# The Influence of physical habitat factors on a near-shore fish community in the lower Muskegon River, Michigan

By

Solomon R. David

A thesis submitted in the partial fulfillment of the requirements
for the degree of Master of Science
in the School of Natural Resources and Environment
of the University of Michigan
January 2008

Thesis Committee:
Dr. Edward S. Rutherford, Chair
Dr. James S. Diana

## Table of Contents

## Acknowledgements

Funding for this study was provided by the Great Lakes Fishery Trust, the Michigan DNR, the Institute for Fisheries Research, and the School of Natural Resources and Environment at the University of Michigan

I would like to thank my advisor, Dr. Edward Rutherford for his support, guidance and motivation during my graduate studies, as well as giving me the opportunity to develop my own study in connection with other Muskegon River research projects. Ed also joined me in the field on several occasions, and his help and enthusiasm were greatly appreciated. I also thank Dr. James Diana, not only for serving on my committee, but for his continual insight, motivation and challenges during my master's work.

I would also like to thank all the fisheries scientists, SNRE faculty, and graduate students who helped me during my master's work. Thanks to Mike Wiley, Kevin Wehrly, Catherine Riseng, Jim Breck, Lizhu Wang, Paul Seelbach, and Dave Allan for their willingness to discuss and provide insight for my research. Thanks to Beth Sparks-Jackson, Shaw Lacy, and Paul Steen for their help with my statistical and spatial analysis questions. Special thanks also goes to Dana Infante for always finding time to discuss multivariate analyses with me.

This study required intensive fieldwork and would not have been possible without the many people who helped with electrofishing and habitat sampling on the Muskegon River. Many thanks to Dave Swank, Ed McCoy, Rob McTear, James Roberts, Lori Ivan, Tomas Hook, Sara Creque, Liza Liversedge and Brad Horne for all their help in the field. Special thanks goes to Jeremy Price, who helped with fieldwork throughout the entire study and helped keep me sane during our many weeks on the Muskegon during summers. Also thanks to Dennis Donahue and others of the NOAA Field Station in Muskegon for allowing us to stay at their facility during field seasons. Thanks also to James “Gappy” Gapczinski, for always making sure all of our field equipment was in top working order, no matter what we did to it in the field.

Many people supported me during my research; I would like to thank my roommates and fellow fish ecology students of “The Tank”, James Roberts and Damon Krueger, for their continual support and insight. I’d also like to thank Ron Oldfield, Damon Duquaine, Matt Ladewig, Rakhi Kasat, Andrea Walther, and Brenda Lin for keeping me motivated and helping me survive graduate school thus far.

I’d like to thank Carl Hoagstrom, Eric Nelson, and Nelson Moore for encouraging me to pursue my interests in field biology and ecology, and special thanks to Terry Keiser for inspiring my fascination with fish ecology and ichthyology during that two-week field course at Ohio Northern University so many years ago. Thanks also to all my Fall 2003 Biology of Fishes Lab students for reminding me why I’m in graduate school and love teaching.

Thanks also to Beau and Eva Harvey, without their support my graduate work would not have been possible. Finally, I would especially like to thank my family, Ignatius, Esther, Rachel and Sarah, for their continual love, support and motivation throughout my graduate career, without them I would not have made it this far.

# List of Tables

**Page**

## List of Figures

## Abstract

The Muskegon River is the second largest tributary to Lake Michigan, and supports a diversity of habitats and fish communities of ecological and economic importance. I hypothesized that spatial heterogeneity in physical habitat characteristics of the river was the major factor affecting fish community composition and species densities in the lower Muskegon River. I further hypothesized that fish community composition and species densities varied temporally due to specific life history patterns as well as seasonal changes in physical habitat. To address these hypotheses, I obtained seasonal estimates of fish abundance at shoreline habitats within mainstem reaches of 5 habitat strata in a 22-km section in the Muskegon River, 64 km upstream from Lake Michigan. I used DC electrofishing and pass depletion methods to estimate fish abundance and species densities at 30 sites (300 $m^2$ in area) within the study area, in summer, fall, and spring from 2001 to 2002. The near-shore fish community of the lower Muskegon River was comprised of 43 species representing 15 families. Functional group classification of the fish community indicated dominant groups were omnivore and benthic invertivore trophic guilds, and species preferring moderate current velocity and rubble substrate. Most species belonged to the warm-water guild, and the majority of fishes were species intolerant of siltation. The fish community varied among strata only in summer 2001 and spring 2002, although several individual species varied among strata in different seasons. Canonical Correspondence Analysis indicated temperature and current velocity explained the most variability in species densities among strata. Fish community composition and species densities varied seasonally due to specific life history patterns, including spawning (spring) and outmigration of adfluvial and potamodromous fishes (spring and summer), as well as seasonal changes in temperature and current velocity.

## Introduction

Relationships between lotic habitats and stream fish communities are both complex and difficult to effectively assess. The appropriate spatial and temporal scales at which these relationships occur also can be difficult to determine, and are contingent on the question or level of detail desired (Stewart et al. 2001). Large-scale analyses are often useful for determining linkages between ecoregions and geographic distribution of fishes (Lyons 1989), the overall status of a fishery in watersheds or across basins (Jude 1992), or regional variation and influence of thermal regime on fish abundance (Wehrly et al. 2003). Conversely, small-scale analyses can determine niche partitioning between similar species (George and Hadley 1979) or food-web interactions among species in patchy environments (Power et al. 1985).

Previous studies have shown that reach-scale habitat variables were more important than regional land use (large-scale) in predicting variability in fish assemblages. In a study of the Raisin River watershed, MI, Lammert and Allan (1999) showed that flow stability and reach-scale land use were better predictors of biotic condition for fish than regional land use. Wang et al. (2003) showed that in the Northern Lakes and Forest Ecoregion, reach-scale variables such as water temperature, gradient, and macrophyte cover better explained patterns in fish assemblages than did riparian land use and watershed scale habitat variables. In Iowa streams, Heitke et al. (2006) found that reach-scale bank stability, hard substrate, and rocky cover better explained variation in fish assemblages compared to land use at the catchment scale. Other studies, however, have demonstrated that large-scale factors were more effective descriptors of fish assemblages. For example, Roth et al. (1996) found that regional land use predicted fish biotic integrity in the Raisin River, MI watershed, while Poff and Allan (1995) found that regional-scale hydrological variability predicted functional organization of stream fish communities.

Fish community composition in lotic habitats also exhibits temporal variability (Schlosser 1991, Wiley et. al 1997, Fausch et al. 2002). Peterson and VanderKooy (1995) found that different groups of fishes in Mississippi spawned in early spring or in summer. Tripe and Guy (1999) showed that species diversity varied temporally in a Kansas stream, with highest values in summer and lowest in fall and spring. Although most studies of fish communities in rivers are typically conducted during low-flow periods, generally summer in the Midwestern region of the United States, changes in species composition can be quite drastic among seasons, and species abundance can range from being very high to complete absence, depending on the species and spatial scale used to study them. Variation in species composition may be due to different life history patterns, such as those exhibited by adfluvial salmonids (Thorpe et al. 1998) which may be present as parr in one season and outmigrate the next, or catadromous eels (Smogor et al. 1995) which mature in freshwater and outmigrate to marine systems to spawn. Species composition also may change because of seasonal migrations associated with growth, food availability and foraging, thermal regime, or flooding (Peterson and VanderKooy 1995, Gido et al. 1997, Snedden et al. 1999).

An intermediate spatial scale has been suggested as appropriate to effectively link landscape-level habitat characteristics with local habitat factors, and to study relationships between stream fishes and their lotic habitats (Fausch et al. 2002). In contrast to large or small spatial scales, Fausch et al. (2002) note habitats that stream fishes generally progress through important stages of their life histories, such as spawning, hatch, larval drift, settlement, foraging and avoidance of predators at intermediate spatial scales of 1-100 km.

A valley segment ecological classification (VSEC) system, fitting general intermediate spatial scale characteristics was developed for Michigan rivers. VSEC units are segments of rivers characterized by relatively homogenous hydrologic, limnologic, riparian, and channel morphology characteristics (Seelbach et al. 1997). Valley segments are relatively large in Michigan rivers, and range from 3 to 60 km (mean length = approximately 6 km), a size that corresponds well with the 1-100 km intermediate spatial scale proposed by Fausch et al. (2002). Fish assemblage data from the Michigan Rivers Inventory (Seelbach and Wiley 1997) and association data by cluster analysis (Zorn et al. 2002) were also included in defining VSEC units. Therefore the VSEC unit should provide an appropriate spatial scale to investigate relationships between fishes and physical habitat variables.

Several physical habitat factors, which may vary at multiple spatial scales, can influence fish assemblages in lotic environments. In the Great Lakes region, physical habitat variables such as hydrological variability and temperature have shown to be important factors influencing fish species assemblages. Wehrly et al. (2003) showed that changes in community composition, species richness, and abundance of stream fishes all occurred across regional gradients of mean temperature and temperature fluctuation in lower Michigan. Zorn et al. (2002) described stream fish assemblages from 226 sites in lower Michigan using low-flow yield (a measure of flow stability) and catchment area, both large-scale hydrology-based variables. Landscape-based measures of mean water temperature were shown to influence salmonids in a study of Michigan rivers by Creque et al. (2005), while Lyons (1996) used reach-scale stream temperature to describe patterns in fish assemblages among Wisconsin streams.

In lotic habitats, particularly large rivers, species within a fish community often further partition themselves between main channel (midstream) and near-shore edge (bank) habitats. Main channel habitats are deeper and have faster current velocities, whereas near-shore edge habitats are generally shallower and have lower current velocities. These near-shore habitats frequently serve as nursery areas for juvenile fishes and are often the preferred habitats of smaller species (Bain et al. 1988, Schlosser 1991, Lamouroux et al. 1999). Juveniles of larger species often have differing habitat preferences from adults (Fladung et al. 2003), and may seek these inshore habitats for protection from predation by larger fishes (Schlosser 1987) which typically reside in deeper main channel habitats (Bain et al. 1988). Therefore the spatial partitioning of species and individuals between midstream and bank habitats could delineate two communities within large rivers, more by local habitat partitioning than by intermediate-scale variables.

The lower Muskegon River represents a dynamic lotic system of diverse habitats and fish species of both ecological and economic importance. The system supports warm, cool, and coldwater fishes, including important game species such as steelhead, walleye, and Chinook salmon (O'Neal 1997) (all species are listed in Table 1). Factors influencing variation in density and composition of the fish community at intermediate temporal and spatial scales are relatively unknown for the lower Muskegon River or for other Great Lakes tributaries. The scale at which these factors are measured in other studies in the same region also varies. For example, to investigate factors influencing fish communities, Wiley et al. (1997) used a multi-scale approach (site- and landscape-scale variables) in Michigan trout streams, Wehrly et al. (2003) used site-scale temperature patterns in Michigan Lower Peninsula tributaries, and Riseng et al. (2006) used several landscape-scale variables (land use, drainage area, presence of wetlands) for tributaries (including the Muskegon) throughout state of Michigan.

I hypothesized that spatial heterogeneity in physical habitat characteristics was the major factor affecting fish community composition and species densities at an intermediate spatial scale in the lower Muskegon River. I further hypothesized that fish community composition and species densities varied temporally, due to specific life history patterns as well as seasonal changes in physical habitat. To test these hypotheses, I determined fish species composition, density and relative abundance among 5 habitat strata (mean length = 3.53 km) within a valley segment in the lower Muskegon River over four seasons from 2001 to 2002. I investigated relationships among component species, and related seasonal and spatial variation within the fish community to physical habitat variables (temperature, current velocity, substrate, vegetation, and woody debris). Because the 5 strata were characterized by physical habitat, I hypothesized that fish community composition and species relative abundance varied among strata within each season. To test this hypothesis, I investigated relationships between variation in species relative abundance and the 5 habitat strata in each season. I did not investigate biotic relationships. Although biotic factors including predation, competition, or prey availability may influence lotic fish communities in small streams (George and Hadley 1979, Schlosser 1991), many of these factors have been shown to be connected with abiotic factors such as substrate, flow, or temperature (George and Hadley 1979, Schlosser and Toth 1984, Godby et al. 2007), and by comparison, may not be important in large streams (Power et al. 1985).

