayev (1997) predicted that several

species found in the middle Huron River, including bluegill, redhorses (*Moxostoma* spp.) and channel catfish (*Ictalurus punctatus*), are potential predators of zebra mussels. A subsequent study carried out by Magoulick and Lewis (2002) in Lake Dardanelle, Arkansas confirmed many of the predictions of Molloy and Karatayev, finding that zebra mussels comprised a large percentage of the diets of blue catfish (*Ictalurus furcatus*), freshwater drum, and redear sunfish (*Lepomis microlophus*). Consequently, related species indigenous to the Huron River may also be capable of shifting their diets to include zebra mussels as a primary food source. Species most likely to feed on zebra mussels include fishes whose main food sources are displaced by zebra mussels, or those that possess molariform pharyngeal teeth, which allows them to process the shells more effectively (Molloy and Karatayev 1997). These factors may explain the increased presence of bluegill and hornyhead chub (*Nocomis biguttatus*) in high mussel density areas.

Other ecological variables appear to be less important in determining whether or not a fish species is capable of adapting to the presence of *Dreissena*. No significant changes in current velocity preferences, substrate preferences, and tolerances to siltation could be detected in the study area as a whole between years, or between high and low *Dreissena* density sites during any of the sampling years. This hypothesis is also supported by the physical habitat data presented in Table 1, which details some of the differences between sampling locations. These observations further support the hypothesis that the introduction of zebra mussels has driven the changes observed in the Huron River's fish communities, rather than any other changes in the physical environment.

In addition, several spatial changes were observed in benthic macroinvertebrate communities that are likely due to the presence of *Dreissena*. Drastic differences in mussel density among sampling sites provide an ideal situation in which to compare benthos with and



without mussels. *Dreissena* cover was densest at sampling locations closest to the source populations in Portage and Baseline lakes, and quickly began to decline between three to four kilometers downriver. Because of the swift current and lack of suitable places for mussel veligers to attach, there is most likely little if any endogenous recruitment from mussels in the river's main channel, making population density a function of proximity to the source population. Consequently, zebra mussels have been unable to attain high population densities throughout most of the middle Huron River, and the spatial patterns that are present today have changed relatively little from when they were first sighted in the river in 1995.

The differences in the overall abundance of benthic organisms between the low and high *Dreissena* density sites were striking. The total number of all non-dreissenid macroinvertebrates was higher in the presence of zebra mussels throughout the study area. This observation is supported by numerous prior studies performed in large lakes, which have indicated that the presence of zebra mussels can actually be beneficial to certain types of benthic invertebrates, primarily deposit feeders and grazers. In southwestern Lake Ontario, for example, the total abundance of non-dreissenid macroinvertebrates, particularly that of the amphipod *Gammarus fasciatus*, was found to be greater after the invasion of zebra and quagga mussels at cobble and artificial reef sites (Stewart and Haynes 1994). A similar phenomenon was observed in the benthos of eastern Lake Erie, where the total number of organisms increased dramatically after the introduction of dreissenids (Dermott and Kerec 1997). This was most likely due to the enhanced spatial complexity and heterogeneity provided by the mussel shells, and to a lesser extent, an increase in food availability in the form of mussel pseudofeces (Ricciardi *et al.* 1997). Bioenergetic models for western Lake Erie proposed by Madenjian (1995) estimate that 1.4 million tons of phytoplankton were deposited in the form of mussel pseudofeces in 1990 alone.

Experiments conducted by Stewart *et al.* (1998) in western Lake Erie determined that organic matter increased three to five times on substrates where live zebra mussels were present compared to the control sites, and that there was a corresponding increase in benthic macroinvertebrate biomass in these areas. However, this study found that habitat complexity was a more important variable than food availability in accounting for the elevated abundance of zoobenthos on mussel beds. There is also evidence suggesting that increased macrophyte density associated with the filtering activity of dreissenids may contribute indirectly to higher benthic macroinvertebrate abundance. Zhu *et al.* (2006) found that zebra mussels caused a significant increase in water clarity in Oneida Lake, leading to increased light penetration and elevated plant growth. In another experiment by Gilinski (1984), enhanced spatial heterogeneity due to the growth of macrophytes was found to be beneficial to multiple groups of zoobenthos, leading to increases in species richness and overall density.

Community composition of zoobenthos was also different in areas with low versus high *Dreissena* density. Benthos samples collected from the middle Huron River study area showed a dramatic increase in chironomid larvae, which is possibly due to the increased availability of food and habitat complexity described above. Additional explanations for this phenomenon may include a commensalism between chironomid larvae and dreissenids similar to the relationship discovered by Ricciardi (1994) in the St. Lawrence River. Gammarid amphipods also increased in abundance in areas with high zebra mussel densities. Previous studies support this observation, suggesting that, like many other benthic invertebrates, some species of amphipods thrive in the complex habitat provided by dreissenid shells. Experiments conducted by González and Downing (1999) in Lake Erie's western basin found that amphipods always preferred substrate with zebra mussels to bare substrate, and that like other zoobenthic taxa, this preference

derived more from increased spatial complexity than food availability. The elevated numbers of snails found in the benthic samples from sites with high *Dreissena* density, as well as the numerous *Campeloma* observed grazing in the immediate vicinity of the zebra mussel beds (Table 1) can most likely be explained by the increased clarity of water exiting Portage and Baseline lakes. This would fuel the growth of epiphytic algae on the riverbed, which is a food source for snails. Lowe and Pillsbury (1995) described a similar phenomenon attributed to dreissenid filtering activity in Lake Huron's Saginaw Bay, where increased light penetration gave rise to heightened benthic primary productivity and algal biomass. The slight decrease in mean relative abundance of clams and oligochaete worms in areas with high zebra mussel density corresponds with the findings of other studies conducted in larger lentic systems. In the deeper areas of Lake Ontario, declines in these two groups and the amphipod *Diporeia* coincided with the growth of zebra and quagga mussels in the mid-1990s (Lozano *et al.* 2001). One possible explanation for the disappearance of clams is that because they are filter feeders, and zebra mussels compete with them for food resources.

Functional feeding classifications appear to be less important in determining which benthic macroinvertebrate taxa will be successful in the presence of *Dreissena*. The data show a relationship between zebra mussel density and increased numbers of macroinvertebrate predators. At the middle Huron River sites, there was a higher relative abundance of turbellarian flatworms in samples collected from the zebra mussel beds, although this difference was not statistically significant. Other studies conducted in lentic systems have demonstrated similar trends (Ward and Ricciardi 2007).

