Effects of Zebra Mussel Invasion on Juvenile Steelhead Distribution, Diet, Growth, and Condition in the Muskegon River, Michigan

by
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Abstract

Dreissenid mussels (zebra mussels *Dreissena polymorpha;* quagga mussel*,* *D. bugensis*) are an invasive species from the Ponto-Caspian region. Since their introduction, zebra mussels have drastically changed Great Lakes aquatic ecosystems by altering nutrient cycling, biomass and species composition of lower trophic levels, with consequent impacts on fish community composition, diet and growth. This study examined zebra mussels' effects on the spatial distribution, diet and growth of age-0 steelhead (*Oncorhynchus mykiss*) in the Muskegon River, a major tributary of Lake Michigan. Densities, spatial distributions, diets, sizes and growth rates of age-0 steelhead were compared from 1998, before zebra mussel invasion, to the 2000-2003 period, post zebra mussel invasion. Before zebra mussel introduction, the majority of age-0 steelhead were found in the upper portion of the study reach in strata 1 and 2. After zebra mussel introduction, age-0 steelhead were found in strata 2 and 5 in the summer and stratum 2 in the fall. Following zebra mussel introduction, mean weights, lengths, condition and growth rates of age-0 steelhead decreased. Significant changes in the diet were observed in the pre- and post-zebra mussel periods (χ^2=21.05, p=0.007). While age-0 steelhead consumed mostly Amphipoda (42%) and Trichoptera (27%) in 1998 before zebra mussel invasion, decreases in the abundance and availability of Trichoptera resulted in a post-zebra mussel diet shift to Diptera (51%) and Amphipoda (30%). Using bioenergetics modeling, it was determined that the change in growth of age-0 steelhead was mainly caused by the changes in diet following the introduction of zebra mussels, rather than differences in water temperature over the study period. Reduced growth of age-0 steelhead has negative implications for steelhead survival and potential recruitment if survival is size-dependent.

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Introduction

Dreissenid mussels (zebra mussel *Dreissena polymorpha;* quagga mussel*, D. bugensis*) are an invasive species from the Ponto-Caspian region, an area which includes the Black and Caspian seas. They were likely introduced to the Great Lakes region via ballast water transfer from ships (Vanderploeg et al. 2002). Since their introduction in the late 1980s to Lake St. Clair, zebra mussels have drastically changed aquatic ecosystems in the region. These changes have included increased water clarity (Fahnenstiel et al. 1995), increased macrophyte densities (Skubinna et al. 1995), and changes in the abundance and diversity of zooplankton (MacIsaac et al. 1995) as well as macroinvertebrate communities (Ricciardi et al. 1997; Barton 2004). How zebra mussels may impact fish distribution, growth, and foraging is less clear.

Recent studies have documented impacts of dreissenid mussels on Great Lakes fish communities. Dreissenid mussels may affect the fish communities of the Great Lakes either directly (i.e. by altering spawning habitat, affecting foraging ability, influencing risk of predation) or indirectly (i.e. by changing food web dynamics). Most studies have focused on lentic fish communities. In western Lake Erie, Gopalan et al. (1998) found that the introduction of zebra mussels did not result in decreases in abundance of most forage fishes. The only fish to decrease in the time frame following zebra mussel introduction was the gizzard shad (*Dorosoma cepedianum*). Trometer and Busch (1999) also did not find any changes in fall abundance of fishes after zebra mussel invasion in the western basin of Lake Erie except for yellow perch (*Perca flavescens*) which increased. In Lake Ontario, Mills et al. (2003) suggested that the shift of slimy sculpin (*Cottus bairdi*) to deeper waters and declines in lake whitefish were the result of

Dreissena introduction, as well as declines in *Diporeia* populations. In Lake Huron, Dobiesz et al. (2005) also suggested *Diporeia* declines were due to zebra mussel invasion and cautioned that effects on the fish community could occur through food web interactions. Indeed, more recent studies indicate profound changes in nutrient cycling (Hecky et al. 2004), biomass and species composition of lower trophic levels (phytoplankton - Fahnenstiel et al. 1995, 2010; zooplankton - Vanderploeg et al. 2002; *Diporeia* spp. - Nalepa et al. 2009a), and consequent impacts on fish community composition, diet and growth (Hondorp et al. 2005, Pothoven and Madenjian 2008, Madenjian et al. 2010).

Fewer studies are available that report the effect of zebra mussels on lotic fish communities. Jennings (1996) found that juvenile fathead minnows (*Pimephales promelas*) grew significantly slower in high zebra mussel treatments than low zebra mussel treatments. Using this information, he postulated that fish growth in the Mississippi River would not be negatively affected at zebra mussel densities between 0-3,000/m^2 but could be negatively affected at densities higher than 3,000/m^2. Strayer et al. (2004) analyzed a long term dataset to evaluate zebra mussel effects on open water and littoral fishes in the St. Lawrence River. Fish species occurring in open water decreased in abundance and were found to shift downriver away from high zebra mussel areas. However, species such as Centrarchids that occupied littoral areas increased in abundance and shifted upstream.

Most studies of zebra mussel impacts on fish growth have been conducted in lentic habitats, and study conclusions vary depending on the mechanism studied. Trometer and Busch (1999) examined growth of various fishes in Lake Erie following zebra mussel introduction and showed no changes in growth for many age-0 fish species, including but not limited to yellow perch, walleye (*Sander vitreus*), and freshwater drum (*Aplodinotus grunniens*). Mayer et al. (2000) examined the effects of zebra mussels on yellow perch in Oneida Lake, NY and found no changes in age-0 yellow perch diet, but did find significant increases in growth. Thayer *et al.* (1997) also found increases in growth of adult yellow perch in the presence of zebra mussels using enclosure experiments that resulted in different benthic prey available between the two enclosure treatments in Lake St. Clair. Richardson and Bartsch (1997), however, like Trometer and Busch (1999), showed no change in growth for age-0 bluegills (*Lepomis macrochirus*) in their experimental mesocosms. Hondorp et al. (2005) found shifts in diets of slimy sculpin (*Cottus cognatus*), alewife (*Alosa pseudoharengus*) and bloater (*Coregonus hoyi*) following the decline of *Diporeia* spp. in southeast Lake Michigan. Pothoven and Madenjian (2008) examined diets of alewives and lake whitefish (*Coregonus clupeaformis*) following the declines of *Diporeia spp.* after dreissenid introduction. Alewives showed decreased consumption and decreased growth. Lake whitefish, though also showing decreased growth, actually consumed more in the post dreissenid mussel period due to increases in dreissenid consumption. Nalepa et al. (2009b) also examined the diets of lake whitefish and found similar increases in dreissenid consumption for medium and large lake whitefish. In one of the few studies of zebra mussel impacts on the growth of a lotic species, Jennings (1996) demonstrated declines in fathead minnow (*Pimephales promelas*) growth in aquaria with zebra mussel compared to controls.

The goal of this study was to document changes in diet and consumption of age-0 steelhead (*Oncorhynchus mykiss*), an economically important target of the recreational fishery in the Great Lakes, that have occurred since the introduction of zebra mussels into the Muskegon River, a major tributary to Lake Michigan. Godby (2000) examined the benthic invertebrate community of the lower Muskegon River in summer and fall of 1998 and spring of 1999 prior to establishment of zebra mussels. During this time period, Chironomidae, Hydropsychidae, and Ephemerellidae were the most abundant families. Though there was higher richness of macroinvertebrate species downstream from Croton Dam, total invertebrate abundance decreased further downstream from the dam (Godby 2000). Since establishment of zebra mussels in the river, there have been large declines in chlorophyll a and density of all macroinvertebrate groups (Luttenton et al. 2006). These declines severely affected the Chironomid and Trichopteran populations, with Hydropsychid caddisflies being the most severely affected group (Luttenton *et al.* 2006).