## Methods

### *Study Area*

The Muskegon River is the second largest tributary to Lake Michigan, draining a basin of 682,200 hectares in west-central Michigan (O'Neal 1997). The study area was a 22-km section of high gradient located within a single valley segment (VSEC unit length approximately 40 km) from Croton Dam to Newaygo, approximately 85 km upstream of the confluence of the Muskegon River and Lake Michigan (O'Neal 1997, Seelbach et al. 1997). Croton Dam is one of 3 major dams on the Muskegon River and serves as the lower-most barrier to migrating fishes.

The study area was divided into five strata (Table 2) based on previous multivariate analysis of riparian and in-stream substrate composition (Ichthyological Associates 1991, Godby et al. 2007). Each stratum was further divided into 100 m sites (or reaches), with a total of 30 sites used for this study. These sites were selected using a stratified random sampling design previously used for Chinook salmon and steelhead surveys (Godby et al. 2007). Each site consisted of 300 $m^2$ of shoreline habitat, 100 m in length and 3 m in width (distance from the stream bank). The number of sites in each stratum were as follows: 11 in stratum 1, 9 in stratum 2, 4 in stratum 3, 2 in stratum 4, and 4 in stratum 5 (Figure 1).

A valley segment (VSEC unit) in the lower Muskegon River immediately downstream of a major impoundment provided an opportunity to examine spatial and temporal variation of the near-shore fish community at an intermediate scale. Given the relative homogenous nature of VSEC unit classification, influence of site-scale physical habitat variables (temperature, current velocity, substrate) should be more evident, whereas larger-scale variables (land-use, riparian cover, surficial geology, groundwater inputs) were relatively consistent. Furthermore, the size and location of the study area within the VSEC unit should present little, if any, longitudinal zonation in the fish community.

### *Fish Community Composition & Density*

An ecological community can be generally defined as a collection of species populations living together in space and time (Begon et al. 2006). Therefore the ecological community is characterized by co-occurrence of species, and not necessarily by interactions among species. In a review of concepts in community ecology, Fauth et al. (1996) supported this view and further explained that communities can be identified as organisms located within areas defined by differences in physical habitat (i.e. temperature) or by arbitrary spatial units (all fishes within a 100 $m^2$ transect) determined by the investigator.

Fish community composition and species densities in the study area were estimated from samples taken in summer (July 20-26), fall (October 13-November 1) 2001, spring (May 21-30), and summer (July 13-16) 2002. Each 300 $m^2$ site was sampled using a 250 volt DC electrofishing barge unit. Density estimates for each site were calculated using the Seber-LeCren two-pass depletion method (Seber and LeCren 1967, Everhart and Youngs 1981). For each species, mean number of individuals per 300 $m^2$ as well as relative density (percent abundance per 300 $m^2$) were estimated.

Average lengths for each species were determined from measurements at two sites per stratum for each season whenever possible. Lengths of 30 individuals were taken for salmonid species at all sites.

### *Physical Habitat Factors*

Physical habitat data were collected using several methods for each site. All habitat measurements were taken at the upstream, middle, and downstream points of each site whenever possible, and then averaged for the entire site. Current velocity (m $sec^{-1}$) was collected after electrofishing each site when possible, and extrapolated for 8 other sites (fall 2001) using streamflow data from USGS gauges and data from the same sites and season in the following year. Water temperature (°C) data were collected using a data sonde device or an analog thermometer at each site during each season. Percentage composition of vegetative cover was sampled once during the study period, and determined visually using three $m^2$ quadrats randomly located at downstream, mid, and upstream ends of each site. Percentage composition of woody debris and percentage substrate cover composition were determined (boulder, cobble, gravel, sand) during previous studies (Godby et al. 2007) using the same sampling method. The percent substrate cover composed of boulder, cobble and gravel values were combined to create a percent hard substrate value, with soft substrate, composed of sand and silt, making up the remaining percentage. Values for substrate composition, woody debris, and vegetation were assumed to be constant at an individual site among all seasons.

### *Data Analysis*

To describe overall characteristics of the fish assemblage, all species were placed into categories within 5 functional guilds developed by Poff and Allan (1995) and further supplemented by other species life history accounts (Hocutt 1973, Trautman 1981, Becker 1983, Trial et al. 1983, Page and Burr 1991, Lyons 1992, Miller et al. 2005). Functional guilds used were trophic, substrate preference, current velocity preference, tolerance to siltation, and thermal preference (Table 3). Relative densities for all species collected were used in combination with functional guild membership to describe the fish community at both spatial and temporal scales. Relative density values for each species were averaged for each stratum and season, as well as combined into an overall estimate for the study.

From the entire fish assemblage, 14 “focus species” were chosen to represent the fish community in further analyses. Twelve of these species consistently occurred throughout all seasons of the study period. Two additional species, Chinook salmon and longnose gar, were also included in the analysis as representative species of adfluvial and potamodromous life histories, respectively.

Fish relative density and physical habitat variables were tested for normality and homogeneity of variance using SAS (2001a) software. MANOVA tests of relative density data for the 14 focus species were performed to determine significance of fish community variation within or among strata and seasons. Two test statistics, Wilks’ Lambda and Pillai’s Trace, were used to determine significance of results. All five physical habitat variables were also tested for variation among strata, and temperature and current velocity were tested for variation among seasons. Level of significance was set at $\alpha = 0.05$ for all tests.

Hierarchical Cluster Analysis by Ward’s minimum variance method (Ward 1963) was used to explore natural groupings of fishes within the 14-species subset of the fish community. Relative density data for all 14 focus species (for each season) were used in cluster analysis. The number of significant clusters was determined visually and statistically based on the first inflection point of the resulting profile curve, and further determined based on functional guild membership. The inflection point of the profile curve was the point at which the slope drastically changed, generally indicating a noticeable difference in variance explained by the number of clusters leading up to and including the inflection point. Ward's method determines cluster distance using ANOVA sum of squares, therefore the amount of variance explained by each cluster was calculated by dividing the between-clusters sum of squares by the total sum of squares (Romesburg 1990, SAS 2001b, Zorn et al. 2002). The resulting $R^2$ value was used to determine number of clusters as well as indicate the fit of the clusters to the relative abundance data (Zorn et al. 2002). Cluster analysis results were also compared with field observations and known life history patterns (Trautman 1981, Poff and Allan 1995) to confirm relevance of cluster groupings.

To further investigate co-occurrence of species within the fish community, pair-wise correlation analysis was performed on the 14 focus species. Correlation tests were performed on species relative density for individual seasons. Pearson's correlation coefficient ($R^2$) and significance were reported for each species pair, as well as the mean correlation value for each season. Relevance of significant species pairs and further description were based on $R^2$ values for each season, with correlations of 0.50 or greater considered meaningful.

In order to explore variation in the fish community in better detail, non-parametric tests (Kruskal-Wallis) were performed to test for spatial (stratum-level) and temporal (seasonal-level) variation in relative density of the 14 focus species. Significant variation in relative density was reported for focal species at both spatial (stratum) and temporal scales (summer and fall 2001, spring and summer 2002). Non-parametric tests (Kruskal-Wallis) also were performed to detect stratum and seasonal variation in temperature and current velocity, and variation among strata in percent hard substrate, % vegetation, and % woody debris.

Canonical Correspondence Analysis (CCA) was used to investigate associations among fish species and physical habitat variables for each season. Species density values were coded to their specific sites; and all sites were included in the CCA ($p < 0.05$) to demonstrate the associations, if any, between fish species and five physical habitat variables. Eigenvalues and canonical correlation values were reported and used to calculate the relative variance in fish density explained by the CCA. Densities for each site, along with physical habitat data, were plotted on the resulting first two canonical axes for each season. Canonical axis 1 was the vertical axis, Canonical axis 2 the horizontal axis.

On CCA plots, fish species were shown as centroid points, and physical habitat variables shown as rays. The 95% confidence region for an individual species was represented by a circle around each species' centroid point (Mardia et al. 1979). The strength of association between a fish species with a physical habitat variable was interpreted by perpendicular proximity of the species point to the variable ray. Physical habitat variables with greater ray lengths were considered to explain more variation than those variables with lesser lengths (Ter Braak 1986, 1995). Also, variable rays could be extended in either direction, positive or negative, from the origin (noted as "grand" in ordination plots, representing the grand mean). Relationships between species and physical habitat were based primarily on associations with one or two variable rays. Therefore, the CCA provided an overall picture of the fish community relative to physical habitat variables for each season of the study period.

## Results

### *Fish Community Composition*

The fish community in the Lower Muskegon River study area included 43 species representing 15 families (Table 1). Cyprinids, percids, centrarchids, and salmonids were predominant families comprising the fish community. Most fishes collected were primarily small adult individuals (darters and cyprinids), or young-of-the-year fishes (longnose gar, Chinook salmon) or juvenile (centrarchids and redhorse) life stages of larger species, as indicated by mean lengths (Table 4). The most abundant species throughout the study was the hornyhead chub, followed by common shiner, steelhead, rainbow darter (Table 5). Species richness was highest in stratum 1 (37 species) and lowest in stratum 4 (22, Table 5), and was highest in summer (35 species in 2001, 39 in 2002, Table 6).

Functional group classification summarized fish community composition using 5 categories (Table 7). Across all seasons, the fish community was dominated by omnivores and benthic invertivores, primarily cyprinids, catostomids and darter species (Tables 7 and 9). Conversely, herbivore-detrivores and parasitic trophic guilds were least represented, primarily due to single, rarely-collected species such as brook silverside and sea lamprey, respectively. Piscivores, such as centrarchids and longnose gar also comprised a smaller portion of the fish community. In terms of current velocity preference, species preferring moderate velocities were most abundant, such as hornyhead chub, smallmouth bass, and steelhead. Although the current velocity category of slow-none was most speciose (22, Tables 7, 9), members of this group were the less abundant than members of other current velocity categories. Fishes preferring rubble (rocky, gravel) substrate were most abundant, followed by substrate generalists, and lastly those preferring sand or silt (Table 8). The tolerance functional group was dominated by species in the low tolerance category.  Thermal guilds in the fish community included warm, cool, and cold-water species, with various warm-water cyprinids, percids, and centrarchids accounting for highest relative abundance values (Table 7).

At the stratum level, omnivores and benthic invertivores continued to be the dominant trophic guilds, although omnivores were at their highest level (stratum 2), where benthic invertivores were at their lowest, and vice versa (with the pattern reversing in stratum 1, Table 8).  In stratum 2, general invertivores, primarily steelhead, replaced benthic invertivores as the second most abundant group.  Piscivores were at highest levels in strata 5 and 3, respectively.  Species preferring moderate current velocity were most abundant in all strata, and highest in stratum 2.  Species preferring fast current, such as rainbow darter, were most abundant in stratum 5 (Tables 5, 8), which was also the highest-gradient stratum in the study area (Table 2).  In the substrate preference group, fishes comprising the rubble (rocky, gravel) category were most abundant throughout all strata, and highest in stratum 5.    Fishes in the low-tolerance group were most abundant in all 5 strata, with highest values in strata 2 and 5 (Table 8).  More highly tolerant fishes were abundant in stratum 3, which was characterized by run-pool habitat (Table 2, Ichthyological Associates 1991).  Warm-water fishes dominated each stratum, with highest abundance in stratum 3, run-pool habitat, as opposed to lowest abundance in stratum 2, gravel-riffle habitat.  Conversely, cold-water fishes were most abundant in stratum 2 (Table 8).

At the seasonal (temporal) level, omnivores and benthic invertivores were again the dominant trophic guilds (Table 9).  Similar to spatial patterns, when omnivores were at highest abundance (spring 2002), benthic invertivores were at their lowest, and replaced by general invertivores.  In summer 2001, when benthic invertivores were highest in abundance, omnivores were at their lowest.  Piscivores were highest in summer 2001 and lowest in spring 2002.

Species preferring moderate current velocity were most abundant in summer seasons, followed by those preferring fast current velocity.  In fall 2001, current velocity generalists were dominant.  Spring was dominated by species preferring moderate current velocity, and secondarily by generalists.  In summer and spring seasons, the fish community was primarily dominated by species preferring rubble substrate, and secondarily by substrate generalists; in the fall, these roles were reversed.  Intolerant species were dominant in all seasons.  Warm-water fishes were the most abundant of all thermal guilds among all seasons, with highest abundances in summer.  Cold-water fishes were the second most abundant group in summer and spring seasons, with lowest abundance in the fall.    Cool-water fishes were highest in abundance in the fall (Table 9).