Due to the complexity and large number of variables governing the functioning of river ecosystems, it is difficult in most cases to discern the role that *Dreissena* plays in the changes

that have been observed in lotic fish and benthic macroinvertebrate communities. Much annual and seasonal variability in fish assemblages has been observed in various river systems, and this is frequently attributed to stochastic events such as droughts, floods, and other natural disturbances (Grossman *et al.* 1990). However, no significant differences were detected in the abundance or community composition of fishes in the river between June, July, and August of 2008. Organic and industrial pollution also plays a role in the degradation of river ecosystems. However, this particular stretch of the Huron River system is ideal for this study because it is relatively healthy, and the land use in the immediate vicinity of the study sites has changed little over the past several decades. Several large metropolitan parks are situated along the banks of this stretch of the Huron River, and the surrounding area is predominantly residential or agricultural. The expansion of the Clean Water Act in 1972, which was enacted long before the introduction of *Dreissena* to the watershed, has also helped to reduce the effects of any pollution on the Huron River ecosystem. Although two small lakes are located upstream of the study locations, the closest site is separated from them by a dam and several kilometers of river. Consequently, the aforementioned attributes make it possible to control for many problematic variables and to focus on the role that *Dreissena* may play in the structuring of river ecosystems.

One variable that makes interpreting the results of this study difficult to interpret is gear bias. The 2008 and 1993 fish surveys were conducted using an electrofisher, while the 1997 data set was collected using a seine. Seines are most effective in systems with relatively smooth, sandy bottoms with few obstructions. All of the sampling sites in the Huron River were littered with large, partially submerged boulders and woody debris, which could cause snags and allow smaller bottom dwelling fishes such as darters and sculpins to escape. Correction factors proposed by Grossman *et al.* that take these issues into account were applied to the 1977 data set

in order to address the gear bias problem. In addition, the 1993 electrofishing data set was taken just before zebra mussels colonized the river and can thus provide a snapshot of fish community composition that is comparable to the 2008 data set. For both logperch and rainbow darters, mean abundances are very similar for the 1977 (seine) and 1993 (electrofisher) datasets, followed by dramatic population increases in 2008 (Table 7). This observation supports the hypothesis that any differences we are seeing between years can be attributed more heavily to variables other than gear bias.

### **Implications**

The ability to predict the responses of native species to the introduction of nuisance species and other ecological problems has become increasingly important in recent years, particularly in light of a rapidly globalizing economy. As *Dreissena* continues its spread across North America, fishery managers need to be aware of what potential changes they can expect once these mussels are introduced to their areas so that they can act preemptively to preserve indigenous species.

This study provides much-needed insight into what changes can be expected once *Dreissena* is introduced to a small to medium-sized system such as the Huron River. Although zebra and quagga mussels have drastically changed the fish and benthos communities of the Great Lakes, the results of this study indicate that they do not impact river ecosystems in the same way. Patterns of zebra mussel distribution in the Huron River are consistent with the “source-sink” model described by Horvath *et al.* (1996), which states that order for *Dreissena* to become established in the first place, there must be a lake or reservoir upstream of the river to house a source population from whence veligers are released downstream. In a river with a relatively swift current like the Huron River, *Dreissena* veligers are usually swept away before

they are able to attach themselves to a suitable substrate. Consequently, a pattern develops in which the mussels colonize the first few kilometers directly downstream of the source population but are sparse or absent further downstream (Table 1, Figure 2). This study demonstrated that there are significant differences in fish and benthic community composition in areas of the river with dense mussel coverage, and that current fish communities differ from those that were observed in surveys prior to the introduction of *Dreissena*. However, fish communities that were present at mussel-free locations in the 2008 surveys are similar to those found there in 1977 and 1993, although the abundance of catostomids did decrease at all sampling locations. It appears that fish that prefer not to live in an area with high *Dreissena* density may simply move a few kilometers downstream to a mussel-free area. The results of this study also demonstrate that areas where mussels have colonized are not an ecological wasteland. Several different types of fishes and invertebrates thrive over mussel beds, and these communities are not significantly less diverse than those found in areas where mussels are absent.

In conclusion, as long as river conditions remain constant, the threat to the Huron's fish communities posed by *Dreissena* is low. However, watershed managers should consider how altering the hydrology of this system could alter the pattern of mussel distribution, and consequently, the functioning of the ecosystem as a whole.

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**Table 1.** Physical attributes of Huron River sampling locations used in the collections in 1977, 1993, and 2008.

Location	Width (m)	Avg depth (m)	1977	Average Current Velocity(m/s) 1993	2008	Substrate	<i>Dreissena</i> present	Average # <i>Dreissena</i> / m <sup>2</sup>	Description
Honey Creek	35.7	0.48	0.83	1.90	1.79	Sand/gravel with lg boulders	-	-	Sleep, eroded banks lined with tree roots, woody debris, and boulders. Near Delhi Metropark.
Loch Alpine	34.1	0.74	1.32	3.02	2.85	Gravel w/ lg boulders	L	2	Eroded banks w/ protruding roots and boulders, lined with trees and overhanging branches. Boyden Creek flowing into the mainstem.
Zeab	30.8	0.82	1.64	3.74	3.52	Cobble w/ lg boulders	L	2	Eroded banks lined with tree roots and hanging branches. Island w/woody debris on east bank. Runs under Zeab Rd. bridge.
Dexter-Huron	48.8	0.58	0.73	1.68	1.58	Sand/gravel w/ lg boulders	L	2	Eroded banks lined with fallen woody debris and overhanging branches. Gravel substrate w/ large boulders. Rapids downstream of sampling site. Located in Dexter-Huron Metropark.
Mast	31.7	0.29	0.56	1.27	1.20	Lg cobble w/ boulders	-	-	Eroded banks lined with lg boulders and fallen branches. Located by Mast Rd. bridge in downtown Dexter. Small island by east bank.
Hudson Mills	41.1	0.65	0.97	2.22	2.09	Sand/gravel w/ submerged aquatic vegetation	-	-	Eroded banks lined with grass, tree roots, and overhanging branches. Located in Hudson Mills Metropark.
North Territorial	40.8	0.58	0.86	1.97	1.86	Gravel w/ lg boulders	H	89	Rocky banks with protruding roots and overhanging vegetation, lined with aquatic macrophytes in some places. Submerged boulders covered with <i>Dreissena</i> and <i>Campeloma decisum</i> . Located in Hudson Mills Metropark running underneath North Territorial Rd. bridge.
Bell	28.3	0.74	1.59	3.64	3.43	Cobble w/ lg boulders	H	504	Eroded banks lined with tree roots, rubble, and aquatic macrophytes. Rapids run over ruins of collapsed bridge. Submerged boulders covered with <i>Dreissena</i> and <i>Campeloma decisum</i> . Creek merges with mainstem here.
Fishing Site	32.9	0.81	1.51	3.46	3.26	Gravel w/ lg boulders, submerged aquatic vegetation	H	774	Highly eroded banks lined with overhanging roots and aquatic macrophytes. Rapids upstream of sampling area. House on east bank. Submerged boulders covered with <i>Dreissena</i> and <i>Campeloma decisum</i> .