Changes in the macroinvertebrate community following zebra mussel introduction may have resulted in changes in steelhead growth rate and survival observed from 2000 to 2003 (Godby 2000, Godby et al. 2007). Macroinvertebrate taxa showing the largest declines in Muskegon River were calorically-rich Trichoptera, a main prey item consumed by age-0 steelhead (*Oncorhynchus mykiss*) prior to zebra mussel invasion (Godby et al. 2007). I hypothesized a careful analysis of steelhead stomach contents available for analysis from zebra mussel invasion surveys would reveal changes in age-0 steelhead diet that may have caused observed decreases in steelhead growth, condition and survival. Specific objectives of my study were:

1) Analyze changes in distribution and density of age-0 steelhead between pre- and post-zebra mussel periods.

2) Quantify diets of age-0 steelhead post-zebra mussel invasion and compare with diets in the pre-zebra mussel period.
3) Use a bioenergetics model to quantify steelhead consumption and growth and determine the relative importance of temperature and diet composition on age-0 steelhead consumption and growth.
4) Relate changes in steelhead distribution, diet, and consumption to observed changes in growth and condition.

Methods

Study Area

The Muskegon River is the second largest tributary to Lake Michigan with a watershed of about 5,900 km^2 (O'Neal 1997). The watershed is not heavily developed with 33.4% of the watershed devoted to agriculture and 0.6% to urban development (O'Neal 1997). However, there are five major impoundments on the river, the lowest of which is Croton Dam. The Muskegon River is well known for its salmon and trout fishing and is stocked with brown trout (*Salmo trutta*), steelhead, and Chinook salmon (*Oncorhynchus tshawytscha*) by the Michigan Department of Natural Resources (Godby et al. 2007).

Croton Dam is the furthest downstream of five major impoundments on Muskegon River, and blocks upstream movement of adfluvial salmonids within the watershed. The study reach extends approximately 22 km downstream from Croton Dam to Newaygo and has an average width of 65 m and average annual discharge of approximately 62 m^3/s (O'Neal 1997, Godby et al. 2007). This stretch encompasses most of the important salmonid breeding grounds in the river for steelhead and Chinook salmon (Godby et al. 2007). Previous work classified five distinct strata within this section of river based on multivariate analysis of instream substrate composition and riparian habitats (Figure 1, Table 1, Ichthyological Associates 1991). These strata were used to examine zebra mussel effects on age-0 steelhead abundance and diet within similar habitats and over a gradient from high zebra mussel densities upstream (stratum 1) to lower mussel densities downstream (stratum 5). Luttenton et al. 2006 found that there were very high zebra mussel densities in stratum 1, with approximately 27,000 zebra mussels/m^2 in 2001. Densities were much lower in strata 2 and 4. The source of zebra mussel introduction was the impoundment at Croton Dam.

Fish Collections

Sites for fish collections were chosen using a random stratified design (Godby et al. 2007) in summer and fall of 1998, 2000, 2001, and summer of 2002. The number of randomly selected sites in each stratum was determined by the amount of suitable trout habitat, defined as predominantly gravel/cobble substrates in shallow nearshore areas with flow velocities of 0.5 to 1.0 m/s (Godby et al. 2007). More sites were chosen within strata with suitable trout habitat and fewer sites in less suitable habitat. A band of shoreline one hundred meters long by three meters wide was sampled at each site location using a 250V DC barge electrofishing unit. In the summer, 36 sites were sampled in 1998, 30 in 2000 and 2001, and 29 in 2002. In fall, 33 sites were sampled in 1998, 26 in 2000, and 29 in 2001. In 2003, although not enough fish were sampled within the reach for density estimates, fish were also collected in the summer for diet and growth analysis. At each site, a subsample of up to 30 age-0-steelhead were measured (mm TL), weighed (0.01 g), and stored in either formalin or ethanol for later diet analysis in the laboratory.

Differences in average weights and lengths of age-0 steelhead were compared among years using ANOVA.

Steelhead Density

Steelhead density was estimated using pass depletion techniques (Seber and LeCren 1967) during both the pre- and post-zebra mussel periods. At each site, densities (number/m^2) were estimated using two or three passes to achieve depletion, and were summarized as the average site density (number/m^2) by stratum. Different transformations of the data were performed in order to best achieve normality prior to statistical analysis. The densities in summer were transformed using log(X+1) and densities in fall were transformed using $\sqrt{(X+0.5)}$ to meet assumptions of normality prior to testing for significance using a two-way ANOVA.

Data on average site density of age-0 steelhead by strata were imported into ESRI ArcGIS 9.0 for analysis and visualization.

Instantaneous Growth Rate and Condition

Instantaneous daily growth rate (G) was estimated for age-0 steelhead:

$$G = \ln(W_{t+1} - W_t) / d$$

where W_t is the mean weight at time t, W_{t+1} is the mean weight at time t+1, and d is the number of days between samples.

The condition of age-0-steelhead was defined as the average weight (to 0.01 g) of steelhead collected in the summer divided by the average length (to 0.1 cm) cubed. These average condition values (g/cm^3) were calculated using length and weight measurements collected in the field.

Diet Analysis

Godby et al. (2007) examined non-empty stomachs of 49 age-0 steelhead collected from throughout the Muskegon River during summer 1998, the pre-zebra mussel period. An additional 55 non-empty diet samples were examined from the post-zebra mussel period collected during summer of 2002 and 2003.

In the laboratory, length and weight were remeasured on each fish. Stomachs were excised by making an incision below the esophagus and before the intestine. The excised stomach was weighed (0.1 mg) and stomach contents were removed and stored in ethanol. The stomach was then weighed empty and the weight of the stomach contents for each fish was estimated by subtracting weight of the empty stomach from the full stomach.

Stomach contents were identified to lowest taxonomic level possible, usually family. A subsample of each taxon was taken and average length determined for each prey item. Using length-to-biomass conversions provided by Smock (1980) and Johnston and Cunjak (1999), biomass of each food item was estimated. Differences in the proportions of each prey item in the diets during the pre- and post-zebra mussel periods were tested for significance using the Chi-Square statistic in SPSS. The proportions of diet items from the pre-zebra mussel period were the expected values and the proportions of diet items from the post-zebra mussel period were the observed values for each taxon.

Bioenergetics Modeling

The Wisconsin Bioenergetics software (Version 3, Hanson et al. 1997) was used to simulate relative effects of temperature and prey composition on consumption and growth of age-0 steelhead. The basic energetics equation relating weight and temperature specific growth of fish to consumption is:

$$G = C - R_{tot} - F - U - SDA$$

where G = growth, C = consumption, R_{tot} = total metabolic losses (active and standard), F = egestion, U = excretion, and SDA = specific dynamic action. The species-specific coefficients for age-0 steelhead used in bioenergetics modeling were from Railsback and Rose (1999) and Rand et al. (1993) (Table 2). Estimates of mean fish weight were determined from field samples collected in August and October in 1998 for the pre-zebra mussel period, and July and October 2003 for the post-zebra mussel period (Table 3). The July start weights were corrected using the instantaneous growth equation (shown above) in order to estimate weight of fish in August 2003.

Water temperature measurements were obtained from the USGS gage at Croton Dam on the Muskegon River from August through October in 1998 and 2003. The average daily temperature was input in the model. Diet composition of age-0 steelhead during summer of the pre-zebra mussel period was from Godby et al. (2007) while diet composition from the post-zebra mussel period combined diet data from 2002 and 2003. Prey caloric densities were calculated using biomasses calculated in the diet analysis and converted to caloric densities following conversion coefficients reported in Hanson et al. (1997) and Cummins and Wuycheck (1971) (as cited by Johnson et al. 2006).