***Spatial & Temporal Variation in Fish Community & Physical Habitat Variables***

MANOVA tests using relative density of fish species indicated significant variation among strata during summer 2001 (Table 10).  The two tests used to determine significant spatial variation among strata yielded conflicting results for spring 2002 (Wilks' Lambda $p = 0.04$, Pillai's Trace $p = 0.09$), however, spatial variation in relative density of the fish community was still considered significant.  In fall 2001 and summer 2002, there was no significant difference in the overall fish community among strata (Table 10).  Variation in relative density of fish species was significant among all seasons (Table 10).  MANOVA tests revealed significant variation in physical habitat variables among strata for all seasons, as well as significant variation in physical habitat among all seasons (Table 11).  Results therefore indicated that strata were generally described by differences in physical habitat variables, but not by differences in relative abundance of the fish community.

*Community Characteristics & Relationships Among Focus Fish Species*

Hierarchical cluster analysis revealed 3 clusters explaining a moderate amount of variation ($R^2$ from 0.48 to 0.61) in species relative density for each season of the study period (Table 12, Figures 2-9). The number of clusters was determined by the first inflection point of the resulting profile curve, which was more evident in some seasons than others, and the proportion of variance ($R^2$) explained by all clusters prior to and including the first inflection point. Summer 2001 ($R^2 = 0.48$) and 2002 (0.55) had similar species clusters, but also the lowest $R^2$ values compared to fall 2001 (0.61) and spring 2002 (0.58) (Table 12, Figures 2-9). Summer 2001 had the least distinct inflection point and lowest $R^2$, whereas fall 2001 had the most distinct inflection point and highest $R^2$ (Table 12, Figures 2 and 3).

Clusters were further interpreted by functional group membership, previously used to describe the entire fish community. For example, in summer 2001 the first cluster in was composed of highly abundant, relatively small, warm-water species from the omnivore and benthic invertivore groups (rainbow darter, Johnny darter, and hornyhead chub) (Table 7, Figure 6). The second cluster (9 species) was primarily composed of less abundant species with relatively larger individuals preferring lower current velocity and warmer temperatures. This cluster also included all piscivores. Steelhead was the only species making up the third and final cluster. Steelhead was highly abundant, like species in cluster 1, but preferred higher current velocity and lower temperature than species in other clusters, possibly explaining its singular membership and separation into the last cluster (Table 7, Figure 6).

Clusters for fall 2001 were somewhat less clearly interpretable due to clusters 2 and 3 being comprised of just one species each, spottail shiner and hornyhead chub, respectively (Figure 7). Spottail shiner is an omnivore, was relatively high in abundance ($4^{th}$ highest), and generally prefers slower current velocity (Table 7). Hornyhead chub is also an omnivore and was highly abundant (2nd highest), but in contrast to spottail shiner, prefers moderate current velocity. Cluster 1 was made up of the other 9 species, including highly abundant common shiner and white sucker, and less abundant species including all piscivorous fishes.

Analysis of the community in spring 2002 revealed 3 groupings consisting of a small cluster of highly abundant species (cluster 2), a larger cluster of less abundant species, including all piscivores (cluster 1), and a final cluster made up of a singular cyprinid species (cluster 3) (Figure 8). Hornyhead chub and Chinook salmon both prefer moderate current, rubble substrate and have somewhat similar trophic guild membership, all of which could have contributed to their grouping in cluster 2. Chinook salmon was highly abundant, and was observed and collected in a variety of habitats throughout the spring. High abundance of Chinook salmon parr in many habitats before smolting may have contributed to their strong separation from all but one species (Table 7, Figure 8).

Analysis of species densities for summer 2002 revealed 3 clusters similar to the community in summer 2001 (Figure 9). The first cluster consisted of 3 species (rainbow darter, common shiner, hornyhead chub) that are highly abundant omnivores or benthic invertivores preferring at least moderate current velocity (Table 7). The second cluster consisted of 9 species of a variety of trophic guilds, again including all 3 piscivorous species, which preferred slow to moderate current velocity or were velocity generalists (Table 7, Figure 9). The third cluster in summer 2002 consisted of only steelhead, as in summer 2001, and similar to a singular salmonid cluster in spring 2002 (Chinook salmon, cluster 3).

Pair-wise correlation analysis indicated several species relationships were significant in each season of the study period. Mean correlation value was highest in spring 2002 and lowest in fall 2001 (Table 13). Few species correlations were larger than 0.50, and relationships were not always intuitively meaningful, even if they were significant. Larger values, however, often revealed more interpretable relationships between species (Table 13). Most species correlations agreed with cluster groupings for each season (31 of 35 correlations); positive species correlations indicated the same cluster group membership, and negative correlations indicated different cluster groupings (Table 13).

In summer 2001, there were eight significant species correlations, with strong positive correlations between smallmouth bass and rockbass ($R^2$ = 0.76), and white sucker and spottail shiner (0.54). A relatively strong negative correlation (-0.51) existed between steelhead and bluntnose minnow. There were seven significant species correlations in fall 2001, with strong positive correlations existing between smallmouth bass and rockbass ($R^2$ = 0.56), and between mottled sculpin and Johnny darter (0.54). In spring 2002, more species were significantly correlated (12) than in other seasons (Table 13). The strongest correlations existed between white sucker and bluntnose minnow ($R^2$ = 0.67), white sucker and rainbow darter (0.62), smallmouth bass and Johnny darter (0.61), bluntnose minnow and rainbow darter (0.56), and mottled sculpin with both bluntnose minnow (0.53) and steelhead (0.52). In summer 2002, strong correlations among the eight significant pairings were between white sucker and smallmouth bass ($R^2$ = 0.69), longnose gar with both rockbass (0.58) and common shiner (0.55), and a strong negative correlation between steelhead and common shiner (-0.52).

***Seasonal & Spatial Variation in Focus Fish Species***

Relative density of focus species varied both spatially and seasonally in the study area. Variation in relative density was species-specific, and not consistent over time periods. Relative density of eleven species varied significantly among seasons and among strata. Two species, rockbass and bluntnose minnow, showed no significant variation among strata or seasons (Tables 14 and 15).

During summer 2001, a total of 5 species showed significant variation in relative abundance among strata (Table 15). These included redhorse, mottled sculpin, rainbow darter, longnose gar, and Chinook salmon. Chinook salmon was found in very low abundance and only at a few sites. When present in the study area, longnose gar was often found in slower current velocity habitat, usually pools. In fall 2001, density of only white sucker and spottail shiner varied among strata (Table 15). Both of these species were at highest abundance during fall. The largest number of species (6) significantly varied among strata during spring 2002 (Table 15). The only species to vary among strata in summer 2002 was rainbow darter, which also varied among strata in summer 2001.

***Seasonal & Spatial Variation in Physical Habitat Variables***

Water temperature, current velocity, hard substrate, and woody debris all showed significant variation at the stratum level, with vegetation the only physical habitat variable that showed no significant spatial variation. Temperature and current velocity were measured in each season, with temperature varying significantly among all seasons as well as among strata. Current velocity also varied significantly among all seasons, but only varied among strata in summer 2001 and 2002 (Table 16). Percent hard substrate was highest in stratum 5 and lowest in stratum 3. Conversely, percent woody debris was highest in stratum 3, and lowest in stratum 5 (Table 16). Temperature varied seasonally and was warmest during summer (mean = 22.7°C, 21.9°C), and coldest during fall (10.5°C). During summer, temperature was warmer in stratum 3 and colder in strata 1 and 5. However, stratum 5 was warmest during fall. During spring, temperature was highest in strata 3 and 4, and lowest in stratum 1. Current velocity also varied seasonally and was highest in spring (mean = 0.66 m $sec^{-1}$) and lowest in summer (mean = 0.23 m $sec^{-1}$, 0.24 m $sec^{-1}$). During summer seasons, current velocity was highest in stratum 5 and lowest in strata 3 and 4. Spatial patterns in temperature appeared to be inversely correlated with current velocity; strata 3 and 4 had the lowest mean current velocity and the highest mean temperature (Table 16).

***Relationships between Species and Physical Habitat Variables***

Canonical Correspondence Analysis was performed for each season to examine associations between density of focus fish species and physical habitat variables. CCA results were statistically significant ($p < 0.05$) and indicated several interpretable relationships between fish species and physical habitat variables for each season based on the ordination plots. Some physical habitat variables, such as temperature and current velocity, were more prominent in the plots than others for various seasons.

In the CCA for summer 2001 (Figure 10), the five physical habitat variables explained 53% of the variance and displayed several interpretable associations between fishes and habitat variables. As indicated by length of the variable rays, temperature and current velocity appeared to be major variables creating gradients among the majority of fish species. Longnose gar, smallmouth bass, rockbass, and Johnny darter aligned with higher temperature values as indicated by their proximity to the positive direction of the temperature factor ray, and were negatively correlated with current velocity. In contrast, white sucker, mottled sculpin and steelhead were positively aligned with current velocity and hard substrate, and negatively with temperature.  Spottail shiner was positively aligned with temperature, and negatively with hard substrate.

CCA for other seasons (Figures 11-13) continued to reveal several interpretable relationships between species and physical habitat factors.  Temperatures in the fall were much cooler than summer, current velocity was much higher, and both of these factors again explained significant variability in the fish community.  Rockbass, rainbow darter, redhorse, and smallmouth bass aligned with higher temperatures in the CCA for fall 2001 (Figure 11). Hornyhead chub, mottled sculpin, and Johnny darter were all closely aligned with higher current velocity, and also with woody debris and vegetation.  Steelhead was aligned with lower current velocity, somewhat higher temperature, and lower hard substrate values.

Spring was characterized by cooler temperatures and higher current velocity than summer seasons, and again explained significant variation within the community (Figure 12). Associations were somewhat less apparent between fish species and habitat variables, and may be a result of the lower variance explained for spring (34%) compared to the previous seasons. The 95% confidence circles were also larger for more species during this season than in others.

The CCA for summer 2002 explained 44% of the variance and indicated several associations similar to those of summer 2001 (Figure 13).  Hard substrate, current velocity, and vegetation appeared to be the important variables explaining variation in fish species densities. Similar to the CCA for summer 2001, smallmouth bass, rockbass, longnose gar, and hornyhead chub aligned positively with temperature and negatively with hard substrate.  Steelhead and Johnny darter aligned positively with current velocity and also hard substrate.  Redhorse, white sucker, and mottled sculpin aligned positively with vegetation.

## Discussion

The near-shore fish community of the lower Muskegon River varied significantly at intermediate spatial and temporal scales within an individual valley segment. Spatial variation within the fish community was largely explained by physical habitat variables and correlated factors associated with species functional groups. Variation due to physical habitat was typically characterized by two or three variables in each season. Temporal variation was largely explained by specific life history patterns of component species and seasonal changes in physical habitat. Spatial variation within the fish community was better explained by variation in physical habitat variables than by habitat strata.

### *Importance of Scale & Habitat*

Results of this study support Fausch et al.'s (2002) argument that fish communities should be studied at an intermediate spatial scale (several kilometers), a "riverscape", because it is at this scale that species develop through ontogenetic stages of their life histories. Fausch et al. (2002) further argued that the intermediate spatial scale reveals the heterogeneous nature of stream habitat different from that of traditional local scales. In the present study, species relative abundance and habitat data were analyzed at the local (site) and intermediate scales (strata, the entire study area), which revealed ecologically interpretable relationships between species and habitat. Analysis of the fish community composition revealed that component species used specific habitat types within the study area, as opposed to separate strata. For example, in summer 2001 steelhead density was highest at sites with higher current velocity and higher percent hard substrate, as indicated by significant CCA results. Such habitat was available, in differing degrees, in all of the strata, and as a consequence steelhead did not vary significantly among strata in summer 2001. Temporal scale analysis further revealed that species varied seasonally due to specific life history patterns. For example, longnose gar was only present as young-of-the-year juveniles in summer due to potamodromous life history patterns (Johnson and Noltie 1996), and Chinook salmon was only present in spring due to an adfluvial life history pattern (Carl 1982).