**Table 2.** Adjustment factors by species for sampling gear bias based on those found in Patton et al. (1998). Functional classifications of fish species collected at all Huron River study locations in 1977, 1993, and/or 2008. H/D= Herbivore/Detritivore, P= Piscivore, BI= Benthic Invertivore, S/WC= Surface/Water Column Invertivore, O= Ominvore, GI= General Invertivore, FC= Fast Current, MC= Medium Current, SC= Slow/ No Current, GC= General Current, R= Rubble, Sa= Sand, Si= Silt, G= General Substrate, L= Low Tolerance, M= Medium Tolerance, H= High Tolerance. Categorizations found in Poff and Allan (1995).

<b>Common Name</b>	<b>Adjustment Factor</b>	<b>Trophic Guild</b>	<b>Current</b>	<b>Substratum</b>	<b>Tolerance</b>
Northern Brook Lamprey	1	H/D	M	R	L
Longnose Gar	1	P	S	G	M
Bowfin	1	P	S	Si	L
Western Grass Pickerel	1	P	S	Si	M
Northern Pike	1	P	S	G	L
Central Mudminnow	1	BI	S	Si	H
Black Bullhead	-	O	S	Si	H
Yellow Bullhead	0.5	O	S	G	M
Stonecat	0.35	GI	F	R	L
Brindled Madtom	0.35	BI	F	R	L
Northern Madtom	0.35	BI	F	R	L
Flathead Catfish	1	P	G	Si	M
Rockbass	0.5	P	M	R	L
Green Sunfish	0.27	GI	S	G	H
Pumpkinseed	1	GI	S	G	M
Warmouth	-	P	M	R	L
Bluegill	1	GI	S	G	H
Longear Sunfish	1	GI	S	G	H
Smallmouth Bass	0.5	P	M	R	L
Largemouth Bass	1	P	S	G	M
Black Crappie	1	P	S	G	M
Greenside Darter	0.82	BI	F	R	L
Rainbow Darter	0.82	BI	F	R	L
Iowa Darter	1	BI	S	Si	H
Fantail Darter	-	BI	M	R	M
Johnny Darter	0.82	BI	S	Sa	H
Orangethroat Darter	-	BI	S	R	M
Yellow Perch	0.4	P	S	G	M
Logperch	0.82	BI	M	R	L
Blackside Darter	0.82	BI	M	R	M
Walleye	-	P	S	R	M
White Sucker	0.84	BI	G	G	H
Northern Hogsucker	0.84	BI	F	R	L
Black Redhorse	0.4	BI	F	R	L
Golden Redhorse	0.4	BI	M	R	L
Ohio Stoneroller	-	H/D	M	R	M

**Table 2.** Continued.

<b>Common Name</b>	<b>Adjustment Factor</b>	<b>Trophic Guild</b>	<b>Current</b>	<b>Substratum</b>	<b>Tolerance</b>
Spotfin Shiner	-	S/WC	S	G	H
Common Carp	0.57	O	S	G	H
Striped Shiner	-	O	S	G	M
Common Shiner	1	O	G	G	M
Hornyhead Chub	1	O	M	R	L
River Chub	1	O	M	R	L
Golden Shiner	-	O	S	Si	H
Spottail Shiner	0.97	O	S	Sa	L
Blacknose Shiner	-	O	S	G	L
Rosyface Shiner	0.97	S/WC	F	R	L
Sand Shiner	0.97	O	M	Sa	M
Miscellaneous shiners	-	O	S	R	M
Northern Redbelly					
Dace	-	O	S	Si	M
Bluntnose Minnow	0.79	O	G	G	H
Fathead Minnow	0.79	O	S	Si	H
Eastern Blacknose					
Dace	0.8	O	F	R	M
Creek Chub	0.84	O	M	R	H
Blackstripe					
Topminnow	0.71	S/WC	S	G	H
Mottled Sculpin	1	BI	G	R	L
Brook Silverside	-	S/WC	S	G	L
Cisco	-	PL	S	Si	-

**Table 3.** Species richness and evenness measured for fish communities at all sites in the middle Huron River study area in 2008. Evenness was measured by taking the negative natural log of Simpson's D. LA= Loch Alpine, Z= Zeeb Road, DH= Dexter-Huron Metropark, HM= Hudson Mills Metropark, B= Bell Road, FS= Fishing Site.

	<b>Low Mussel Density</b>			<b>High Mussel Density</b>		
	<b>LA</b>	<b>Z</b>	<b>DH</b>	<b>NT</b>	<b>B</b>	<b>FS</b>
<b>Species Richness</b>						
<b>Mean</b>	<b>17</b>	<b>18</b>	<b>13</b>	<b>16</b>	<b>16</b>	<b>13</b>
June	10	17	*	12	11	7
July	20	21	11	15	18	18
August	20	15	14	20	18	13
<b>Total # Species Captured</b>	<b>29</b>	<b>25</b>	<b>18</b>	<b>25</b>	<b>22</b>	<b>20</b>
<b>Simpson's Index (corr.)</b>						
June	1.17	1.55	*	1.4	1.2	0.72
July	1.88	2.35	1.41	1.81	2.13	1.59
August	2.02	1.90	1.84	1.75	1.44	1.36
<b>Mean</b>	<b>1.69</b>	<b>1.93</b>	<b>1.63</b>	<b>1.65</b>	<b>1.59</b>	<b>1.22</b>

**Table 4.** Mean relative abundance by fish species collected by electrofishing at all middle Huron River study locations, June-August 2008. LA= Loch Alpine, Z= Zeeb Road, DH= Dexter-Huron Metropark, HM= Hudson Mills Metropark, B= Bell Road, FS= Fishing Site.