Differences in observed growth of age-0 steelhead among years could be caused by differences in temperature or diet between the pre- and post-zebra mussel periods. To evaluate this hypothesis, six model simulations were performed using the bioenergetics model to determine the relative effects of temperature and diet composition on consumption and growth of age-0 steelhead (Table 4). The first simulation performed was the “Control” run where the water temperature, mean weight and diet composition values were the actual data from either pre- or post-zebra mussel periods. In subsequent simulations, either temperature or diet was held constant at observed levels, and the other variable was switched to evaluate impacts of each variable on consumption rate given observed changes in growth. Thus, the “Temperature” simulation used mean weights and diet composition data as in the control simulation, but switched the temperature values from the pre- and post-zebra mussel invasion periods to isolate the effect of those different temperature patterns on consumption and growth. The “Diet Composition” simulations kept temperature values as in the control run but switched diet composition values from the pre- and post zebra mussel periods to isolate the effect of the diet change on steelhead consumption and growth. Only proportions of items in the diet were switched; caloric densities of macroinvertebrates in the diet were kept constant.

Results

Steelhead Density

Spatial distributions and densities of age-0 steelhead appeared to change after zebra mussels invaded the lower Muskegon River. In summer, the density of age-0 steelhead in summer was significantly different among years (F=2.997, p=0.035) but not strata (F=1.815, p=0.133) or the interaction (F=1.381, p=0.216). Sampling in 2002 showed significantly higher densities throughout the study area compared to 1998 and 2001. The mapping of age-0 steelhead density prior to zebra mussel introduction showed the majority of steelhead in the summer were caught in strata 1 and 2 with very few steelhead caught in strata 3, 4, and 5 (Figure 2). Following zebra mussel introduction in

2001, age-0 steelhead density declined (32.2 ± 21.1/m^2) in stratum 1, remained high (141.7 ± 136.3/m^2) in stratum 2, and increased to 125.2 ± 72.6/m^2 in stratum 5.

In fall, prior to zebra mussel introduction, the highest densities of age-0 steelhead were found in strata 1, 2, and 3 (Figure 3). By fall 2001, steelhead densities had dropped in strata 1 (2.7 ± 1.8/m^2) and 3 (0.0/m^2) and to a lesser extent in stratum 2, though stratum 2 densities were lower than those in 1998 (mean = 32.3 ± 48.2/m^2 in 1998, 12.8 ± 20.5/ m^2 in 2001). The two-way ANOVA showed significant differences in the fall among strata (F=4.183, p=0.004) and year (F=3.914, p=0.024) but not the interaction (F=1.178, p=0.326). In the fall, age-0 steelhead density in stratum 2 was significantly different from stratum 5, but the post hoc tests used were unable to detect where the statistical differences occurred.

Growth and Condition

Changes in mean weight, growth rate, length, and condition of age-0 steelhead also were observed after zebra mussel introduction. Average weight in the summer was significantly different among years (F=302.4, p<0.0001). In August 1998, the average weight of age-0 steelhead was 2.36 ± 0.05 g, significantly larger than the corrected July weights of age-0 steelhead in 2001, 2002, and 2003 (Table 5). The fall average weights were also significantly different between years (F=27.6, p<0.0001) (Table 5). Age-0 steelhead were smallest in fall 2003 with an average weight of 4.95 ± 0.7 g, significantly smaller than in 1998 and 2001. Instantaneous daily growth rate (G) was 0.017 g/day in 1998 and 2001, but dropped to G = 0.011 g/day in 2003. There were no fish weights measured in fall 2000 or 2002 to allow estimates of G in those years.

Average length of age-0 steelhead decreased after the introduction of zebra mussels and there were significant differences between years. In summer 1998, prior to zebra mussel introduction, the average length of age-0 steelhead was 5.9 ± 0.04 cm (Table 6), significantly longer than the average lengths of age-0 steelhead in summer 2000-2002 ($F=13.9$, $p<0.0001$). Significant differences also were found among average lengths of age-0 steelhead in fall ($F=60.9$, $p<0.0001$). In October 1998, the average length of age-0 steelhead was 9.0 ± 0.02 cm. By 2003, the average length of steelhead had declined to 8.1 ± 0.4 cm.

Condition of age-0 steelhead also was higher in the pre-zebra mussel period than in the post-invasion period. While significant differences in summer condition of age-0 steelhead were detected among years ($F=16.6$, $p<0.0001$), there was no temporal trend in condition. In 1998, prior to zebra mussel introduction, the summer condition of age-0 steelhead was 10.5 ± 0.09 g/cm^3*10^{-3} (Table 7), increased in 2000, and declined to a low in 2001-2002 before increasing again in 2003. Condition of age-0 steelhead in fall declined after 1998 and differences among years were significant ($F=6.3$, $p=0.02$). In the pre-zebra mussel period (1998), the condition of age-0 steelhead in fall was approximately 10.3 ± 0.1 g/cm^3*10^{-3}. Following zebra mussel introduction (2001-2003), the condition of age-0 steelhead in the fall significantly decreased to 9.9 ± 0.7 g/cm^3*10^{-3}.

Diet Analysis

Significant changes in the diet composition of age-0 steelhead were observed between the pre- and post zebra mussel periods ($\chi^2=21.054$, $p=0.007$). The main prey items consumed during the pre-ZM period by wet weight were Amphipoda (41.8%) and Trichoptera (26.6%), specifically Hydropsychidae (17.3%) (Table 8). After zebra mussel invasion, the percentage of Trichopterans (mainly Hydropsychidae) declined in steelhead diets, as did Amphipods (to 30.4%) and zooplankton, but percentages increased of Diptera (50.1% - mainly Chironomidae), Ephemeroptera (7.2%), and Plecoptera (3.6%).

Though results should be interpreted with caution due to small sample sizes within strata, interesting spatial patterns in diet composition of age-0 steelhead were observed (Figure 4). In the pre-zebra mussel period, the proportion of zooplankton (Cladocerans) in the diet was high in strata 1 (near Croton Dam) and decreased downstream. The proportion of amphipods in the diet increased with distance downstream. Diets of age-0 steelhead from stratum 4 in the pre-zebra mussel period showed the greatest variety of items in the summer. In the post-zebra mussel data, amphipods became more prevalent in diets closer to the dam in the high zebra mussel areas and decreased in prevalence further downstream away from the zebra mussels. The percentage of Dipterans in the diet also decreased with distance downstream after zebra mussel invasion.

Bioenergetics Modeling

Bioenergetics modeling showed that age-0 steelhead had a lower average daily consumption rate in the pre-zebra mussel period compared to the post-zebra mussel period (Figure 5). The control simulation indicated that age-0-steelhead specific consumption rate would be only 0.159 g/g/day in the pre-zebra mussel time period to achieve observed growth, compared to a higher specific consumption rate of 0.218 g/g/day in the post-zebra mussel time period to achieve less growth (Table 3). The temperature run, designed to look solely at the effect of temperature in the two time periods, showed that temperature did not explain the differences in specific consumption and growth of age-0 steelhead observed between the two periods. Using pre-zebra mussel diet data, 1998 weight parameters, and 2003 temperature data, age-0-steelhead would have to consume just 3.7% less per day to achieve the same growth. Using post-zebra mussel diet and weight data, using the 1998 temperature data, fish would have to consume just 4.2% more per day to achieve the same growth. In contrast, changes in diet composition explained much of the observed decreases in age-0 steelhead growth observed following zebra mussel invasion. If age-0 steelhead diet compositions were switched from pre- to post-ZM invasion periods and all other pre-zebra mussel parameters stayed the same, steelhead specific consumption rate would have to increase by 39% (0.221 g/g/day) to grow the same amount during the pre-invasion period. In contrast, age-0 steelhead during the post-invasion period would consume 72% (0.157 g/g/day) less per day to grow the amount observed in the field if they had been eating the pre-zebra mussel diet.