VSEC units for Michigan rivers (Seelbach et al. 1997) combine both landscape-scale and site-scale habitat features along with fish assemblages and closely match the intermediate scale suggested by Fausch et al. (2002). The VSEC unit system considers each unit to be relatively homogenous in physical habitat and fish assemblages (Seelbach et al. 1997). The area examined for this study was 22 km long and located within a single 40-km long VSEC unit in the lower Muskegon River, and was further delineated into 5 strata (mean length = 3.53 km) (Ichthyological Associates 1991, Seelbach et al. 1997). The present study found that abundance of some species within the fish community varied spatially even within a VSEC unit. For example, rainbow darter was more abundant in the higher-gradient habitat of stratum 5 than in most other strata within the study area. Other species, such as rockbass and bluntnose minnow, showed no significant variation within the study area, which implies that variation for these species may exist among valley segments, other larger scales, or that they are habitat generalists.

Analysis also indicated physical habitat varied spatially within the VSEC unit. Mean temperature varied among all strata in all seasons, and current velocity varied among strata in summer. Percent hard substrate and woody debris also varied significantly among strata. Variation in physical habitat within a VSEC unit suggests that a spatial unit smaller than the valley segment, such as strata within the study area (mean length 3.53 km), may be more appropriate in some analyses of relationships between fish communities and physical habitat variables. The average length of valley segments in Michigan is approximately 6 km (Seelbach et al. 1997), much smaller than that of this study (40 km), therefore the spatial unit used to investigate other fish communities may need to be specific to the valley segment.

In this study, physical habitat variables at the reach (site)-scale explained significant variation within the fish community and its component species. In a study of multiple spatial scales within the relatively pristine Northern Lakes and Forest Ecoregion, Wang et al. (2003) found that reach-scale variables also best explained patterns in stream fish presence/absence, abundance, and community characteristics. Wang et al. (2003) used CCA to analyze relationships between fish assemblage data for 79 watersheds and several environmental factors at the watershed, riparian land-use, and reach-scales. Among the most important reach-scale variables influencing fish assemblages were temperature, gradient, and macrophyte coverage, all variables included (temperature, percent vegetation) or correlated with (gradient with current velocity) those analyzed in the present study.

***Spatial variation***

Temperature had a dominant influence on spatial distributions of fishes in this study and other studies of Michigan streams. Wehrly et al. (2003) used stream fish community patterns to classify regional variation in thermal regime of lower Michigan rivers, and found that differences in community structure among sites were largely related to spatial variation in mean temperature as well as temperature fluctuation. In the present study, temperature was a primary factor in most CCA analyses relating physical factors to focus species (summer 2001, fall 2001, spring 2002), and thermal guild was often used to explain species correlations and cluster groupings. For example, in the CCA plot for summer 2001, smallmouth bass, rockbass, and longnose gar, all warm-water piscivores, were positively correlated with temperature. Steelhead, a coldwater species preferring rubble substrate and higher current velocity was positively correlated with hard substrate, current velocity, and negatively correlated with temperature. Pair-wise correlations for smallmouth bass and rockbass, as well as longnose gar and rockbass were also largely explained by temperature preference. The differences were surprising given the relatively small difference in mean temperature among strata (Table 16), but may occur because temperature effects on metabolism and consumption for cold and warm water fishes increase sharply at 21-23°C (Hokanson et al. 1977, Magnuson et al. 1979). Spatial variability in cold (10°C) groundwater inflows within and among strata also may enhance variation in species distributions (Wehrly et al. 1998, Wiley et al. 1997).

Correlates of temperature and current velocity also explained distribution and community composition in other studies of Michigan fishes. Zorn et al. (2002) used low-flow yield (LFY) and catchment area (CA) in a study of stream fish distribution in relation to stream size and hydrology in lower Michigan. LFY was defined as the 90% exceedence-flow discharge divided by catchment area of a given stream site, and is an index of temperature and correlated with current velocity. Zorn et al. (2002) used cluster analysis based on fish species abundance and identified general fish assemblage patterns when clusters were plotted against LFY and CA. Although the overall relationship between LFY and CA was meaningful, much of the variance in fish species abundance (61%) was unexplained. Further analysis indicated that cluster membership did not equally represent abundance of constituent species, and further species-specific study was suggested (Zorn et al. 2002). The present study used some methods similar to Zorn et al. (2002), with correlates of LFY (temperature, current velocity) as physical habitat variables and cluster analysis based on species abundance, albeit at a smaller scale. Temperature and current velocity both explained a large portion of spatial variation in fishes (functional group membership and CCA for summer 2001-spring 2002), however cluster analysis did not explain much variation in fishes, nor was cluster membership the same as in Zorn et al.'s (2002) study. Several species found within the same cluster in this study were found in separate clusters in the Zorn et al. (2002) study, and vice versa. For example, in summer 2002, hornyhead chub, common shiner, and rainbow darter constituted one cluster, whereas Zorn et al. (2002) found these species to be part of separate clusters. Some of the disagreement in cluster membership is very likely due to the different scale and size of datasets between the two studies. Zorn et al. (2002) looked at abundance of 69 species at 226 stream sites throughout lower Michigan, compared to the present study which analyzed relative abundance of 14 species at 30 sites within one river; although this unexplained discrepancy further justifies species-specific analysis. The present study addressed this issue by using CCA to investigate individual species relationships with physical habitat variables, and the results explained a larger portion of variance in species distributions as well as provided interpretable species-habitat relationships.

Redhorse, mottled sculpin, and rainbow darter, all benthic invertivores, varied spatially in summer 2001, possibly owing to patchiness of habitat and resulting habitat shifts by the species. All three of these benthic invertivores prefer rubble substrate, but prefer different current velocities as indicated by functional groups. The low-flow period of summer may have created patchiness in rubble substrate habitats (typically riffles), causing species to shift to other areas, therefore contributing to spatial variation. In a study investigating relationships and population ecology of rainbow and fantail darters (*Etheostoma flabellare*) in a temporally variable Illinois stream, Schlosser and Toth (1984) showed that distributions of rainbow darter varied during summer low-flow periods because of movement to deeper habitat, emigration out of the study area, or mortality.  Furthermore, it was shown that rainbow darter and fantail darter varied independently of one another, and that fluctuation in discharge was the primary factor influencing relative abundance of each species.  These findings provide a possible explanation for spatial variation in relative abundance of rainbow darter, and possibly other species in the present study, particularly in summer seasons.  Findings by Schlosser and Toth (1984) also support the larger effects of physical habitat as opposed to competition with similar species.

The fish community (focus species only) significantly varied at the spatial scale in summer 2001 when mean current velocity was lowest, and also varied among strata.  The fish community also varied among strata in spring 2002, when mean current velocity was highest (0.66 m $sec^{-1}$).  In a review of stream fish ecology from a landscape perspective, Schlosser (1991) stated that the most dramatic aspects of temporal variation in physical habitat of streams are those associated with stream flow.  He further stated that near-shore habitats of streams exhibit high levels of variability due to fluctuations in stream flow and associated changes in depth.  In spring, higher flows increase the habitat available to fishes, whereas low flows of summer may cause shifts in some species due to lack of preferred habitat.  These findings could explain spatial variation at the community level during summer 2001 and spring 2002 in the present study.

Spawning periods and emergence of juveniles likely contributed to significant spatial variation of several species, and may also explain associations between species and physical habitat variables which were somewhat contrary to functional group membership.  In the present study, the most species, primarily darters and cyprinids, varied spatially during spring 2002 and summer 2001; these fishes are known to spawn primarily in spring and summer (Peterson and VanderKooy 1995).   In the lower Muskegon River, steelhead spawn in early spring, and young of the year emerge from the gravel within several weeks. CCA results for spring 2002 indicated steelhead density was negatively correlated with current velocity. In a study of the effects of flow regime on juvenile abundance and assemblage structure of stream fishes, Schlosser (1985) found that variation in stream flow, particularly during spawning periods, strongly affected fish assemblage structure. Furthermore, Schlosser (1985) suggested that influence of stream flow varies among age groups of fishes, having different effects on young of the year and juveniles, than on adult individuals. Although juvenile and adult steelhead generally prefer higher current velocity (Poff and Allan 1995), Close and Anderson (1997) suggested that young-of-the-year steelhead avoid high current velocity. Differences in habitat preference by young-of-the-year individuals during higher-flow periods could contribute to spatial variation in steelhead as well as other species.

***Seasonal Variation***

The fish community varied significantly among all seasons over the course of the study period primarily due to life history patterns and seasonal variation in physical habitat. During summer, flow was low and temperature was high, whereas in fall temperatures were lowest, and in spring flows were highest and temperatures were cooler. From a biological perspective, summer presents a period of settlement and growth for many species, including juvenile and young-of-the-year individuals. Low-flow periods of summer may also cause habitat shifts in some species (Schlosser and Toth 1984, Schlosser 1991). In fall, most species continue growing but shift habitat, emigrate, or die (Johnson and Kucera 1985). The spring season is generally a spawning period for most fishes.

Ontogenetic changes in survival and habitat dependence may explain seasonal variation found in this study. In summer 2001 and 2002, rainbow darters were at their highest abundances compared to fall and spring. Rainbow darters are known to spawn in the late spring and summer months, with juveniles developing over mid to late summer (Trautman 1981, Peterson and VanderKooy 1995). Schlosser and Toth (1984) showed the decline in abundance in rainbow darter from summer to fall could also be related to juvenile mortality. Similar ontogenetic differences in survival explained seasonal variation in steelhead. Steelhead spawn in early spring, and therefore young of the year were highly abundant in the summer seasons, but much lower in the fall. Godby et al. (2007) showed that this variation in juvenile steelhead abundance was primarily due to juvenile mortality related to intolerance of increased temperatures from late summer into fall in the Muskegon River. Godby et al. (2007) explained that juvenile steelhead sought thermal refugia in cooler tributary creek habitats, which would further contribute to a decrease in abundance within the study area from summer to fall.

Abundance of other species such as smallmouth bass may have varied seasonally due to local migrations. Smallmouth bass are known to move upstream from local pools to spawn in higher gradient habitat, after which the adults move back down to lower gradient habitat (Trautman 1981, Todd and Rabeni 1989). Individuals from lower gradient habitat downstream of Newaygo may have migrated upstream into the study area for spawning. Smallmouth bass spawn in the summer months, with larvae developing into juveniles by late summer (Peterson and Vanderkooy 1995). Therefore juvenile recruitment can add to the overall abundance of smallmouth bass in the fall (Schlosser 1985), which would explain the increase in smallmouth bass relative density from summer 2001 to fall 2001.

Presence or absence of some species varied seasonally due to life history patterns. Juvenile Chinook salmon, an adfluvial species, were only present and highly abundant in the spring season during their outmigration from the river to lake habitat, in this case to Muskegon Lake and Lake Michigan. In the Muskegon River, adult Chinook salmon (not sampled in our study) migrate upstream from Lake Michigan in the fall to spawn and eventually die. The eggs hatch and fry develop through the spring into smolts, when they migrate en masse to Lake Michigan (O'Neal 1997). Chinook salmon were highly abundant in the spring and did not vary spatially, likely because smolts move in large groups downstream to reach the lake during this period (Bjornn 1971).

The potamodromous life history pattern of longnose gar populations may explain their presence and absence during the study period. Longnose gar was only present in summer. This species generally prefers lower-gradient, slower-moving waters often found near downstream habitats in medium to large rivers (Page and Burr 1991, Hubbs et al. 2004). Studies by Netsch and Witt (1962) and Johnson and Noltie (1996, 1997) showed that some populations exhibit potamadromous life history patterns and are known to migrate upstream in the spring to spawn in higher gradient habitat. Eggs are scattered and attach to vegetation and hard substrate (Trautman 1981), and the adults eventually move back downstream to larger pools (Netsch and Witt 1962). This spawning behavior takes place in late spring and early summer on the Muskegon River (personal observation). After hatch, juveniles aggressively feed, grow rapidly and move downstream to pools and habitats with lower current velocity. Outmigration of juveniles probably takes place during the fall or winter of the first year (Netsch and Witt 1962, Echelle and Riggs 1972).