Common Name	Low Mussel Density			High Mussel Density		
	LA	Z	DH	NT	B	FS
American Brook Lamprey	*	0.92	*	*	*	*
Longnose Gar	0.14	*	*	*	*	*
Bowfin	0.44	*	*	0.34	0.20	*
Western Grass Pickerel	0.17	*	*	*	*	*
Northern Pike	0.31	1.07	*	*	*	*
Central Mudminnow	*	*	*	*	0.33	*
Yellow Bullhead	0.27	*	*	0.71	1.47	0.33
Stonecat	*	1.28	*	0.23	8.45	0.93
Brindled Madtom	0.14	0.56	0.23	0.52	*	*
Northern Madtom	*	0.71	0.23	0.48	1.42	0.51
Flathead Catfish	0.17	*	*	*	*	*
Rockbass	22.21	20.64	11.78	29.6	41.3	49.36
Green Sunfish	1.75	0.77	0.23	0.81	2.22	*
Pumpkinseed	0.17	0.35	*	1.55	0.53	*
Bluegill	2.80	1.28	0.52	6.18	6.44	8.68
Northern Longear Sunfish	*	0.21	*	3.00	2.53	0.34
Smallmouth Bass	10.22	9.28	4.53	1.91	3.36	2.72
Largemouth Bass	0.55	2.84	*	0.64	0.87	0.33
Black Crappie	0.17	*	*	*	*	0.17
Northern Greenside Darter	12.94	25.74	20.58	11.64	13.64	8.56
Rainbow Darter	11.66	14.95	12.93	30.02	5.83	8.10
Iowa Darter	*	*	0.23	*	*	0.50
Central Johnny Darter	2.33	0.62	*	1.17	*	*
Yellow Perch	1.33	*	*	1.24	0.80	0.88
Northern Logperch	3.19	*	2.61	2.35	4.32	15.10
Blackside Darter	0.27	0.57	*	0.17	0.87	0.50
White Sucker	10.11	0.71	*	0.31	1.11	*
Northern Hogsucker	12.2	5.79	0.94	2.69	1.09	0.67
Greater Redhorse	0.17	2.41	1.02	*	*	*
Spotfin Shiner	*	1.55	0.70	0.47	1.27	*
Carp	*	*	*	0.17	*	*
Hornyhead Chub	2.91	2.26	1.77	*	0.60	0.17
Spottail Shiner	*	1.04	*	*	*	0.51
Shiner spp.	0.34	2.07	0.52	*	*	*
Bluntnose Minnow	0.82	*	7.04	*	1.33	0.51
Northern Creek Chub	0.75	1.63	0.52	0.65	*	*
Blackstripe Topminnow	1.19	*	0.26	2.81	*	1.15
Northern Mottled Sculpin	0.27	1.13	*	0.34	*	*

\* value < 0.01

**Table 5.** Relative abundance of fish functional guilds across all middle Huron River sampling locations, June – August 2008. LA= Loch Alpine, Z= Zeeb Road, DH= Dexter-Huron Metropark, HM= Hudson Mills Metropark, B= Bell Road, FS= Fishing Site.

	<b>Low <i>Dreissena</i> density</b>			<b>High <i>Dreissena</i> density</b>		
	<b>LA</b>	<b>Z</b>	<b>DH</b>	<b>NT</b>	<b>B</b>	<b>FS</b>
<b>Trophic Guild</b>						
Herbivore/Detritivore	*	0.86	*	*	*	*
Omnivore	5.84	8.02	15.19	1.57	3.99	1.89
General Invertivore	4.28	3.72	1.11	11.91	21.17	12.16
S/WC Invertivore	0.78	1.72	1.48	3.37	1.53	1.47
Benthic Invertivore	61.28	51.86	57.78	49.21	27.61	36.27
Piscivore	27.82	33.81	24.44	33.93	45.71	48.22
<b>Substrate Preference</b>						
Rubble	75.7	88.5	85.93	80.22	80.06	84.49
Sand	3.30	2.30	*	1.12	*	0.63
Silt	0.60	*	0.37	0.45	0.61	0.63
General	20.40	9.48	13.70	18.20	19.33	14.26
<b>Current Preference</b>						
Low	12.65	14.08	3.7	19.33	20.55	16.14
Medium	33.07	36.78	33.33	35.06	49.39	66.04
High	42.61	47.41	51.85	44.94	29.45	17.82
General	11.67	1.72	1.11	0.67	0.61	*
<b>Tolerance</b>						
Low	74.90	83.33	84.44	80.00	78.22	83.86
Medium	0.45	7.47	0.74	4.72	6.75	2.73
High	20.43	6.90	14.81	15.28	15.03	13.42



**Table 6.** List of fish species collected within the Huron River study area in 1977 (Humphries & Smith), 1993 (Bailey & Latta), and 2008 (this study).

Common Name	Scientific Name	Family	1977	1993	2008
Northern Brook Lamprey	<i>Ichthyomyzon fossor</i>	Petromyzontidae	P	P	P
Longnose Gar	<i>Lepisosteus osseus</i>	Lepisosteidae	P	P	P
Bowfin	<i>Amia calva</i>	Amiidae	-	-	P
Western Grass Pickerel	<i>Esox americanus vermiculatus</i>	Esocidae	-	-	P
Northern Pike	<i>Esox lucius</i>	Esocidae	P	P	P
Central Mudminnow	<i>Umbra limi</i>	Umbridae	P	P	P
Black Bullhead	<i>Ameiurus melas</i>	Ictaluridae	P	-	-
Yellow Bullhead	<i>Ameiurus natalis</i>	Ictaluridae	P	P	P
Stonecat	<i>Noturus flavus</i>	Ictaluridae	P	P	P
Brindled Madtom	<i>Noturus miurus</i>	Ictaluridae	-	-	P
Northern Madtom	<i>Noturus stigmosus</i>	Ictaluridae	-	-	P
Flathead Catfish	<i>Pylodictis olivaris</i>	Ictaluridae	-	-	P
Rockbass	<i>Ambloplites rupestris</i>	Centrarchidae	P	P	P
Green Sunfish	<i>Lepomis cyanellus</i>	Centrarchidae	P	P	P
Pumpkinseed	<i>Lepomis gibbosus</i>	Centrarchidae	P	-	P
Warmouth	<i>Lepomis gulosus</i>	Centrarchidae	P	-	-
Bluegill	<i>Lepomis macrochirus</i>	Centrarchidae	P	P	P
Longear Sunfish	<i>Lepomis peltastes</i>	Centrarchidae	P	P	P
Smallmouth Bass	<i>Micropterus dolomieu</i>	Centrarchidae	P	P	P
Largemouth Bass	<i>Micropterus salmoides</i>	Centrarchidae	P	P	P
Black Crappie	<i>Pomoxis nigromaculatus</i>	Centrarchidae	P	P	P
Greenside Darter	<i>Etheostoma blennioides</i>	Percidae	P	P	P
Rainbow Darter	<i>Etheostoma caeruleum</i>	Percidae	P	P	P
Iowa Darter	<i>Etheostoma exile</i>	Percidae	-	-	P
Fantail Darter	<i>Etheostoma fabellare</i>	Percidae	P	-	-
Johnny Darter	<i>Etheostoma nigrum nigrum</i>	Percidae	P	P	P
Orangethroat Darter	<i>Etheostoma spectabile</i>	Percidae	P	-	-
Yellow Perch	<i>Perca flavescens</i>	Percidae	P	-	P
Logperch	<i>Percina caprodes</i>	Percidae	P	P	P
Blackside Darter	<i>Percina maculata</i>	Percidae	P	-	P
Walleye	<i>Sander vitreus</i>	Percidae	P	-	-
White Sucker	<i>Catostomus commersoni</i>	Catostomidae	P	-	P
Northern Hogsucker	<i>Hypentelium nigricans</i>	Catostomidae	P	P	P
Black Redhorse	<i>Moxostoma duquesnei</i>	Catostomidae	-	P	-
Golden Redhorse	<i>Moxostoma erythrurum</i>	Catostomidae	P	P	P
Ohio Stoneroller	<i>Campostoma anomalum</i>	Cyprinidae	P	P	-
Spotfin Shiner	<i>Cyprinella spiloptera</i>	Cyprinidae	P	P	P
Common Carp	<i>Cyprinus carpio</i>	Cyprinidae	P	P	P
Striped Shiner	<i>Luxilus chrysocephalus</i>	Cyprinidae	P	P	-
Common Shiner	<i>Luxilus cornutus</i>	Cyprinidae	P	P	-
Hornyhead Chub	<i>Nocomis biguttatus</i>	Cyprinidae	P	P	P