Discussion

Steelhead density prior to zebra mussel introduction was highest upstream near Croton Dam (in strata 1 and 2) but shifted downstream after zebra mussel introduction, consistent with the claims of guides and anglers on the river. The diet, average weight, length, condition and instantaneous growth rate of age-0 steelhead decreased concurrently with the introduction of zebra mussels to the Muskegon River. Diet composition of age-0 steelhead in the post-zebra mussel period was significantly different from that in the pre-zebra mussel period. There was a 98% decrease of Trichoptera in the diet from 1998 to 2002-2003. Bioenergetics analysis showed that the change in the proportions of prey items in the diet affected estimated daily consumption to a greater degree than differences in water temperature between the two years. The differences in macroinvertebrate density and distribution resulting from zebra mussel invasion may have greatly affected foraging success, growth and survival of age-0 steelhead.

Spatial Analysis of Steelhead Abundance

Spatial aggregation was an important tool to visualize how steelhead density changed through time and within a stratum along the zebra mussel gradient. The data support the contention that peak locations of steelhead abundance have been displaced downstream since the introduction of zebra mussels. These results coincide with the distribution of zebra mussels described by Luttenton *et al.* (2006) which showed the highest densities of zebra mussels upstream and much lower densities downstream, starting in stratum 2. There are two possible explanations for these trends. First, if the habitat is no longer suitable for digging redds, adult steelhead may be spawning eggs further downstream where the substrate is less affected. Second, these numbers may not reflect the number of eggs laid or hatched but rather differences in survival between time of hatch and when steelhead parr were sampled. Godby *et al.* (2007) documented a post-invasion decrease in age-0 steelhead survival in this section of river from summer to fall. Movement of steelhead parr was believed to be limited before the fall because water temperatures rarely fell below 10°C and there was abundant habitat in the reach suitable for overwintering. Fraction survival was 0.163 in 1998 prior to zebra mussel introduction and dropped to 0.038 in 2000 and 0.006 in 2001 after zebra mussel introduction (Godby et al. 2007). The drop in survival from summer to fall could be due to resource limitation, steelhead growth if survival is size-dependent, changes in water temperature or flow, or increased predation. While some of these changes may be related to changes caused by the zebra mussel introduction, others may act independently to result in the observed trends.

Growth, Condition, and Survival

The decreased growth and condition of age-0 steelhead could result in decreased survival and abundance of the wild population. Assuming survival of age-0 steelhead is size-dependent (McFadden 1961; Clark and Rose 1997; Post et al. 1998; Van Winkle et al. 1998), the decreased growth resulting from zebra mussel introduction will result in increased predation risk. Also, the decreased condition could negatively affect temperature-dependent survival during winter (Seelbach 1987; Biro et al. 2004). Biro et al. (2004) found that smaller rainbow trout had lower lipid reserves which were depleted more quickly than those of larger trout, resulting in increased mortality.

Godby et al. (2007) concluded that discharge and summer temperatures were significant factors influencing age-0-steelhead growth and survival in the Muskegon River. Though these are important factors, in my study temperature was found to not be as important a factor as a change in diet composition.

Diet Changes

Diets of age-0 steelhead changed significantly from pre- to post-zebra mussel invasion, with a large decrease in consumption of Trichopterans and increase in comsumption of Dipterans. The decrease in Trichoptera consumption is consistent with the available information on the abundance of Trichoptera in the overall invertebrate community, particularly the large decline in Hydropsychidae. The only Trichopterans found in the diets of age-0-steelhead in the summer were *Hydroptila,* a member of the

Hydroptilidae. These caddisflies have cases made of sand and are much smaller than other caddisflies. Godby (2000) found that age-0 steelhead in the study area were opportunistic feeders. It is likely that that age-0-steelhead are selecting *Hydroptila* as prey due to their availability compared to Hydropsychids and other larger caddisflies. This is supported by the Luttenton *et al.* (2006) study which found that Hydropsychid densities had dropped sharply in 2001 after zebra mussel introduction.

The other difference between the pre- and post-zebra mussel diets was the increase in Dipterans. Luttenton *et al.* (2006) showed a decrease in abundance for all invertebrate groups following zebra mussel introduction. As steelhead have been shown to be opportunistic feeders, it is likely that Dipterans are more readily available than other prey and their abundance was not as affected by the presence of zebra mussels.

In the post-zebra mussel period, the proportions of amphipods and Dipterans in the diet were higher in the upstream sites which had higher densities of zebra mussels. Increases in amphipods around zebra mussel beds have been shown in other systems (Ricciardi et al. 1997; Mills et al. 2003; Barton 2004) suggesting that the increase in these prey items is likely related to the presence of zebra mussels. As other invertebrate groups are likely to be more severely affected in high density zebra mussel areas and the abundance of amphipods is likely higher here than in other areas of the study reach, the higher proportion in the diet would be reasonable. As the proportion of Dipterans in the diet follows a similar trend, it is possible that this is also tied to the presence of zebra mussels.

In this study, steelhead collected from stratum 4, where zebra mussel densities were low, had a greater diversity of prey in diets than steelhead collected from stratum 1 where zebra mussel densities were high. Assuming the diversity of invertebrates in the upstream portion of the study area was related to zebra mussel presence, it follows that the diversity of available prey would be higher downstream where zebra mussel densities are lower. However, as macroinvertebrate species richness was already higher downstream in stratum 4 than in stratum 1 prior to zebra mussel introduction (Godby 2000), it is not possible to attribute spatial differences in richness to the presence of zebra mussels.

Changes in Growth

Bioenergetics modeling demonstrated that age-0-steelhead in Muskegon River in consumed 138% more and grew 39% less during the post-zebra mussel period than during the pre-zebra mussel period. McNickle et al. (2006) examined changes in the benthic community of South Bay, Lake Huron following zebra mussel invasion, especially the decline in *Diporeia*, and predicted a 14-43% decline in energy content of prey in the diet of lake whitefish.

The bioenergetics model was used to determine the relative contributions of temperature and diet composition to the changes in growth. Temperatures were not very different in the pre- and post-study periods and hence were unlikely to cause the observed changes in steelhead growth. When the diet compositions were switched, there was a much larger difference in specific consumption necessary to obtain the observed growth. In the post-zebra mussel period, fish could eat 28% less and grow the same amount if the diet consisted of the composition of prey items found in the pre-zebra mussel period. During the pre-zebra mussel period, on the other hand, fish would have to eat 39% more of the post-zebra mussel diet to grow the same amount as they were predicted to do under the pre-zebra mussel diet. These data suggest that the change in diet composition had a larger effect on the observed change in growth than changes in temperature.

I assumed that the prey caloric density stayed constant during pre- and post-zebra mussel periods. It has been suggested by others that some invertebrate groups may be resource limited. Luttenton et al. (2006) showed that chlorophyll a levels declined below Croton Dam in the Muskegon River owing to filtration by zebra mussels. As zebra mussels filter out these particles, they are no longer available for consumption by other macroinvertebrates. The decrease in available food would likely negatively affect the growth and survival of macroinvertebrates and decrease the caloric value of some of them. This means that the estimated differences observed in specific consumption when diets were switched may be conservative as the differences would become larger had caloric densities of prey items decreased in the post-zebra mussel period.