### *Potential Influence of Other Factors*

Several other factors may influence variation within lotic fish communities including biotic factors such as competition and prey availability, or anthropogenic factors such as stream impoundment. Some of these factors may have contributed to spatial and seasonal variation in the fish community, but were likely correlated with physical habitat variables measured in this study and may not significantly change overall results.

In a review of landscape influence on stream fish population and community dynamics, Schlosser (1991) suggested three primary factors are important for growth and survival of early life stages of stream fishes; trophic interactions, spatial environmental heterogeneity, and temporal environmental heterogeneity. The latter two factors were investigated in-depth for this study and explained significant variation in fish distributions in the lower Muskegon River. Trophic interactions were accounted for to an extent in the form of functional group classification of species, and used to further describe community composition and species relationships.

Biotic interactions such as competition, predator avoidance, and prey availability influence fish communities, but were likely explained by functional group classification or correlated with variables measured in this study. For example, pair-wise correlation analysis of focus species indicated a strong positive relationship between relative abundance of smallmouth bass and rockbass. Both species are warm-water piscivores, therefore a strong positive correlation may imply competition between the two species. In a study on food and habitat partitioning between young-of-the-year smallmouth bass and rockbass, George and Hadley (1979) showed that the two species were ecologically segregated by prey size and habitat. While sharing similar habitat, smallmouth bass grew faster and were able to consume larger prey, whereas rockbass grew slower and consumed smaller prey items. Smallmouth bass eventually moved away from near-shore habitat as they grew larger, whereas rockbass remained in the shallower habitat. The strong positive correlation between these two species detected in the present study likely occurred during the period when both species had similar habitat preference (warmer temperature), but different prey size preference (summers 2001 and 2002, fall 2001), although no diets were analyzed to confirm this.

Prey availability can also affect spatial and temporal variation in fish species, but was likely correlated with physical habitat variables in this study. In the lower Muskegon River, Godby et al. (2007) showed that the dominant prey of young steelhead were invertebrates, particularly hydropsychid caddisflies. Hydropsychids are generally more abundant in cooler, higher velocity, and hard substrate habitats (Hildrew and Edington 1979). Furthermore, Godby et al. (2007) found that macroinvertebrate prey densities in the lower Muskegon River were large enough to support high densities of juvenile steelhead; this suggests that food availability may have been sufficient to support several invertivore species.

Schlosser (1991) also suggested that predator avoidance is likely a major factor causing segregation of small fishes to shallow near-shore habitats and large fishes to deeper main-channel habitats. Small fishes risk predation by larger fishes if they enter into deeper waters, and large fishes actually risk predation by terrestrial predators, such as herons, if they move into shallow habitats. In a concurrent study of the lower Muskegon River, Riseng et al. (2006) found abundant populations of walleye and brown trout (*Salmo trutta*), both piscivorous species (Poff and Allan 1995), in the main channel habitat within the same valley segment as the present study; neither species, however, were collected in near-shore habitats. This disjunct distribution of large and small fishes in river habitats may partially account for lack of predators found in near-shore habitats in the present study.

Anthropogenic effects may also influence variation in the fish community. Croton Dam is the lower-most impoundment on the Muskegon River before draining into Lake Michigan and did appear to have localized impacts. One of the main effects observable was the abundance of centrarchids, particularly sunfishes, at sites just below Croton Dam. Sunfishes, a warm-water group of species, were relatively low in abundance throughout the study area, but some species, such as bluegill, appeared to be locally abundant at sites immediately below the dam. Other than the obvious impact of the dam on flow regime, the proliferation of centrarchids could be related to the fact that Croton impoundment is a top-draw dam; therefore water discharged just below the dam can be warmer than that further downstream (O'Neal 1997). These effects would provide suitable thermal habitat and flow regime for sunfishes as opposed to salmonids, which were abundant throughout the rest of stratum 1. Similar results were found by Taylor et al. (2001) in a study of stream impoundment on fish communities in an Illinois stream. Taylor et al. (2001) compared several pre-and post-impoundment fish collections to find that the fish community changed from one previously dominated by cyprinids to a post-impoundment community dominated by centrarchids. Among other factors, alteration of thermal regime by impoundment was believed to influence the community shift. Although Croton Dam likely alters localized thermal regime in the lower Muskegon River, the observed increase in local abundance of sunfishes would not affect results of this study since they were not abundant enough to be included in analyses of focus species.

***Comparison to the Main Channel Fish Community***

Analysis of main channel habitats and community would likely produce different, although somewhat related, results to the present study of the near-shore fish community. The main channel of the Lower Muskegon River is populated with many of the same species, but at a later stage of development, generally sub-adults and adult fishes (O'Neill 1997). Therefore individuals would be larger and more mature, and in many cases would have different behaviors and habitat preferences. In a study of life history patterns of three redhorse species in the Des Moine River in Iowa, Meyer (1962) observed that young redhorses often remained near shoreline habitats including both vegetated areas and riffles, but as they matured would move into main channel habitat and larger deeper pools. Redhorse species were collected during all seasons during the present study, with highest relative abundance in spring. During these sampling periods larger individuals could often be observed in the main channel.

The main channel was deeper than our study sites and may provide less cover for fishes than near-shore habitats. In a study of seasonal and size-related variation in microhabitat use by South Victorian stream fishes, Koehn et al. (1994) showed that depth can play a large role in the areas of a stream fishes will enter, even within a single species, with smaller individuals remaining nearer to the shoreline, and larger individuals in deeper waters. A comparison of species richness with the main channel habitat of the Muskegon River found in summer 2002 by Riseng et al. (2006) reveals that many of the same species occurred in both main channel and near-shore habitats, although the near-shore habitat included almost 33% more species than the main channel (Tables 5, 17).

### ***Importance of Species-specific Analyses***

Although the fish community within the study area was effectively described by functional group classification and varied among seasons, analyses at the species level revealed the most meaningful relationships between fishes and physical habitat variables. Species-specific analyses were also more ecologically meaningful than cluster groupings. Zorn et al. (2002) suggested species-specific analyses may explain more variability in fish distributions than the hierarchical cluster analysis used in their study of stream fish assemblages. In their multi-scale study of aquatic communities in Michigan trout streams, Wiley et al. (2007) emphasized that variance structure in aquatic communities is a species-specific property. Analyses of long-term, spatially- and temporally-extensive datasets of three macroinvertebrates and two fish species showed that each species had a distinctive overall variance structure. They further suggested that difference between variance structures of component species indicates inherent ecological differences, and these characteristics may be useful to managers. The findings of Wiley et al. (2007) are also important because they suggest that no singular variance structure exists for the community as a whole. In the case of the present study, variation of the whole community at the spatial scale did not accurately represent variation of component species.

### ***Biases & Limitations***

Sampling efficiency was likely a major bias in this study as it could vary greatly among habitats and species, and therefore may have influenced estimates of relative abundance within strata or seasons. Certain types of habitats were easier to effectively sample, such as shallower hard-substrate habitats, as opposed to deeper, soft-substrate habitats. The former habitat type allows for easier location and collection of fishes due to better visibility and navigation, whereas the latter can be much more difficult due to factors such as clouding of the water while navigating the site. Certain species also are more easily collected than others (Larimore 1961); for example, salmonids were drawn to the electrical current and remained near the surface for longer periods of time, and were therefore collected more effectively than fishes that lack gas-bladders and remain on the bottom, such as darters and sculpin.

Sampling efficiency also may have been lowered because sites were located in a large river. Electrofishing gear is generally limited by stream depth (Angermeier and Smogor 1991); although the width of a given site was 3 meters, if fishes were able to out-swim the electrical current, they could seek refuge in deeper water, outside the range of our sampling gear. Schooling fishes, such as common shiners, were also observed to have entered and exited sites during sampling passes. Since block nets were not used, and are relatively impractical and inefficient on large rivers, fishes could also move from one site to an adjacent site. I assumed that neither emigration nor immigration would significantly influence my depletion estimates. Additional sampling using a small boom-electrofishing boat could be used for future sampling, as this type of sampling gear may help contain fishes to near-shore areas, although collection by this method would likely be cumbersome in shallow water.

Some physical habitat variables were collected for each site in each season, such as temperature and current velocity (or extrapolated from other data), however, data for other variables (percent hard substrate, % woody debris, % vegetation) were collected only once over the study period. In-stream vegetative cover is an important reach-scale variable influencing fish assemblages (Wang et al. 2003), and likely varies seasonally to a greater degree than substrate or woody debris. Vegetation was observably more abundant in spring and summer than in fall, and would have likely had greater influence on fish species densities during those seasons, therefore percent vegetation should be sampled seasonally at each site in future work.

This study was conducted in conjunction with a salmonid (Chinook salmon and steelhead) population survey, therefore the stratified random sampling design used was primarily based on salmonid spawning habitat, with optimal spawning areas given more weight. Therefore a major bias of the study was the variable number of sites sampled in each stratum, ranging from 11 in stratum 1, which contained optimal salmonid spawning habitat, to only 2 in stratum 4, which had less optimal salmonid spawning habitat. Although sites sampled were biased toward salmonid spawning habitat, primarily gravel and rubble substrates, many other species in this study also utilized similar habitat, such as darters, cyprinids, and catostomids, and therefore were likely well-represented. Other species that did not utilize habitat similar to salmonid spawning areas may have been less well-represented, such as smallmouth bass and longnose gar.

Although site selection was biased toward salmonid spawning habitat, species within the fish community still showed considerable variation among sites in strata and seasons. Variation in relative abundance of species within the fish community was better explained by physical habitat variables than strata and was statistically significant, suggesting that a variety of habitat types were still likely represented. Given the bias and assumptions in sampling design, more sites in less well-represented strata should be sampled for further analysis.

***Implications & Future Work***

This study demonstrated some of the complex relationships between a near-shore fish community and its component species with physical habitat variables at an intermediate scale. Given the degree of species-specific variation with multiple physical habitat variables and correlated factors, it is important to manage not only for functional groups of fishes, such as thermal and trophic guilds, but for individual species. In a study of biological integrity in water resource management, Karr (1991) observed that in streams, functional or community-level variables are less responsive to environmental change than community composition. This observation supports the importance of understanding fish communities at a component species level. Species must also be studied at the temporal scale, due to varying life history patterns ranging from local habitat-scale shifts to seasonal absence altogether. Variation in fish community composition at the temporal-scale reiterates the need for species-specific management to maintain biotic integrity.

In order to effectively study physical habitat variables influencing fish communities and species, it is also suggested that thorough investigation and classification of the physical habitat types at intermediate scales be determined *a priori*. In the present study, detailed instream habitat analyses had already been conducted for the entire study area (Ichthyological Associates 1991) and allowed efficient sampling of a variety of general habitat types without the need for sampling every site. Once physical habitat types were categorized and mapped, representative sites could be selected and species sampled with confidence in their representation of the area at the intermediate scale. Previously-established sampling units are not always available for valley segments, but landscape classification and GIS techniques may permit identification of general habitat types and aid in site selection for intensive sampling (Brenden et al. 2006).

Although the VSEC unit presents a scale similar to the intermediate scale suggested by Fausch et al. (2002), significant spatial variation in physical habitat and individual fish species still existed within a valley segment. Units smaller than individual valley segments, but larger than 100 m sites, should be used for assessment of fish community characteristics. In the present study, the entire 22-km study area served this purpose, although the size of the study unit should be relative to that of the specific river system.  Using an intermediate scale places site-scale variables, such as species relative abundance and physical habitat, into a larger context, therefore revealing ecologically interpretable relationships between species and habitat.  These relationships may not be detectable at several individually disjoint sites, and may be lost at the scale of an entire watershed.  It will also be necessary to study adjacent VSEC units to determine variation in species that do not vary spatially within a valley segment, including game fishes such as Chinook salmon or smallmouth bass, or forage fishes such as bluntnose minnow.

Seasonal changes in physical habitat variables also contribute to variation in the fish community and component species, and may vary from year to year.  Further analyses are needed over longer time scales to accurately assess temporal variation and pattern in fish communities and species.  Management decisions should be made with knowledge of the primary physical habitat variables influencing fish communities, as well as the specific life history patterns of component species.  By studying and managing for fish communities and species at the intermediate scale, complex relationships between fishes and their lotic habitats can be better understood.