**Table 6.** Continued

<b>Common Name</b>	<b>Scientific Name</b>	<b>Family</b>	<b>1977</b>	<b>1993</b>	<b>2008</b>
River Chub	<i>Nocomis micropogon</i>	Cyprinidae	P	-	-
Golden Shiner	<i>Notemigonus crysoleucas</i>	Cyprinidae	P	-	-
Blacknose shiner	<i>Notropis heterolepis</i>	Cyprinidae	P	-	-
Spottail Shiner	<i>Notropis hudsonius</i>	Cyprinidae	P	P	P
Rosyface Shiner	<i>Notropis rubellus</i>	Cyprinidae	P	P	P
Sand Shiner	<i>Notropis stramineus</i>	Cyprinidae	P	P	-
Unidentified shiner	<i>Notropis sp.</i>	Cyprinidae	P	-	P
Northern Redbelly Dace	<i>Phoxinus eos</i>	Cyprinidae	P	-	-
Bluntnose Minnow	<i>Pimephales notatus</i>	Cyprinidae	P	P	P
Fathead Minnow	<i>Pimephales promelas</i>	Cyprinidae	P	P	-
Eastern Blacknose Dace	<i>Rhinichthys atratulus</i>	Cyprinidae	P	P	-
Creek Chub	<i>Semotilus atromaculatus</i>	Cyprinidae	P	P	P
Blackstripe Topminnow	<i>Fundulus notatus</i>	Fundulidae	P	P	P
Northern Mottled Sculpin	<i>Cottus bairdii bairdii</i>	Cottidae	P	P	P
Brook Silverside	<i>Labidesthes sicculus</i>	Atherinopsidae	P	P	-
Cisco	<i>Coregonus artedi</i>	Salmonidae	P	-	-

**Table 7.** Results of Kruskal-Wallis tests comparing differences in mean numbers of individual fish belonging to different families and functional groups from each year of collection. Significant results are highlighted in gray.

		Mean			p-value
		1977	1993	2008	
General Information	Total Catch	235.9	75.9	127.6	<b>0.004</b>
	Species Richness	15.6	15.5	16.5	0.47741
	Inverse Simpson's D	5.3	8.4	5.7	0.80116
Fish Family	Cyprinidae	147.7	40.6	9.3	<b>0.00157</b>
	Centrarchidae	59.3	3.7	43.9	<b>0.02589</b>
	Percidae	23.6	5.5	61.1	<b>0.00051</b>
	Catostomidae	14.7	5.1	7.7	0.45215
	Ictaluridae	3.6	1.3	3.4	0.45727
Fish Species	<i>Percina caprodes</i>	0	0.4	11.3	<b>0.01551</b>
	<i>Etheostoma blennioides</i>	14.6	2.7	22.1	<b>0.00996</b>
	<i>Etheostoma caeruleum</i>	2.6	2.1	23.5	<b>0.00677</b>
	<i>Ambloplites rupestris</i>	3.9	0.5	44.5	<b>0.00998</b>
	<i>Lepomis macrochirus</i>	1.1	0.5	10.3	0.05684
Functional Feeding	Omnivore	107.9	35.9	8.8	<b>0.00933</b>
	General Invertivore	4	2.2	15.7	0.17503
	Benthic Invertivore	43	27.1	69.9	0.10464
	Piscivore	21	3.5	30.25	0.07322
	Surface/Water Column	55.3	7	4.26	0.07753
	Herbivore/Detritivore	0	0.25	1.6	0.13407
Current Preference	Fast	49.5	15.9	54.7	0.06364
	Medium	70.1	24.4	48.1	0.21166
	Slow	78.7	12.23	23.1	<b>0.00665</b>
	General	43	23.4	0.1	<b>0.01258</b>
Substrate Preference	Rubble	93.4	54.8	103	0.27056
	Sand	33.6	2.1	2.3	<b>0.00935</b>
	Silt	8.3	3.4	1	<b>0.0382</b>
	General	98	15.5	21.3	<b>0.00098</b>
Siltation Tolerance	High	82	18	19.5	<b>0.00056</b>
	Medium	66.7	7.2	5.1	<b>0.02246</b>
	Low	80	26	103.3	0.193261

**Table 8.** Wilcoxon rank-sum comparisons of total catch, species diversity, fish families, and functional feeding groups for 1977 collection data between sites with high and low zebra mussel abundances in 2008.

	<b>High Density</b>	<b>Low Density</b>	<b>p-value</b>
Total Catch	174.5	367.5	0.2667
Simpson's D	5.2	5.6	0.8000
Species Richness	15.3	16	0.4667
<b>Family</b>			
Centrarchidae	14	36.3	0.6286
Percidae	21	27	0.8571
Catostomidae	19.25	12.5	0.9333
Cyprinidae	91.25	223	0.0571
Ictaluridae	3.25	4	1.0000
<b>Trophic Guild</b>			
Piscivore	44.3	9.75	0.1429
Benthic Invertivore	166.3	64	0.22857
General			
Invertivore	4	4	0.7419
Omnivore	31.7	51.5	0.8571
Sfc/Water Column	36.3	37.25	0.7000

**Table 9.** Mean number of benthic organisms collected from each major taxonomic category at the middle Huron River study locations, June-August 2008, August 2009. Significant p-values of Kruskal-Wallis tests for differences between sites are given in bold. Chiron= chironomid, amph= amphipod, olig=oligochaete, flat=flatworm.