Other factors including flow variability may have affected the growth of age-0-steelhead either separate from, or in conjunction with, zebra mussel effects. Higher flow rates could increase fish swimming speeds and metabolic costs and thus negatively affect fish growth. Increased flow velocities could also increase the delivery rate of prey to age-0 steelhead but due to decreased abundance of macroinvertebrates in the river, it seems unlikely that this would be enough to increase growth. In 1998, the average daily flow rate from the USGS gage was 1,641 ft^3/s. It increased to 2,157 ft^3/s in 2001 and decreased to 1,853 ft^3/s in 2002 and 1,477 ft^3/s in 2003. The higher water velocities in 2001 and 2002 compared to 1998 likely negatively affected the growth of age-0 steelhead in conjunction with the diet change. Because the flow rate was lower in 2003 than 1998, water velocity was probably less of a factor in that year.

Conclusions and Management Implications

Since the introduction of zebra mussels to the Muskegon River, there has been a decline in age-0 steelhead density and growth. Based on the results of this analysis, this appears to be more related to a change in diet following the introduction of zebra mussels rather than effects of annual temperature patterns. Within the Great Lakes region, efforts to eliminate zebra mussels have been unsuccessful. Zebra mussel densities were found to decrease in the river following a flood event in 2004, however, the densities of other macroinvertebrates decreased as well (Luttenton *et al.* 2006). Evidence suggests that despite some natural reproduction in the river, the main source of the zebra mussel population is the impoundment upstream of Croton Dam (Luttenton *et al.* 2006). As long as this source exists, zebra mussels will be able to re-colonize the upper river easily after flood events. These flood events followed by re-colonization will likely result in oscillations of the zebra mussel population over time, with consequent oscillating effects on steelhead growth and survival.

The results of this study provide some evidence of changes which have occurred since the zebra mussel invasion of the Muskegon River, but more work needs to be done to examine mechanistic causes. Targeted laboratory and field experiments are needed to relate effects of changes in the macroinvertebrate community on foraging behavior of age-0 steelhead. Also, continued sampling of age-0 steelhead densities would be important in determining whether trends in distribution and survival hold true over a longer time frame. In order to determine whether these shifts in distribution are due to changes in spawning substrate, additional studies would have to be done to determine where adult steelhead are spawning eggs and what is the relative hatching success of these eggs among zebra mussel colonies. These additional studies would strengthen the argument that the introduction of zebra mussels has affected the distribution, growth, and survival of age-0 steelhead in the Muskegon River.

Literature Cited

Barton, D.R. 2004. Differences in wave-zone benthic invertebrate communities in Lake Huron and Georgian Bay, 1974-2003. J. Great Lakes Res. 30: 508-518.

Biro, P.A., A.E. Morton, J.R. Post, and E.A. Parkinson. 2004. Over-winter lipid depletion and mortality of age-0 rainbow trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci.: 61: 1513-1519.

Clark, M.E. and K.A. Rose. 1997. Factors affecting competitive dominance of rainbow trout over brook trout in Southern Appalachian streams: implications of an individual-based model. Trans. Am. Fish. Soc. 126: 1-20.

Dobiesz, N.E., D.A. McLeish, R.L. Eshenroder, J.R. Bence, L.C. Mohr, M.P. Ebener, T.F. Nalepa, A.P. Woldt, J.E. Johnson, R.L. Argyle, and J.C. Makarewicz. 2005. Ecology of the Lake Huron fish community, 1970-1999. Can. J. Fish. Aquat. Sci. 62: 1432-1451.

Fahnenstiel, G.L., G.L. Lang, T.F. Nalepa, and T.H. Johengen. 1995. Effects of zebra mussel (*Dreissena polymorpha*) colonization on water quality parameters in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21: 435-448.

Fahnenstiel, G., S. Pothoven, H. Vanderploeg, D. Klarer, T. Nalepa, D. Scavia. 2010. Recent changes in primary production and phytoplankton in the offshore region of southeastern Lake Michigan. J. Great Lakes Res. 36: 20-29.

Godby, N. 2000. Growth, diet, and prey availability for juvenile steelhead in the Muskegon River and Bigelow Creek, Michigan. M.S. Thesis, School of Natural Resources and Environment, University of Michigan, Ann Arbor, MI.

Godby, N.A., E.S. Rutherford, and D.M. Mason. 2007. Diet, consumption, growth, mortality and production of juvenile steelhead in a Lake Michigan tributary. North American Journal of Fisheries Management 27: 578-592.

Gopalan, G., D.A. Culver, L.Wu, and B.K. Trauben. 1998. Effects of recent ecosystem changes on the recruitment of young-of-year fish in western Lake Erie. Can. J. Fish. Aquat. Sci. 55: 2572-2579.

Hanson, P. C., T. B. Johnson, et al. (1997). Wisconsin Fish Bioenergetics 3.0 manual. Madison, UW Sea Grant Institute.

Hecky, R.E., R.E.H. Smith, D.R. Barton, S.J. Guildford, W.D. Taylor, M.N. Charlton, and T. Howell. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. 61: 1285-1293.

Hondorp, D.W., S.A. Pothoven, and S.B. Brandt. 2005. Influence of *Diporeia* density on diet composition, relative abundance, and energy density of planktivorous fishes in southeast Lake Michigan. Trans. Am. Fish. Soc. 134: 588-601.

Ichthyological Associates. 1991. Habitat Mapping Report for the Croton Project, FERC Project No. 2468, Muskegon River, Michigan. New York, Ichthyological Associates, Inc.

Jennings, C.A. 1996. Effects of zebra mussel (*Dreissena polymorpha*) density on the survival and growth of juvenile fathead minnows (*Pimephales promelas*): implications for North American river fishes. Hydrobiologia 324: 157-161.

Johnson, R.L., S.C. Blumenshine, and S.M. Coghlan. 2006. A bioenergetic analysis of factors limiting brown trout growth in an Ozark tailwater river. Environ. Biol. Fish. 77:121-132.

Johnston, T.A. and R.A. Cunjak. 1999. Dry mass-length relationships for benthic insects: a review with new data from Catamaran Brook, New Brunswick, Canada. Freshwater Biology 41: 653-674.

Luttenton, M., N. Godby, E. Rutherford, and A. Bosch. 2006. Changes in benthic macroinvertebrates in an impounded Michigan river following the introduction of zebra mussels and a large flow event. Presentation at the North American Benthological Society 54th Annual Meeting, June 4-9, Anchorage, Alaska.

MacIsaac, H.J., C.J. Lonnee, J.H. Leach. 1995. Suppression of microzooplankton by zebra mussels: importance of mussel size. Freshwater Biol. 34: 379-387.

Madenjian, C.P., S.A. Pothoven, P.J. Schneeberger, M.P. Ebener, L.C. Mohr, T.F. Nalepa, and J.R. Bence. 2010. Dreissenid mussels are not a “dead end” in Great Lakes food webs. J. Great Lakes Res. 36: 73-77.

Mayer, C.M., A.J. VanDeValk, J.L. Forney, L.G. Rudstam, and E.L. Mills. 2000. Response of yellow perch (*Perca flavescens*) in Oneida Lake, New York, to the establishment of zebra mussels (*Dreissena polymorpha*). Can. J. Fish. Aquat. Sci. 57: 742-754.

McFadden, J.T. 1961. A population study of the brook trout, *Salvelinus fontinalis*. Wildlife Monographs 7: 3-73.

McNickle, G.G, M.D. Rennie, and W.G. Sprules. 2006. Changes in the benthic invertebrate communities of South Bay, Lake Huron following invasion by zebra mussels (*Dreissena polymorpha*), and the potential effects on lake whitefish (*Coregonus clupeaformis*) diet and growth. J. Great Lakes Res. 32: 180-193.