## Literature Cited


Angermeier, P.L., and R.A. Smogor. 1991. An electric seine for collecting fish in streams. North American Journal of Fisheries Management 11: 352-357.

Bain, M.B., J.T. Finn, and H.E. Booke. 1988. Streamflow regulation and fish community Structure. Ecology 69: 382-392.

Becker, G.C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison.

Begon, M., C.R. Townsend, and J.L. Harper. 2006. Ecology: From Individuals to Ecosystems. Blackwell Publishing, Oxford.

Bjornn, T. C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. Transactions of the American Fisheries Society 100: 423–438.

Brenden, T., R.D. Clark, A. Cooper, P.W. Seelbach, L. Wang, S. Aichele, E. Bissell, and J.Stewart. 2006. A GIS framework for collecting, managing, and analyzing multi-scale landscape variables across large regions for river conservation and management. Pages 49-74 *In* R. Hughes, L. Wang, and P.W. Seelbach, editors. Landscape influences on stream habitats and biological communities. American Fisheries Society, Symposium 48, Bethesda, Maryland.

Carl, L. M. 1982. Natural reproduction of coho salmon and Chinook salmon in some Michigan streams. North American Journal of Fisheries Management 2: 375–380.

Close, T.L., and C.S. Anderson. 1997. Factors limiting juvenile steelhead survival in streams tributary to Minnesota waters of Lake Superior. Minnesota Department of Natural Resources, Investigational Report no. 462, St. Paul.

Creque, S.M., E.S. Rutherford, and T.G. Zorn. 2005. Use of GIS-derived landscape-scale habitat features to explain spatial patterns of fish density in Michigan rivers. North American Journal of Fisheries Management 25:1411-1425.

Echelle, A.A., and C.D. Riggs. 1972. Aspects of the early life history of gars (*Lepisosteus*) in Lake Texoma. Transactions of the American Fisheries Society 101: 106-112.

Everhart, W.H., and W.D. Youngs. 1981. Principles of Fishery Science. Comstock Publishing, Ithaca, New York.

Fausch, K.D., C.E. Torgersen, C.V. Baxter, and H.W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream Fishes. BioScience 52: 483-498.

Fauth, J.E., J. Bernardo, M. Camara, W.J. Resetarits, Jr., J. Van Buskirk, and S.A. McCollum. 1996. Simplifying the jargon of community ecology: a conceptual approach. The American Naturalist 147: 282-286.

Fladung, E., M. Scholten, and R. Thiel. 2003. Modelling the habitat preferences of preadult and adult fishes on the shoreline of the large, lowland Elbe River. Journal of Applied Ichthyology 19: 303-314.

George, E.L., and W.F. Hadley. 1979. Food and habitat partitioning between rockbass (*Ambloplites rupestris*) and smallmouth bass (*Micropterus dolomieui*) young of the year. Transactions of the American Fisheries Society 108: 253-261.

Gido, K.B., D.L. Propst, and M.C. Molles, Jr. 1997. Spatial and temporal variation of fish communities in secondary channels of the San Juan River, New Mexico and Utah. Environmental Biology of Fishes 49: 417-434.

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

Heitke, J.D., C.L. Pierce, G.T. Gelwicks, G.A. Simmons, and G.L. Siegwarth. 2006. Habitat, land use, and fish assemblage relationships in Iowa streams: preliminary assessment in an agricultural landscape. American Fisheries Society Symposium 48: 287-303.

Hildrew, A.G., and J.M. Edington. 1979. Factors facilitating the coexistence of hydropsychid caddis larvae (Trichoptera) in the same river system. Journal of Animal Ecology 48: 557-576.

Hocutt, C.H. 1973. Swimming performance of three warmwater fishes exposed to a rapid temperature change. Chesapeake Science 14: 11-16.

Hokanson, K.E.F., C.E. Kleines, and T.W. Thorslund. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile rainbow trout, *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 34: 639-648.

Hubbs, C.L., K.F. Lagler, and G.R. Smith. 2004. Fishes of the Great Lakes Region, revised edition. The University of Michigan Press, Ann Arbor, Michigan.

Ichthyological Associates. 1991. Habitat mapping report for the Croton Project, FERC Project No. 2468, Muskegon River, Michigan. Ichthyological Associates, New York.

Johnson, J. H., and P. A. Kucera. 1985. Summer-autumn utilization of subyearling steelhead trout in tributaries of the Clearwater River, Idaho. Canadian Journal of Zoology 63: 2283-2290.

Johnson, B.L., and D.B. Noltie. 1996. Migratory dynamics of stream-spawning longnose gar (*Lepisosteus osseus*). Ecology of Freshwater Fish 5: 97-107.

Johnson, B.L., and D.B. Noltie. 1997. Demography, growth, and reproductive allocation in stream-spawning longnose gar. Transactions of the American Fisheries Society 126: 438-466.

Jude, D.J. 1992. Evidence for natural reproduction by stocked walleyes in the Saginaw River tributary system, Michigan. North American Journal of Fisheries Management 12:386-395.

Karr, J.R. 1991. Biological integrity: a long-neglected aspect of water resource management. Ecological Applications 1: 66-84.

Koehn, J.D., N.A. O'Connor, and P.D. Jackson. 1994. seasonal and size-related variation in microhabitat use by a southern Victorian stream fish assemblage. Australian Journal of Marine and Freshwater Research 45: 1353-66.

Lammert, M., and J.D. Allan. 1999. Assessing biotic integrity of streams: effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. Environmental Management 23: 257-270.

Lamouroux, N., H. Capra, M. Pouilly, and Y. Souchon. 1999. Fish habitat preferences in large streams of southern France. Freshwater Biology 42: 673-687.

Larimore, R.W. 1961. Fish population and electrofishing success in a warm-water stream. The Journal of Wildlife Management 25: 1-12.

Lyons, J. 1989. Correspondence between the distribution of fish assemblages in Wisconsin streams and Omernik's Ecoregions. American Midland Naturalist 122: 163-182.

Lyons, J. 1992. Using the index of biotic integrity (IBI) to measure environmental quality in warmwater streams of Wisconsin. U.S. Department of Agriculture, Forest Service, Gen. Technical Report NC-149, North Central Forest Experiment Station, St. Paul, Minnesota.

Lyons, J. 1996. Patterns in the species composition of fish assemblages among Wisconsin streams. Environmental Biology of Fishes 45: 329-341.

Magnuson, J.J., L.B. Crowder, and P.A. Medvick. 1979. Temperature as an ecological resource. American Zoologist 19: 331-343.

Mardia, K.V., J.T. Kent, and J.M. Bibby. 1979. Multivariate Analysis. Academic Press, London.

Meyer, W.H. 1962. Life history of three species of redhorse (*Moxostoma*) in the Des Moines River, Iowa. Transactions of the American Fisheries Society 91: 412-419.

Miller, W.J., D.E. Rees, R.J. Carr, and D.S. Berube. 2005. Hornyhead chub (*Nocomis biguttatus*): a technical conservation assessment. USDA Forest Service, Rocky Mountain Region, Fort Collins, Colorado.

Netsch, N.F., and A. Witt, Jr. 1962. Contributions to the life history of the longnose gar, (*Lepisosteus osseus*) in Missouri. Transactions of the American Fisheries Society 91: 251-262.

O'Neal, R.P. 1997. Muskegon River Watershed Assessment. Michigan Department of Natural Resources, Special Report no. 19, Fisheries Division, Lansing.

Page, L.M., and B.M. Burr. 1991. A Field Guide to Freshwater Fishes. Houghton Mifflin Company, Boston.

Peterson, M.S., and S.J. VanderKooy. 1995. Phenology and spatial and temporal distribution of larval fishes in a partially channelized warmwater stream. Ecology of Freshwater Fish 4: 93-105.

Poff, N.L., and J.D. Allan. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76: 606-627.

Power, M.E., W.J. Matthews, and A.J. Stewart. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. Ecology 66: 1448-1456.

Riseng, C.M., M.J. Wiley, R.J. Stevenson, T.G. Zorn, and P.W. Seelbach. 2006. Comparison of coarse versus fine scale sampling on statistical modeling of landscape effects and assessment of fish assemblages of the Muskegon River, Michigan. American Fisheries Society Symposium 48: 555-575.

Romesburg, H.C. 1990. Cluster Analysis for Researchers. Krieger Publishing Company, Malabar, Florida.

Roth, N.E., J.D. Allan, and D.L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11: 141-156.

SAS. 2001a. JMP version 4. SAS Institute Incorporated, Cary, North Carolina.

SAS. 2001b. JMP Statistics and Graphics Guide, Version 4. SAS Institute Incorporated, Cary, North Carolina.

Schlosser, I.J. 1985. Flow regime, juvenile abundance, and the assemblage structure of stream fishes. Ecology 66: 1484-1490.

Schlosser, I.J. 1987. The role of predation in age- and size-related habitat use by stream fishes. Ecology 68: 651-659.

Schlosser, I.J. 1991. Stream fish ecology: a landscape perspective. BioScience 41: 704-712.

Schlosser, I.J., and L.A. Toth. 1984. Niche relationships and population ecology of rainbow (*Etheostoma caeruleum*) and fantail (*E. flabellare*) darters in a temporally variable environment. Oikos 42: 229-238.

Seber, G.A.F., and E.D. Le Cren. 1967. Estimating population parameters from catches large relative to the population. The Journal of Animal Ecology 36: 631-643.

Seelbach, P.W., and M.J. Wiley. 1997. Overview of the Michigan rivers inventory project. Michigan Department of Natural Resources, Fisheries Technical Report no. 97-3, Ann Arbor.

Seelbach, P.W., M.J. Wiley, J.C. Kotanchik, and M.E. Baker. 1997. A landscape-based ecological classification system for river valley segments in lower Michigan (MI-VSEC Version 1.0). Michigan Department of Natural Resources, Fisheries Research Report no. 2036, Ann Arbor.

Smogor, R.A., P.L. Angermeier, and C.K. Gaylord. 1995. Distribution and abundance of American eels in Virginia streams: tests of null models across spatial scales. Transactions of the American Fisheries Society 124: 789-803.

Snedden, G.A., W.E. Kelso, and D.A. Rutherford. 1999. Diel and seasonal patterns of spotted gar movement and habitat use in the lower Atchafalaya River Basin, Louisiana. Transactions of the American Fisheries Society 128: 144-154.

Stewart, J.S., L. Wang, J. Lyons, J.A. Horwatich, and R. Bannerman. 2001. Influences of watershed, riparian-corridor, and reach-scale characteristics on aquatic biota in agricultural watersheds. Journal of the American Water Resources Association 37: 1457-1487.

Taylor, C.A., J.H. Knouft, and T.M. Hiland. 2001. Consequences of stream impoundment on fish communities in a small North American drainage. Regulated Rivers: Research and Managment 17: 687-698.

Ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.

Ter Braak, C.J.F. 1995. Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquatic Sciences – Research Across Boundaries 57: 255-289.

Thorpe, J.E., M. Mangel, N.B. Metcalfe, and F.A. Huntingford. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology 12: 581-599.

Todd, B.L., and C.F. Rabeni. 1989. Movement and habitat use by stream-dwelling smallmouth bass. Transactions of the American Fisheries Society 118: 229-242.

Trautman, M.B. 1981. The Fishes of Ohio, revised edition. Ohio State University Press, Columbus.

Trial, J.G., C.S. Wade, J.G. Stanley, and P.C. Nelson. 1983. Habitat and suitability information: common shiner. United States Department of the Interior, Fish and Wildlife Service no. 82/10.40, Orono, Maine.

Tripe, J.A., and C.S. Guy. 1999. Spatial and temporal variation in habitat and fish community characteristics in a Kansas Flint Hills stream. Ecology of Freshwater Fish 8: 216-226.

Wang, L., J. Lyons, P. Rasmussen, P. Seelbach, T. Simon, M. Wiley, P. Kanehl, E. Baker, S. Niemela, and P.M. Stewart. 2003. Watershed, reach, and riparian influences on stream fish assemblages in the Northern Lakes and Forest Ecoregion, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 60: 491-505.