			<b>Chiron</b>	<b>Amph</b>	<b>Olig</b>	<b>Flat</b>	<b>Clam</b>	<b>Snail</b>	<b>TOTAL</b>
Low-Density	Loch Alpine	Mean	24.38	3.38	22.75	*	2.5	*	<b>61</b>
		SE	3.96	2.26	11.8	*	0.82	*	<b>15.6</b>
	Zeeb	Mean	28.38	1.75	8.25	0.75	1.38	*	<b>51.6</b>
		SE	7.9	0.7	3.33	0.62	0.82	*	<b>10.6</b>
	Dexter-Huron	Mean	16.5	3.63	23.13	0.13	4.63	0.25	<b>44.6</b>
		SE	7.33	2.17	8.16	0.13	3.42	0.16	<b>16.4</b>
High-Density	North Territorial	Mean	145.5	1.5	10.38	1.2	1.56	2.55	<b>171.8</b>
		SE	41.6	0.5	3.77	1.1	0.38	1.02	<b>45.1</b>
	Bell	Mean	71	8.63	5.5	2.5	0.75	0.5	<b>93.6</b>
		SE	20.69	2.69	2.32	1	0.41	0.27	<b>20.3</b>
	Fishing Site	Mean	147	5.88	9.5	2.38	0.63	4.93	<b>1.09</b>
		SE	29.02	1.54	4.37	1.08	0.38	1.09	<b>26.69</b>
	p-value		0.0001	0.0094	0.2050	0.2352	0.4872	0.0051	<b>0.0020</b>

**Table 10.** Relative abundance of benthic invertebrates by functional feeding guild at study locations in the middle Huron River. LA= Loch Alpine, Z= Zeeb Road, DH= Dexter-Huron Metropark, HM= Hudson Mills Metropark, B= Bell Road, FS= Fishing Site.

<b>Functional Group</b>	<b>LA</b>	<b>Z</b>	<b>DH</b>	<b>NT</b>	<b>B</b>	<b>FS</b>
<b>S</b>	5.89	5.92	7.85	2.55	9.89	3.84
<b>FC/SF</b>	5.89	4.98	9.87	1.31	2.03	0.52
<b>CG/DF</b>	82.32	80.57	72.41	93.44	84.96	93.5
<b>G</b>	5.05	6.87	9.37	1.24	0.27	0.22
<b>P</b>	0.84	1.66	0.51	1.46	2.85	1.92

**Table 11.** Species richness and evenness values for study locations in the 1977 and 1993 surveys. Evenness was measured by taking the negative natural log of Simpson’s D. Values for 1993 were based on data adjusted for sampling bias. NT= North Territorial Road., HM= Hudson Mills, M=Mast Rd., DH=Dexter-Huron Metropark, Z= Zeeb Road., LA=Loch Alpine, D=Delhi Metropark, and HC=Honey Creek.

Metric	Year	Low Mussel Density				High Mussel Density			
		NT	HM	M	DH	Z	LA	D	HC
Richness	1977	17	15	16	-	13	13	21	14
	1993	-	13	-	10	26	13	-	-
Evenness	1977	4.9	6.2	5.3	-	3.9	3.2	7.5	6.2
	1993	-	7.1	-	4.4	20	2.1	-	-

**Table 12.** Mean number of individuals and standard error from fish families collected from the middle Huron River study area, June – August 2008. Results of a Wilcoxon rank sum (WRS) test for mean number of individuals from high and low zebra mussel density sites are listed in the right-hand column. Ict= Ictaluridae, Cent= Centrarchidae, Perc= Percidae, Cat= Catostomidae, Cyp= Cyprinidae. LA= Loch Alpine, Z= Zeeb Road, DH= Dexter-Huron Metropark, HM= Hudson Mills Metropark, B= Bell Road, FS= Fishing Site.

Family	Low ZM Density						High ZM Density						WRS p
	LA		Z		DH		NT		B		FS		
	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE	
Ict	1.33	0.90	2.67	0.3	1.00	1.22	3.00	1.22	12.0	3.00	3.00	1.00	<b>0.01</b>
Cent	50.3	3.30	41.3	9.3	35.0	15.7	65.0	15.7	62.0	20.0	94.0	20.0	<b>0.02</b>
Perc	63.0	37.0	47.7	6.8	73.0	10.6	68.0	10.6	28.0	8.15	56.0	17.6	0.31
Cat	43.7	24.0	10.0	1.2	4.00	3.49	4.00	3.49	2.00	0.67	1.30	0.67	<b>0.00</b>
Cyp	9.33	5.60	11.3	6.4	22.0	0.71	2.00	0.71	4.00	2.00	2.30	2.33	<b>0.01</b>

**Table 13.** Mean number of individuals belonging to different functional groups of fishes found in the middle Huron River study area, June – August 2008. Results of a Wilcoxon test for mean number of individuals from high and low zebra mussel density sites are listed in the right-hand column. Sites as in Table 3.

F(x) Group	Low <i>Dreissena</i> Density						High <i>Dreissena</i> Density						WRS p	
	LA		Z		DH		NT		B		FS			
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
<b>Trophic Guild</b>														
H/D	*	*	1.00	*	*	*	*	*	*	*	*	*	*	<b>0.032</b>
O	10.0	5.5	9.3	5.3	20.5	11.5	2.3	0.9	4.3	2.2	3.0	2.5	<b>0.0</b>	
GI	7.3	1.9	4.3	0.3	1.5	0.5	17.7	3.5	23.0	8.1	19.3	9.5	<b>0.0</b>	
S/SC	1.3	0.3	2.0	1.2	2.0	1.0	5.0	2.3	1.7	0.9	2.3	1.9	0.4	
BI	105.0	45.4	60.3	8.3	78.0	6.0	73.0	10.4	30.0	6.7	57.7	19.4	0.1	
P	47.7	0.3	39.3	8.5	33.0	1.0	50.3	9.6	49.7	17.3	76.7	10.9	0.1	
<b>Substrate Pref</b>														
R	130.0	40.0	103.0	15.2	116.0	9.0	119.0	26.0	87.0	22.2	134.3	30.6	0.3	
Sa	5.7	5.7	2.7	2.7	*	*	1.7	2.0	*	*	1.0	1.0	0.4	
Si	1.0	0.6	*	*	0.5	0.5	0.7	0.8	0.7	0.3	1.0	0.6	0.2	
G	35.0	20.0	10.7	4.8	18.5	15.5	27.0	6.8	21.0	9.1	22.7	10.6	0.2	
<b>Current Velocity</b>														
High	73.0	35.0	55.0	6.7	57.5	10.2	66.7	10.8	32.0	7.2	28.3	5.7	0.1	
Medium	56.7	4.9	42.7	5.4	25.0	2.0	52.0	14.1	54.0	17.2	105.0	24.6	0.4	
Low	21.7	8.8	16.3	10.8	10.0	*	28.7	9.2	22.0	10.4	25.7	12.4	0.2	
General	20.0	18.0	2.0	*	15.0	15.0	1.0	0.7	0.7	0.7	*	*	<b>0.0</b>	
<b>Tolerance</b>														
High	35.3	16.0	8.0	2.3	20.0	15.0	22.7	6.4	16.0	6.3	21.3	10.8	0.4	
Medium	7.7	3.9	8.7	7.2	1.0	1.0	7.0	3.5	7.3	3.7	4.3	1.5	0.3	
Low	128.0	40.0	96.7	15.1	114.0	7.0	119.0	25.6	85.0	22.8	133.3	30.0	0.4	