Mills, E.L., J.M. Casselman, R. Dermott, J.D. Fitzsimons, G. Gal, K.T. Holeck, J.A. Hoyle, O.E. Johannsson, B.F. Lantry, J.C. Makarewicz, E.S. Millard, I.F. Munawar, M. Munawar, R. O'Gorman, R.W. Owens, L.G. Rudstam, T. Schaner, and T.J. Stewart. 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970-2000). Can. J. Fish. Aquat. Sci. 60: 471-490.

Nalepa, T.F., D.L. Fanslow, and G.A. Lang. 2009a. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia spp.* to the invasive mussel *Dreissena rostriformis bugensis*. Freshwater Biology 54: 466-479.

Nalepa, T.F., S.A. Pothoven, and D.L. Fanslow. 2009b. Recent changes in benthic macroinvertebrate populations in Lake Huron and impact on the diet of lake whitefish (*Coregonus clupeaformis*). Aquatic Ecosystem Health and Management 12: 2-10.

O'Neal, R.P. 1997. Muskegon River Watershed Assessment. Lansing, Michigan Department of Natural Resources Fisheries Division.

Pothoven, S.A. and C.P. Madenjian. 2008. Changes in consumption by alewives and lake whitefish after dreissenid mussel invasions in Lakes Michigan and Huron. North American Journal of Fisheries Management 28: 308-320.

Post, J.R., E.A. Parkinson, and N.T. Johnston. 1998. Spatial and temporal variation in risk to piscivory of age-0 rainbow trout: patterns and population level consequences. Trans. Am. Fish. Soc. 127: 932-942.

Railsback, S.F. and K.A. Rose. 1999. Bioenergetics modeling of stream trout growth: temperature and food consumption effects. Trans. Am. Fish. Soc. 128: 241-256.

Rand, P.S., D.J. Stewart, P.W. Seelback, M.L. Jones, and L.R. Wedge. 1993. Modeling steelhead population energetics in Lakes Michigan and Ontario. Trans. Am. Fish. Soc. 122: 977-1001.

Ricciardi, A., F.G. Whoriskey, and J.B. Rasmussen. 1997. The role of zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. Can. J. Fish. Aquat. Sci. 54: 2596-2608.

Richardson, W.B. and L.A. Bartsch. 1997. Effects of zebra mussels on food webs: interactions with juvenile bluegills and water residence time. Hydrobiologia 354: 141-150.

Seber, G.A.F. and E.D. LeCren. 1967. Estimating population parameters from catches large relative to the population. J. Animal Ecology 36: 631-643.

Seelbach, P.W. 1987. Effect of winter severity on steelhead smolt yield in Michigan: an example of the importance of environmental factors in determining smolt yield. American Fisheries Society Symposium 1: 441-450.

Skubinna, J.P., T.G. Coon, and T.R. Batterson. 1995. Increased abundance and depth of submersed macrophytes in response to decreased turbidity in Saginaw Bay, Lake Huron. J. Great Lakes Res. 21: 476-488.

Smock, L.A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biology 10: 375-383.

Strayer, D.L., K.A. Hattala, and A.W. Kahnle. 2004. Effects of an invasive bivalve (*Dreissena polymorpha*) on fish in the Hudson River estuary. Can. J. Fish. Aquat. Sci. 61: 924-941.

Thayer, S.A., R.C. Haas, R.D. Hunter, and R.H. Kushler. 1997. Zebra mussel (*Dreissena polymorpha*) effects on sediment, other zoobenthos, and the diet and growth of adult yellow perch (*Perca flavescens*) in pond enclosures. Can. J. Fish. Aquat. Sci. 54: 1903-1915.

Trometer, E.S. and W.-D. N. Busch. 1999. Changes in age-0 fish growth and abundance following the introduction of zebra mussels *Dreissena polymorpha* in the western basin of Lake Erie. North American Journal of Fisheries Management 19: 604-609.

Vanderploeg, H.A., T.F. Nalepa, D.J. Jude, E.L. Mills, K.T. Holeck, J.R. Liebig, I.A. Grigorovich, and H. Ojaveer. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. 59: 1209-1228.

Van Winkle, W., H.I. Jager, S.F. Railsback, B.D. Holcomb, T.K. Studley, and J.E. Baldrige. 1998. Individual-based model of sympatric populations of brown and rainbow trout for instream flow assessment: model description and calibration. Ecological Modelling 110: 175-207.

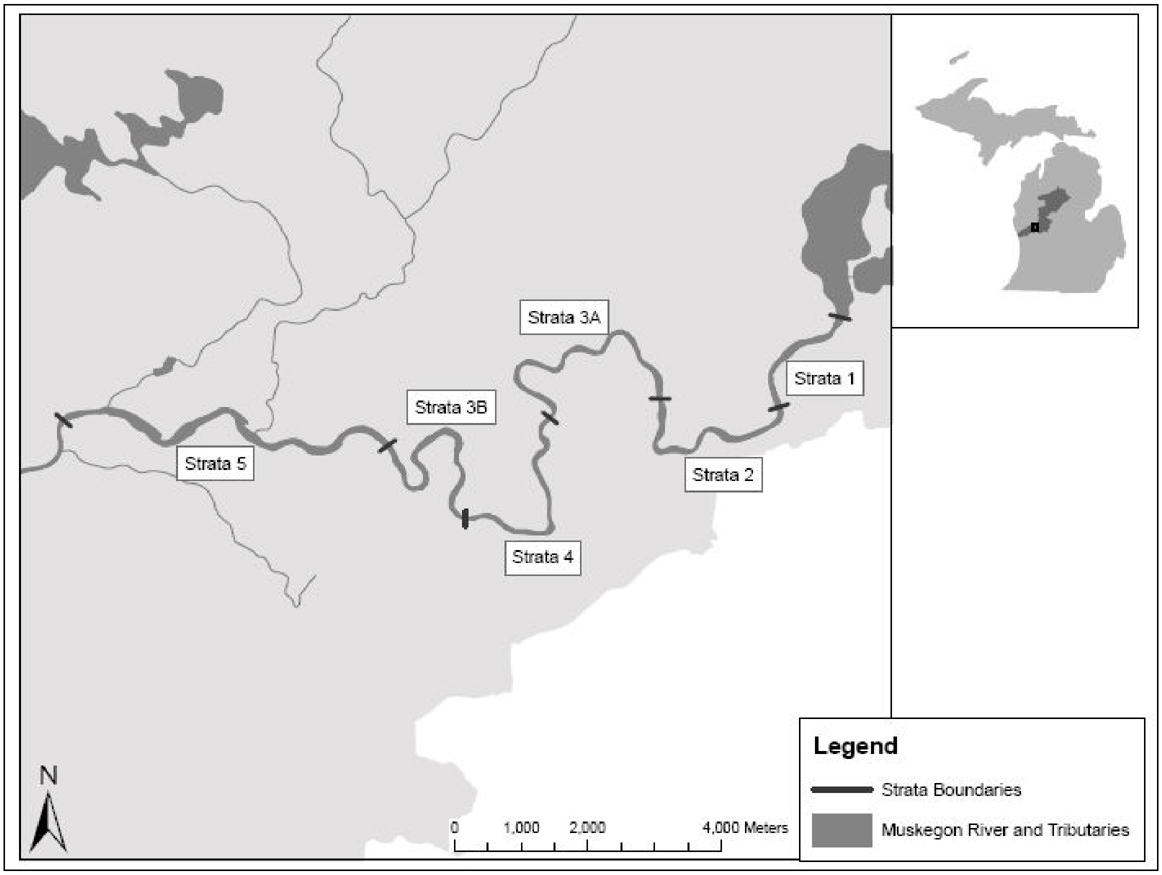

Figure 1. Map showing the study reach and locations of strata in the Muskegon River, Michigan. Croton Dam marks the upstream boundary of stratum 1.