Ward, J.H. Jr. 1963. Hierarchical grouping to optimize an objective function. Journal of the American Statistical Association 58: 236-244.

Wehrly, K.E., M.J. Wiley, and P.W. Seelbach. 1998. Landscape-based models that predict July thermal characteristics in lower Michigan rivers. Michigan Department of Natural Resources, Fisheries Research Report 2037, Ann Arbor.

Wehrly, K.E., M.J. Wiley, and P.W. Seelbach. 2003. Classifying regional variation in thermal regime based on stream fish community patterns. Transactions of the American Fisheries Society 132: 18-38.

Wiley, M.J., S.L. Kohler, and P.W. Seelbach. 1997. Reconciling landscape and local views of aquatic communities: lessons from Michigan trout streams. Freshwater Biology 37: 133-148.

Zorn, T.G., P.W. Seelbach, and M.J. Wiley. 2002. Distributions of Stream Fishes and their Relationship to Stream Size and Hydrology in Michigan's Lower Peninsula. Transactions of the American Fisheries Society 131: 70-85.

Table 1. List of species collected by electrofishing in the lower Muskegon River study area 2001-2002.

| Common Name* | FAMILY | Scientific Name |
|---|---|---|
| Bowfin | Amiidae | *Amia calva* |
| Brook Silversides | Atherinidae | *Labidesthes sicculus* |
| Northern Hogsucker | Catostomidae | *Hypentelium nigricans* |
| Redhorse spp. (RH) | Catostomidae | *Moxostoma spp.* |
| White Sucker (WS) | Catostomidae | *Catostomus commersoni* |
| Rock Bass (RB) | Centrarchidae | *Ambloplites rupestris* |
| Green Sunfish | Centrarchidae | *Lepomis cyanellus* |
| Pumpkinseed | Centrarchidae | *Lepomis gibbosus* |
| Bluegill | Centrarchidae | *Lepomis macrochirus* |
| Smallmouth Bass (SMB) | Centrarchidae | *Micropterus dolomieu* |
| Largemouth Bass | Centrarchidae | *Micropterus salmoides* |
| White Crappie | Centrarchidae | *Pomoxis annularis* |
| Black Crappie | Centrarchidae | *Pomoxis nigromaculatus* |
| Mottled Sculpin (MS) | Cottidae | *Cottus bairdi* |
| Central Stoneroller | Cyprinidae | *Campostoma anomalum* |
| Spotfin Shiner | Cyprinidae | *Cyprinella spiloptera* |
| Common Carp | Cyprinidae | *Cyprinus carpio* |
| Common Shiner (CS) | Cyprinidae | *Luxilus cornutus* |
| Hornyhead Chub (HHC) | Cyprinidae | *Nocomis biguttatus* |
| Golden Shiner | Cyprinidae | *Notemigonus crysoleucas* |
| Emerald Shiner | Cyprinidae | *Notropis atherinoides* |
| Spottail Shiner (SPTS) | Cyprinidae | *Notropis hudsonius* |
| Rosyface Shiner | Cyprinidae | *Notropis rubellus* |
| Sand Shiner | Cyprinidae | *Notropis stramineus* |
| Northern Redbelly Dace | Cyprinidae | *Phoxinus eos* |
| Bluntnose Minnow (BNM) | Cyprinidae | *Pimephales notatus* |
| Fathead Minnow | Cyprinidae | *Pimephales promelas* |
| Longnose Dace | Cyprinidae | *Rhinichthys cataractae* |
| Creek Chub | Cyprinidae | *Semotilus atromaculatus* |
| Banded Killifish | Fundulidae | *Fundulus diaphanus* |
| Burbot | Gadidae | *Lota lota* |
| Brook Stickleback | Gasterosteidae | *Culea inconstans* |
| Yellow Bullhead | Ictaluridae | *Amerius natalis* |
| Longnose Gar (LNG) | Lepisosteidae | *Lepisosteus osseus* |
| Rainbow Darter (RBD) | Percidae | *Etheostoma caeruleum* |
| Johnny Darter (JD) | Percidae | *Etheostoma nigrum* |
| Yellow Perch | Percidae | *Perca flavescens* |
| Logperch | Percidae | *Percina caprodes* |
| Blackside Darter | Percidae | *Percina maculata* |
| Sea Lamprey | Petromyzontidae | *Petromyzon marinus* |
| Steelhead (RBT) | Salmonidae | *Oncorhynchus mykiss* |
| Chinook Salmon (CHK) | Salmonidae | *Oncorhynchus tshawytscha* |
| Central Mudminnow | Umbridae | *Umbra limi* |

*abbreviations created for focus species.

Table 2. Strata location and substrate description in Muskegon River study area 2001-2002 (Ichthyological Associates 1991).

| Stratum | Distance (m) downstream of Croton Dam | Substrate / Habitat |
|---|---|---|
| 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<br>and<br>11,582 to 15,240 | Run and 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 |

*indicates primarily salmonid spawning habitat.

Table 3. Functional group categories and abbreviations used to classify all 43 species collected in the lower Muskegon River 2001-2002. Functional group categories were primarily based on those used by Poff and Allan (1995).

| Group | Abbreviation |
|---|---|
| Trophic Guild | |
| Herbivore-detrivore | herb-detrivore |
| Omnivore | omnivore |
| General invertivore | gen invert |
| Surface/water column invertivore | s/wc invertivore |
| Benthic invertivore | benthic invert |
| Piscivore* | piscivore |
| Parasite | parasite |
| | |
| Current velocity preference | |
| Fast | fast |
| Moderate | mod |
| Slow-none | slow |
| General | gen |
| | |
| Substrate preference | |
| Rubble (rocky, gravel) | rub |
| Sand | sand |
| Silt | silt |
| General | gen |
| | |
| Tolerance to siltation | |
| High | high |
| Medium | med |
| Low | low |
| | |
| Thermal Guild | |
| Warm-water | warm |
| Cool-water | cool |
| Cold-water | cold |

*Includes fishes feeding on crayfish.

Table 4. Mean lengths (± 1 SE) of focus species by season for lower Muskegon River 2001-2002.

| | Summer 2001 | | Fall 2001 | | Spring 2002 | | Summer 2002 | |
|---|---|---|---|---|---|---|---|---|
| SPECIES | Mean | SE | Mean | SE | Mean | SE | Mean | SE |
| Rainbow Darter | 5.1 | 0.9 | * | * | 4.4 | 0.6 | 4.9 | 0.1 |
| Johnny Darter | 4.8 | 0.2 | 5.3 | 0.2 | 5.3 | 0.2 | 5.5 | 0.1 |
| Common Shiner | 8.4 | 0.3 | 11.4 | 0.5 | 8.0 | 0.5 | 6.1 | 0.1 |
| Hornyhead Chub | 6.2 | 0.2 | 6.1 | 0.7 | 7.1 | 0.5 | 6.3 | 0.2 |
| Bluntnose Minnow | 5.3 | 0.1 | * | * | 6.5 | 0.4 | 5.6 | 0.4 |
| Spottail Shiner | 3.8 | 0.2 | * | * | 4.7 | 0.2 | 4.8 | 1.8 |
| Rockbass | 10.6 | 3.3 | 5.2 | 0.9 | 5.5 | 1.0 | 7.8 | 0.6 |
| Smallmouth Bass | 5.0 | 0.5 | 8.0 | 0.3 | 7.2 | 0.2 | 4.9 | 0.6 |
| Redhorse | 4.3 | 0.2 | 15.3 | 0.4 | 5.5 | 0.2 | 7.6 | 0.3 |
| White Sucker | 5.4 | 0.4 | 5.9 | 0.2 | 6.4 | 0.5 | 5.7 | 1.1 |
| Steelhead | 4.9 | 0.1 | 10.2 | 0.4 | 3.1 | 0.1 | 4.0 | 0.1 |
| Chinook Salmon | 8.5 | 0.0 | x | x | 5.3 | 0.1 | x | x |
| Mottled Sculpin | 4.3 | 0.3 | 10.5 | 0.0 | 7.4 | 0.5 | 3.6 | 0.3 |
| Longnose Gar | * | * | x | x | x | x | 7.2 | 0.2 |

* indicates species was collected during season but not measured.
x indicates species was not collected during season.

Table 5. Mean relative abundance for all species by stratum, collected by electrofishing in the lower Muskegon River 2001-2002.

| Common Name | Stratum 1 | Stratum 2 | Stratum 3 | Stratum 4 | Stratum 5 | All Strata |
|---|---|---|---|---|---|---|
| Bowfin | 0.00 | * | 0.00 | 0.00 | 0.00 | * |
| Brook Silversides | 0.01 | 0.00 | 0.02 | 0.00 | 0.00 | 0.01 |
| White Sucker | 5.58 | 1.29 | 10.19 | 2.72 | 2.30 | 4.41 |
| Northern Hogsucker | 0.02 | 0.02 | 0.05 | 0.05 | 0.56 | 0.14 |
| Redhorse | 12.24 | 1.15 | 0.74 | 0.44 | 2.54 | 3.42 |
| Rock Bass | 1.20 | 1.07 | 3.13 | 1.42 | 4.00 | 2.16 |
| Green Sunfish | 0.02 | 0.00 | 0.01 | 0.00 | 0.03 | 0.01 |
| Pumpkinseed | 0.03 | 0.01 | 0.06 | 0.00 | 0.07 | 0.04 |
| Bluegill | 0.18 | 0.14 | 0.01 | 0.03 | 0.08 | 0.09 |
| Smallmouth Bass | 0.30 | 0.65 | 2.53 | 1.40 | 2.26 | 1.43 |
| Largemouth Bass | 0.94 | 0.14 | 0.13 | 2.03 | 2.02 | 1.05 |
| White Crappie | * | * | 0.00 | 0.00 | 0.00 | * |
| Black Crappie | * | 0.00 | 0.00 | 0.00 | 0.00 | * |
| Mottled Sculpin | 2.02 | 1.81 | 0.65 | 0.82 | 0.16 | 1.09 |
| Central Stoneroller | * | 0.00 | 0.01 | 0.00 | 0.00 | * |
| Spotfin Shiner | 0.01 | 0.00 | 0.01 | 0.00 | 0.00 | * |
| Common Carp | 0.00 | 0.00 | 0.02 | 0.00 | 0.02 | 0.01 |
| Common Shiner | 3.73 | 24.61 | 13.56 | 27.89 | 19.70 | 17.90 |
| Hornyhead Chub | 11.39 | 22.11 | 32.36 | 21.29 | 15.04 | 20.44 |
| Golden Shiner | 0.01 | * | 0.01 | 0.00 | 0.01 | 0.01 |
| Emerald Shiner | 0.78 | 0.13 | 0.49 | 0.98 | 2.57 | 0.99 |
| Spottail Shiner | 7.25 | 8.74 | * | 0.00 | 1.21 | 4.30 |
| Rosyface Shiner | 0.68 | 0.17 | 0.58 | 0.04 | 0.23 | 0.34 |
| Sand Shiner | 0.29 | 0.05 | 0.10 | 0.00 | 0.04 | 0.10 |
| Northern Redbelly Dace | 0.00 | 0.09 | 0.00 | 0.00 | 0.00 | 0.02 |
| Bluntnose Minnow | 2.41 | 0.82 | 0.76 | 2.33 | 0.05 | 1.28 |
| Fathead Minnow | 0.01 | 0.01 | 0.00 | 0.00 | 0.00 | * |
| Longnose Dace | 0.00 | 0.00 | 0.00 | 0.03 | 0.16 | 0.04 |
| Creek Chub | 0.04 | * | 0.00 | 0.00 | 0.00 | 0.01 |
| Banded Killifish | 0.00 | 0.00 | 0.01 | 0.03 | 0.00 | 0.01 |
| Burbot | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | * |
| Brook Stickleback | 0.39 | 0.14 | 0.03 | 0.00 | 0.00 | 0.11 |
| Yellow Bullhead | 0.01 | 0.05 | 0.00 | 0.00 | 0.02 | 0.01 |
| Longnose Gar | 0.00 | 0.00 | 2.08 | 0.07 | 0.08 | 0.44 |
| Rainbow Darter | 3.43 | 3.61 | 12.83 | 16.70 | 21.18 | 11.55 |
| Johnny Darter | 6.93 | 3.03 | 7.31 | 5.58 | 2.45 | 5.06 |
| Yellow Perch | 0.33 | 0.09 | 0.02 | 0.00 | 0.02 | 0.09 |