**Table 14.** Mean relative abundance of benthic macroinvertebrate taxa collected at all middle Huron River sampling locations, June – August 2008 and August 2009 (\* value <0.01).

Taxonomic Group	Low <i>Dreissena</i> Density			High <i>Dreissena</i> density		
	LA	Z	DH	NT	B	FS
<b>Scuds (Amphipoda)</b>	<b>4.64</b>	<b>3.90</b>	<b>5.33</b>	<b>2.92</b>	<b>9.21</b>	<b>6.34</b>
<b>Flatworms (Platyhelminthes)</b>	*	<b>0.90</b>	<b>0.09</b>	<b>3.02</b>	<b>5.22</b>	<b>1.96</b>
<b>Leeches (Euhirudinea)</b>	*	*	<b>0.09</b>	<b>0.06</b>	*	<b>0.05</b>
<b>Beetles (Coleoptera)</b>	<b>0.95</b>	<b>7.11</b>	<b>0.09</b>	<b>2.36</b>	<b>1.76</b>	<b>0.68</b>
Elmidae	0.95	5.90	0.09	2.26	1.76	0.68
Psephenidae	*	1.20	*	0.10	*	*
<b>Flies (Diptera)</b>	<b>52.87</b>	<b>56.20</b>	<b>19.51</b>	<b>69.70</b>	<b>64.76</b>	<b>78.90</b>
Chironomidae	52.61	56.20	19.51	76.64	64.60	78.70
Tabanidae	*	*	*	0.06	0.16	0.20
Empididae	0.26	*	*	*	*	*
<b>Mayflies (Ephemeroptera)</b>	<b>1.41</b>	<b>4.73</b>	<b>0.33</b>	<b>0.75</b>	<b>2.49</b>	<b>0.14</b>
Baetidae	0.26	*	*	*	0.94	*
Caenidae	0.41	*	*	0.14	*	0.09
Ephemeridae	0.26	1.09	0.19	*	1.25	*
Heptageniidae	0.40	3.64	*	0.60	0.94	0.05
Leptohyphidae	0.26	*	*	*	*	*
Potamanthidae	*	*	0.09	*	*	*
<b>Moths (Lepidoptera)</b>	*	<b>0.54</b>	*	*	*	*
Pyrilidae	*	0.54	*	*	*	*
<b>Dragonflies (Odonata)</b>	*	*	*	*	*	<b>0.13</b>
Aeshnidae	*	*	*	*	*	0.13
<b>Stoneflies (Plecoptera)</b>	<b>0.40</b>	<b>0.15</b>	*	<b>0.45</b>	*	*
Perlidae	0.40	*	*	0.29	*	*
Perlodidae	*	*	*	0.16	*	*
Taeniopterygidae	*	0.15	*	*	*	*
<b>Caddisflies (Trichoptera)</b>	<b>8.71</b>	<b>4.68</b>	*	<b>2.39</b>	<b>2.34</b>	<b>0.25</b>
Brachycentridae	*	*	*	0.06	*	0.05
Glossosomatidae	6.18	2.65	*	0.91	*	0.10
Hydropsychidae	1.93	1.60	*	1.14	0.83	0.10
Leptoceridae	*	1.5	*	*	0.63	*
Limnephilidae	0.26	*	*	*	*	*
Philopotamidae	*	0.15	*	*	*	*
Polycentropodidae	0.26	*	*	0.15	*	*
Pyschomyidae	*	*	*	0.06	*	*
<b>Woodlice (Isopoda)</b>	<b>0.26</b>	<b>0.15</b>	*	<b>0.06</b>	<b>0.49</b>	*
<b>Mollusks (Mollusca)</b>	<b>5.22</b>	<b>3.17</b>	<b>5.60</b>	<b>3.94</b>	<b>2.8</b>	<b>5.75</b>
Fingernail Clams (Sphaeriidae)	5.22	3.17	5.26	1.42	1.17	1.07
Snails (Gastropoda)	*	*	0.19	2.44	0.39	2.20
Zebra Mussels (Dreissenidae)	*	*	*	0.06	1.24	2.47
<b>Earthworms/ Tubifex Worms (Oligochaeta)</b>	<b>25.55</b>	<b>18.46</b>	<b>66.01</b>	<b>7.09</b>	<b>10.92</b>	<b>5.74</b>