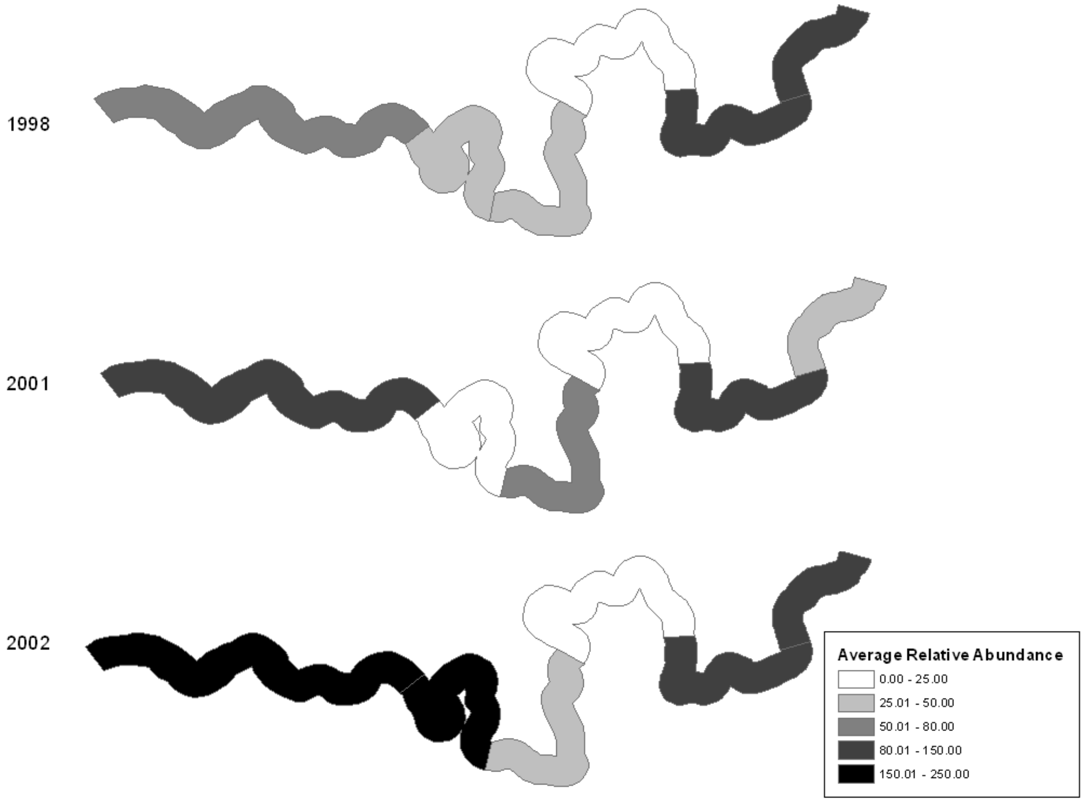

Figure 2. Density estimates of age-0 steelhead averaged by strata in the summer before (1998) and after (2001, 2002) zebra mussel introduction.

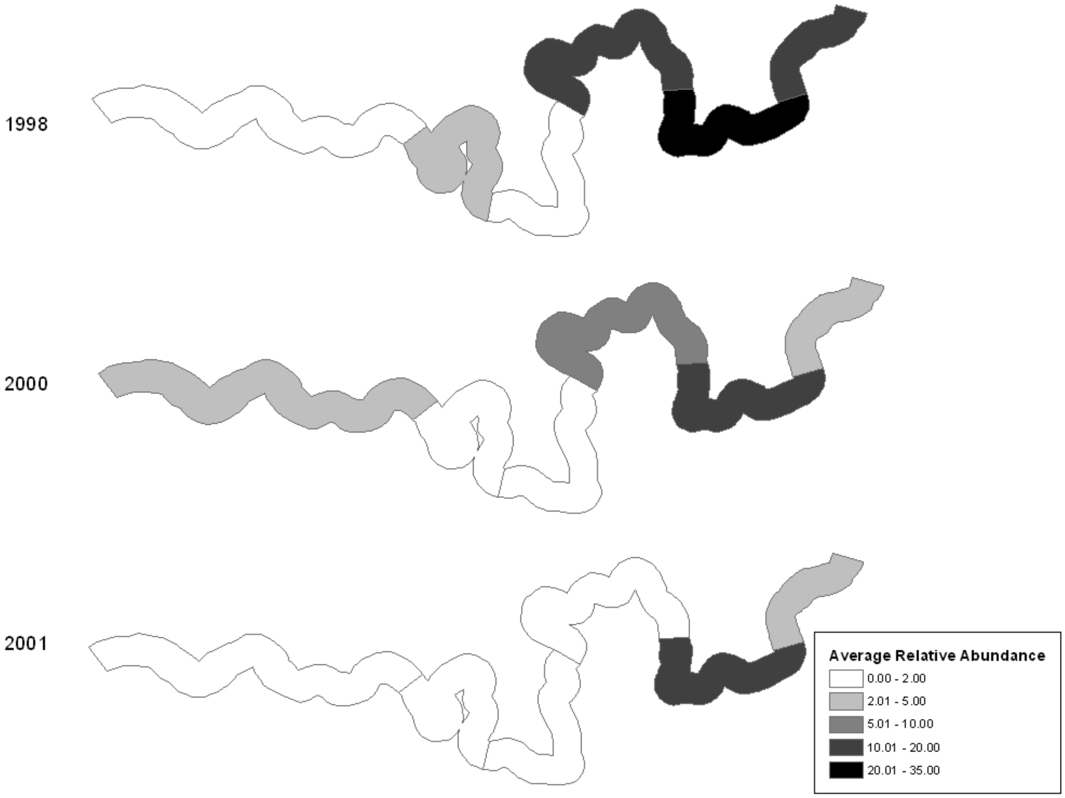

Figure 3. Density estimates of age-0 steelhead averaged by strata in the fall before (1998) and after (2000, 2001) zebra mussel introduction.

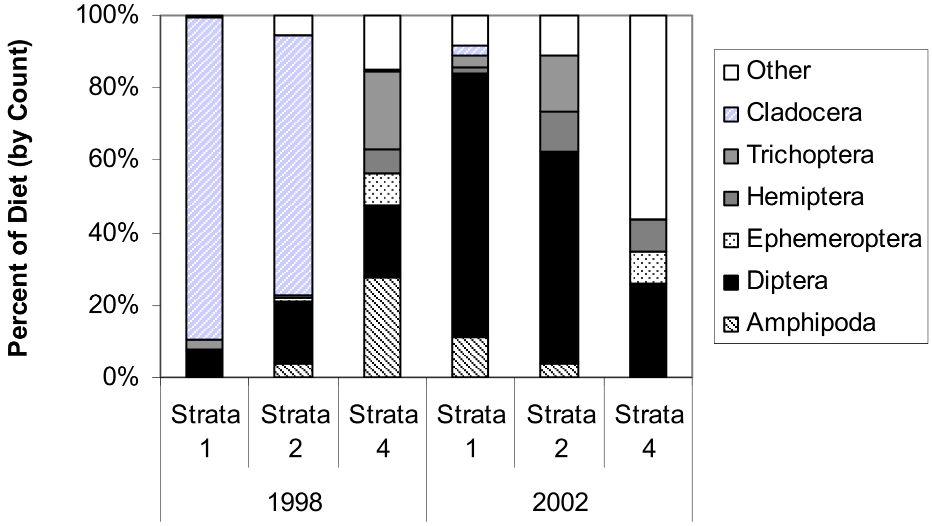

Figure 4. Percent abundance of macroinvertebrate prey found in the diets of age-0 steelhead in summer before (1998) and after (2002) zebra mussel introduction. "Other" includes members of Coleoptera, Isopoda, Plecoptera and items of terrestrial origin.

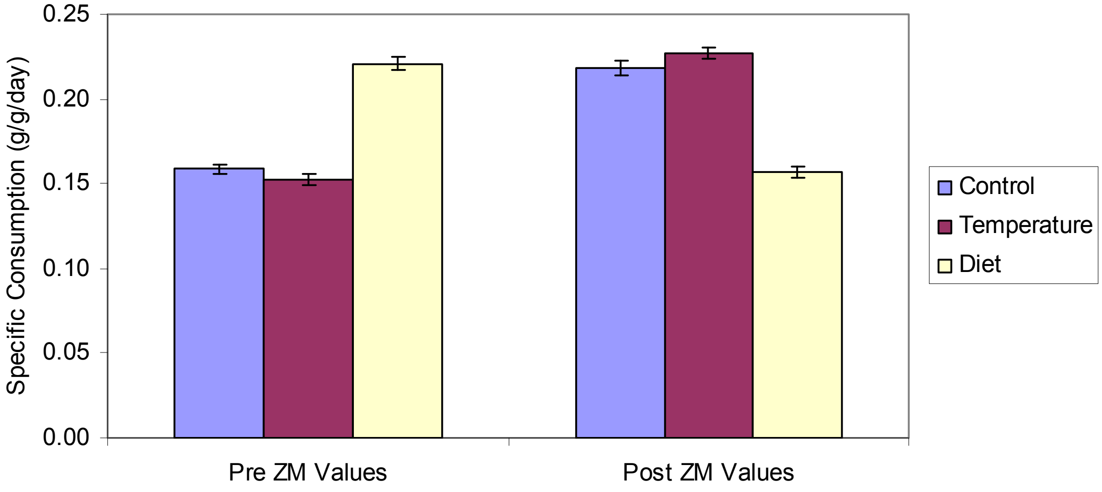

Figure 5. Average daily consumption (g/g/day) (±2 SE) of age-0 steelhead before and after zebra mussel introduction in the Muskegon River, Michigan under three bioenergetics model scenarios.

Table 1. Strata location and substrate description of the study area in Muskegon River, Michigan from Croton Dam to Newaygo (Ichthyological Associates 1991).

Stratum	Location (m downstream of Croton Dam)	Substrate / Habitat Description of River Segments
1	305 to 1,829	Gravel riffle spawning habitat
2	1,829 to 4,267	Spawning habitat with run holding habitat
3	4,267 to 8,534 and 11,582 to 15,240	Run / pool with some high banks
4	8,534 to 11,582	Deep and shallow runs with spawning gravel
5	18,288 to 21,031	Higher gradient reach with instream cover provided by man-made log/rock cribs

Table 2. Coefficients for weight- and temperature-specific parameters of consumption, egestion, excretion, and respiration for steelhead used in the Wisconsin bioenergetics model. Parameters were taken from Rand et al. (1993) and Railsback and Rose (1999).

Parameter	**Value**
Consumption Equations	
Ca:	0.628
Cb:	-0.3
Ck1:	0.33
Ck4:	0.2
Cq:	5
Ctl:	24
Ctm:	20
Cto:	20
Eq:	3
Egestion, excretion Equations	
Eq:	3
Fa:	0.212
Fb:	-0.222
Fg:	0.631
Ua:	0.031
Ub:	0.58
Ug:	-0.299
Respiration Equation	
Act:	9.7
Bact:	0.041
Eq:	1
Ra:	0.003
Rb:	-0.217
Rk1:	1
Rk4:	0.13
Rq:	0.068
Rt1:	25
Rtm:	0
Rto:	0.023
Sda:	0.172

Table 3. Values for start and end weights (g) and average daily temperatures (°C) used to simulate changes in age-0 steelhead consumption and growth from summer to fall in the Muskegon River, Michigan using the Wisconsin bioenergetics model (version 3, Hansen et al. 1997). Estimated start weight in 2003 was calculated using observed mean weight during the July survey and the instantaneous growth rate from July to October, 2003.

	Start Weight (g)	End Weight (g)	Average Temperature (°C)	Diet Composition Source
Pre-Zebra Mussel Period (August-October 1998)	2.36	8.05	20.7	Godby (2000)
Post-Zebra Mussel Period (August-October 2003)	1.46	4.95	19.7	This study

Table 4. Descriptions of the six bioenergetics model simulations to distinguish relative effects of water temperature and prey composition on age-0 steelhead consumption and growth.

	Variable	Control Run	Temperature Run	Diet Composition Run
Pre-Zebra Mussel Period	Growth	Pre-Values	Pre-Values	Pre-Values
	Temperature	Pre-Values	Post-Values	Pre-Values
	Diet	Pre-Values	Pre-Values	Post-Values
Post-Zebra Mussel Period	Growth	Post-Values	Post-Values	Post-Values
	Temperature	Post-Values	Pre-Values	Post-Values
	Diet	Post-Values	Post-Values	Pre-Values

Table 5. Average weights (0.01 g, ±2 s.e.) and instantaneous growth rates (G, ln weight/day) of age-0 steelhead collected from the Muskegon River, Michigan by year and season. Average weights of steelhead in July of 2000-2003 were adjusted to August weights using instantaneous growth rates (assumed G=0.017 for 2000 and 2002).

Year	Summer	Fall	G
1998	2.36 ± 0.05	8.05 ± 0.36	0.017
2000	2.21 ± 0.2	n.d.	n.d.
2001	1.75 ± 0.1	7.09 ± 1.16	0.017
2002	1.35 ± 0.1	n.d.	n.d.
2003	1.46 ± 0.1	4.95 ± 0.7	0.011

Table 6. Average lengths (0.1 cm, ±2 s.e.) of age-0 steelhead collected from the Muskegon River, Michigan by year and season. In summer 1998, fish were sampled in August, and in July in summers of 2000-2003. In fall, fish were sampled in October in all years. ‘n.d.’ indicates no samples were collected.

Year	Summer	Fall
1998	5.9 ± 0.04	9.0 ± 0.02
2000	4.7 ± 0.07	10.7 ± 0.4
2001	5.0 ± 0.01	8.8 ± 0.4
2002	4.2 ± 0.1	n.d.
2003	4.8 ± 1.2	7.8 ± 0.3

Table 7. Average condition ($g/cm^3 * 10^{-3}$, ±2 s.e.) of age-0 steelhead collected from the Muskegon River, Michigan by year and season. In summer 1998, fish were sampled in August, and in July in summers of 2000-2003. In fall, fish were sampled in October in all years. ‘n.d.’ indicates no samples were collected.

Year	Summer	Fall
1998	10.5 ± 0.09	10.3 ± 0.1
2000	10.9 ± 0.3	n.d.
2001	9.7 ± 0.1	9.7 ± 0.8
2002	9.7 ± 0.3	n.d.
2003	10.9 ± 2.3	9.9 ± 0.7

Table 8. The percent composition of macroinvertebrate prey taxa (by wet weight) in diets of age-0 steelhead during summer, before (1998) and after (2003) zebra mussel introduction in the Muskegon River, Michigan. The "Other Trichoptera" category includes all Trichoptera other than Hydropsychidae and the "Other" category includes terrestrial items, Cladocerans, Odonata, and unidentified items. The pre-zebra mussel data were from Godby *et al.* (2007).

Taxa	Pre-ZM (N=49)	Post-ZM (N=55)
Hydropsychidae	17.3	0
Other Trichoptera	9.3	0.5
Ephemeroptera	4.4	7.2
Diptera	2.9	50.1
Coleoptera	3.8	1.1
Plecoptera	0.7	3.6
Hemiptera	5.5	5.5
Amphipoda	41.8	30.4
Other	14.3	1.58