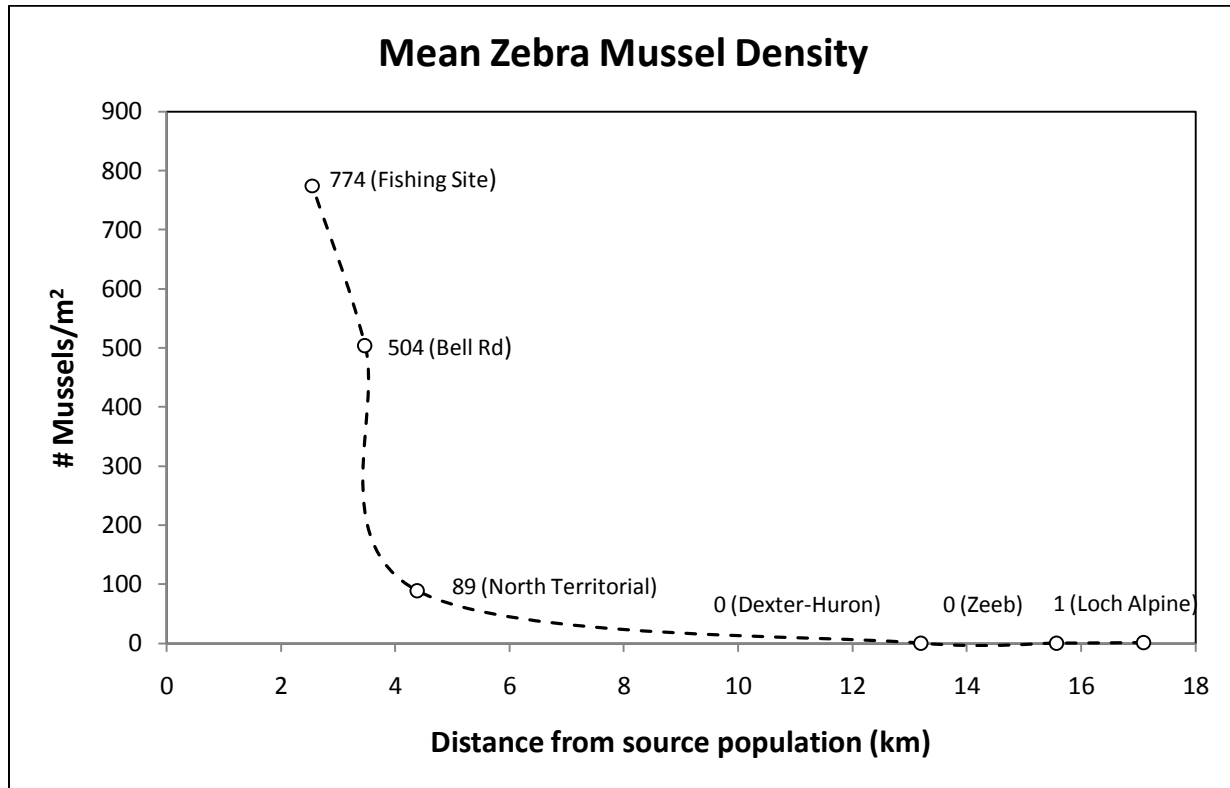


**Figure 1.** Composition of fish communities in the Huron River from surveys taken in 1977, 1993, and August 2008. Datasets from 1993 and 2008 were adjusted for gear bias.

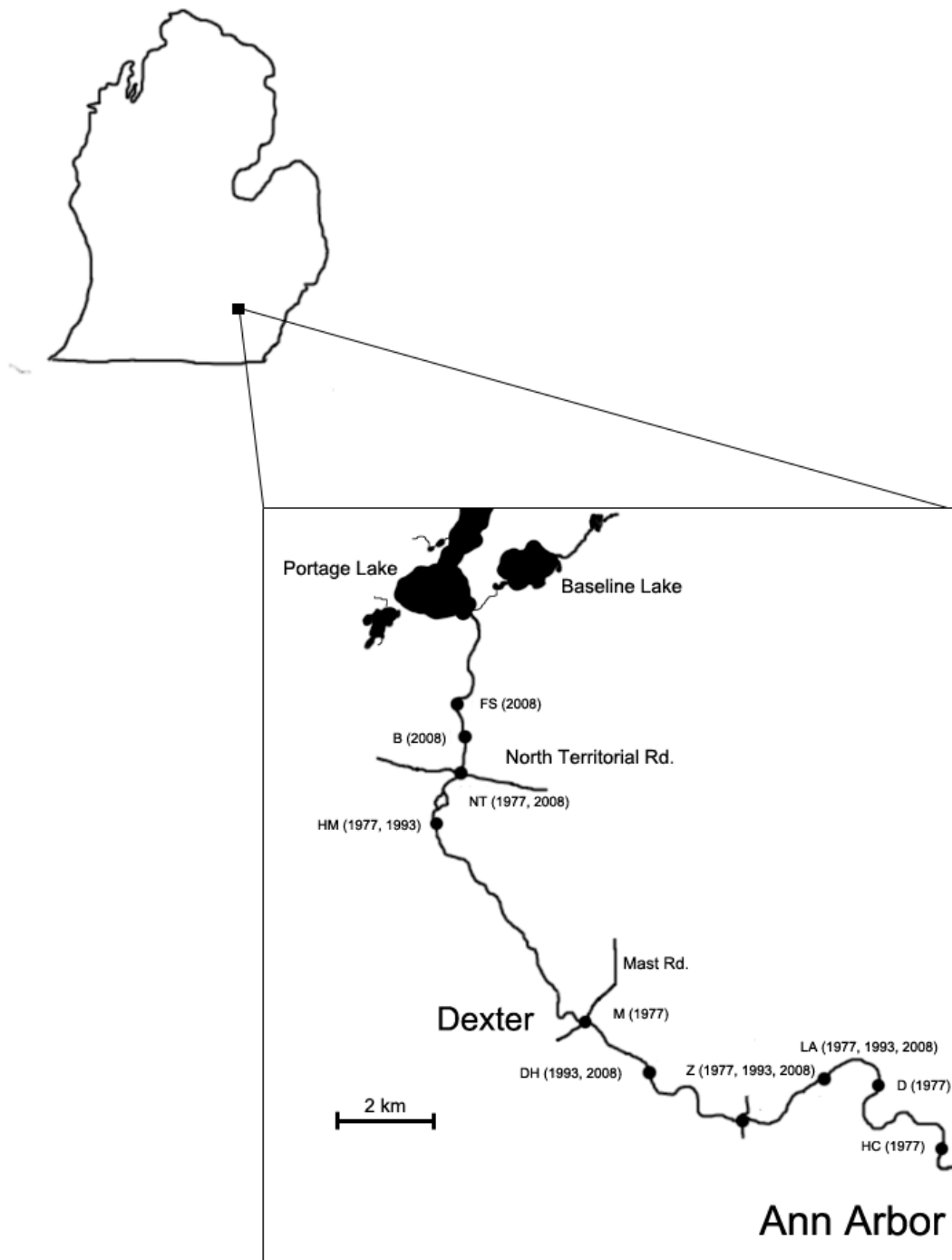
### % Fish Community Composition by Family - 1977, 1993, and 2008



**Figure 2.** Mean zebra mussel density on the riverbed at sampling locations in the middle Huron River study area, plotted as a function of distance from the source population in Baseline and Portage lakes.



**Figure 3.** Map of the middle Huron River study area. HC= Honey Creek (1977), D= Delhi Metropark (1977), LA= Loch Alpine (1977, 1993, 2008), Z= Zeeb Road (1977, 1993, 2008), DH= Dexter-Huron Metropark(1993, 2008), M= Mast Road (1977), HM= Hudson Mills Metropark (1977, 1993), NT= North Territorial Road (1977, 2008), B= Bell Road (2008), FS= Fishing Site (2008).



**Figure 4.** Relative abundances of major benthic macroinvertebrates groups at all middle Huron River study sites, June – August 2008, August 2009. BC= Loch Alpine, Z= Zeeb Rd., DH= Dexter-Huron, HM=North Territorial, B= Bell Rd., FS= Fishing Site.