*indicates <0.01

Table 5.  Continued.

| Common Name | Stratum 1 | Stratum 2 | Stratum 3 | Stratum 4 | Stratum 5 | All Strata |
|---|---|---|---|---|---|---|
| Logperch | 0.06 | 0.01 | 0.05 | 0.00 | 0.00 | 0.02 |
| Blackside Darter | 0.08 | 0.05 | 0.50 | 0.44 | 2.28 | 0.67 |
| Sea Lamprey | 0.01 | 0.00 | 0.03 | 0.00 | 0.04 | 0.02 |
| Steelhead | 11.74 | 25.04 | 5.13 | 9.20 | 12.98 | 12.82 |
| Chinook | 5.37 | 4.97 | 5.96 | 6.53 | 7.88 | 6.14 |
| Central Mudminnow | 0.00 | 0.00 | 0.61 | 0.00 | 0.01 | 0.12 |
| Number of Species | 37 | 32 | 35 | 22 | 31 | 43 |

*indicates <0.01

Table 6. Mean relative abundance values for all species by season, collected by electrofishing in the lower Muskegon River 2001-2002.

| Common Name | Summer 2001 | Fall 2001 | Spring 2002 | Summer 2002 |
|---|---|---|---|---|
| Bowfin | 0.00 | 0.00 | * | 0.00 |
| Brook Silversides | 0.00 | 0.03 | 0.00 | 0.00 |
| White Sucker | 3.80 | 15.45 | 1.42 | 0.84 |
| Northern Hogsucker | 0.11 | 0.32 | 0.05 | 0.03 |
| Redhorse spp. | 2.97 | 1.98 | 0.73 | 6.22 |
| Rockbass | 1.87 | 2.51 | 0.53 | 1.53 |
| Green Sunfish | 0.04 | 0.00 | 0.00 | 0.01 |
| Pumpkinseed | 0.07 | 0.07 | 0.00 | 0.03 |
| Bluegill | 0.05 | 0.15 | 0.10 | 0.02 |
| Smallmouth Bass | 2.74 | 3.48 | 1.49 | 1.58 |
| Largemouth Bass | 1.81 | 0.08 | 0.03 | 1.67 |
| White Crappie | 0.00 | * | * | 0.00 |
| Black Crappie | 0.01 | * | * | * |
| Mottled Sculpin | 2.15 | 0.20 | 0.20 | 1.52 |
| Central Stoneroller | 0.00 | * | 0.00 | 0.01 |
| Spotfin Shiner | 0.01 | 0.00 | 0.00 | 0.01 |
| Common Carp | 0.00 | 0.03 | 0.00 | 0.01 |
| Common Shiner | 5.05 | 26.45 | 22.80 | 14.40 |
| Hornyhead Chub | 17.54 | 17.27 | 35.07 | 19.83 |
| Golden Shiner | 0.01 | 0.02 | 0.00 | * |
| Emerald Shiner | 0.69 | 2.18 | 0.72 | 0.02 |
| Spottail Shiner | 0.17 | 6.62 | 3.23 | 1.44 |
| Rosyface Shiner | 0.00 | 0.00 | 0.35 | 1.16 |
| Sand Shiner | 0.17 | 0.07 | 0.06 | 0.09 |
| Northern Redbelly Dace | 0.04 | 0.01 | 0.01 | 0.01 |
| Bluntnose Minnow | 3.01 | 0.58 | 0.46 | 0.71 |
| Fathead Minnow | 0.01 | 0.00 | 0.00 | * |
| Longnose Dace | 0.08 | 0.03 | 0.01 | * |
| Creek Chub | 0.00 | * | 0.02 | 0.00 |
| Banded Killifish | 0.02 | 0.00 | 0.00 | 0.02 |
| Burbot | 0.00 | 0.00 | 0.00 | * |
| Brook Stickleback | 0.09 | 0.09 | 0.19 | 0.02 |
| Yellow Bullhead | 0.01 | 0.03 | * | 0.01 |
| Longnose Gar | 2.27 | 0.00 | 0.00 | 0.60 |
| Rainbow Darter | 21.68 | 4.01 | 4.36 | 17.00 |
| Johnny Darter | 10.42 | 2.87 | 3.24 | 5.20 |
| Yellow Perch | 0.22 | 0.02 | 0.04 | 0.05 |

Table 6. Continued.

| Common Name | Summer 2001 | Fall 2001 | Spring 2002 | Summer 2002 |
|---|---|---|---|---|
| Logperch | 0.10 | * | 0.00 | 0.01 |
| Blackside Darter | 1.61 | 0.31 | 0.19 | 0.46 |
| Sea Lamprey | 0.03 | 0.00 | 0.01 | 0.04 |
| Steelhead | 20.28 | 0.15 | 0.35 | 25.37 |
| Chinook salmon | 0.08 | 0.00 | 24.34 | 0.02 |
| Central Mudminnow | 0.80 | 0.00 | 0.00 | 0.02 |
| Number of Species | 35 | 32 | 30 | 39 |

*value <0.01

Table 7. Functional group membership for all 43 species collected in the lower Muskegon River 2001-2002.

| Common Name | Trophic Guild | Current Preference | Substrate Preference | Tolerance | Temperature Guild |
|---|---|---|---|---|---|
| Bowfin | piscivore | slow | silt | high | warm |
| Brook Silversides | s/wc invertivore | slow | gen | low | warm |
| White Sucker | benthic invert | gen | gen | high | cool |
| Northern Hogsucker | benthic invert | fast | rub | low | warm |
| Redhorse spp. | benthic invert | mod | rub | low | warm |
| Rockbass | piscivore | mod | rub | low | warm |
| Green Sunfish | gen invert | slow | gen | high | warm |
| Pumpkinseed | gen invert | slow | gen | med | warm |
| Bluegill | gen invert | slow | gen | high | warm |
| Smallmouth Bass | piscivore | mod | rub | low | warm |
| Largemouth Bass | piscivore | slow | gen | med | warm |
| White Crappie | piscivore | slow | silt | high | cool |
| Black Crappie | piscivore | slow | gen | med | cool |
| Mottled Sculpin | benthic invert | gen | rub | low | cold |
| Central Stoneroller | herb-detrivore | mod | rub | med | warm |
| Spotfin Shiner | s/wc invertivore | slow | gen | high | warm |
| Common Carp | omnivore | slow | gen | high | warm |
| Common Shiner | omnivore | gen | gen | med | cool |
| Hornyhead Chub | omnivore | mod | rub | low | warm |
| Golden Shiner | omnivore | slow | silt | high | warm |
| Emerald Shiner | s/wc invertivore | slow | sand | med | warm |
| Spottail Shiner | omnivore | slow | sand | low | warm |
| Rosyface Shiner | gen invert | fast | rub | low | cool |
| Sand Shiner | omnivore | mod | sand | med | warm |
| Northern Redbelly Dace | omnivore | slow | silt | med | cool |
| Bluntnose Minnow | omnivore | gen | gen | high | warm |
| Fathead Minnow | omnivore | slow | silt | high | warm |
| Longnose Dace | benthic invert | fast | rub | low | cool |
| Creek Chub | omnivore | mod | rub | high | warm |
| Banded Killifish | s/wc invertivore | slow | gen | low | warm |
| Burbot | piscivore | mod | rub | med | cool |
| Brook Stickleback | gen invert | slow | silt | low | cool |
| Yellow Bullhead | omnivore | slow | gen | med | warm |
| Longnose Gar | piscivore | slow | gen | med | warm |
| Rainbow Darter | benthic invert | fast | rub | low | warm |
| Johnny Darter | benthic invert | slow | sand | high | warm |
| Yellow Perch | piscivore | slow | gen | med | cool |
| Logperch | benthic invert | mod | rub | low | warm |
| Blackside Darter | s/wc invertivore | mod | rub | med | warm |
| Sea Lamprey | parasite | mod | rub | low | cool |
| Steelhead | gen invert | mod | rub | low | cold |
| Chinook | gen invert | mod | rub | low | cold |
| Central Mudminnow | benthic invert | slow | silt | high | cool |

Table 8. Mean relative abundance of each functional group in each stratum for all 43 species collected in the lower Muskegon River 2001-2002.

| Functional Group | Stratum 1 | Stratum 2 | Stratum 3 | Stratum 4 | Stratum 5 | ALL |
|---|---|---|---|---|---|---|
| Trophic Guild | | | | | | |
| herbivore-detrivore | * | x | 0.01 | x | x | * |
| omnivore | 25.13 | 56.48 | 46.83 | 51.51 | 36.09 | 43.21 |
| general invertivore | 18.40 | 30.47 | 11.78 | 15.79 | 21.28 | 19.54 |
| surface/water column invertivore | 0.88 | 0.18 | 1.03 | 1.46 | 4.84 | 1.68 |
| benthic invertivore | 30.28 | 10.92 | 32.42 | 26.33 | 29.36 | 25.87 |
| piscivore | 2.80 | 1.95 | 7.90 | 4.91 | 8.38 | 5.19 |
| parasite | 0.01 | x | 0.03 | x | 0.04 | 0.02 |
| Current Preference | | | | | | |
| fast | 4.13 | 3.80 | 13.45 | 16.82 | 22.13 | 12.07 |
| moderate | 42.73 | 55.10 | 50.55 | 40.72 | 47.05 | 47.23 |
| slow-none | 16.91 | 12.57 | 10.83 | 8.71 | 8.61 | 11.53 |
| general | 13.74 | 28.53 | 25.17 | 33.75 | 22.21 | 24.68 |
| Substrate Preference | | | | | | |
| rubble (rocky,gravel) | 48.58 | 60.66 | 64.55 | 58.35 | 69.30 | 60.29 |
| sand | 15.25 | 11.94 | 7.91 | 6.56 | 6.27 | 9.58 |
| silt | 0.40 | 0.24 | 0.65 | x | 0.02 | 0.26 |
| general | 13.27 | 27.15 | 26.90 | 35.09 | 24.41 | 25.36 |
| Tolerance to siltation | | | | | | |
| high | 15.19 | 5.30 | 18.93 | 10.65 | 4.97 | 11.01 |
| medium | 6.22 | 25.21 | 16.96 | 31.41 | 26.79 | 21.32 |
| low | 56.10 | 69.48 | 64.11 | 57.94 | 68.24 | 63.17 |
| Temperature | | | | | | |
| cold-water | 19.12 | 31.82 | 11.74 | 16.54 | 21.02 | 20.05 |
| cool-water | 10.74 | 26.38 | 25.02 | 30.68 | 22.46 | 23.06 |
| warm-water | 47.64 | 41.80 | 63.23 | 52.78 | 56.52 | 52.39 |
| Total Species per stratum | 37 | 32 | 35 | 22 | 31 | 43 |

* indicates <0.01
x indicates functional group not collected.

Table 9. Mean relative abundance of each functional group during each season for all 43 species collected in the lower Muskegon River 2001-2002.

| Functional Group | Summer 2001 | Fall 2001 | Spring 2002 | Summer 2002 | Number of species |
|---|---|---|---|---|---|
| Trophic Guild | | | | | |
| herbivore-detrivore | 0.00 | * | 0.00 | 0.01 | 1 |
| omnivore | 26.00 | 51.08 | 61.65 | 36.53 | 11 |
| general invertivore | 20.60 | 0.45 | 25.32 | 26.63 | 7 |
| surface/water column invertivore | 2.33 | 2.52 | 0.91 | 0.51 | 5 |
| benthic invertivore | 42.12 | 24.86 | 10.01 | 30.84 | 9 |
| piscivore | 8.93 | 6.09 | 2.10 | 5.44 | 9 |
| parasite | 0.03 | 0.00 | * | 0.04 | 1 |
| Current Preference | | | | | |
| fast | 21.87 | 4.36 | 4.77 | 18.19 | 4 |
| moderate | 47.40 | 25.76 | 62.78 | 55.17 | 13 |
| slow-none | 16.73 | 12.19 | 7.57 | 9.16 | 22 |
| general | 14.01 | 42.68 | 24.88 | 17.47 | 4 |
| Substrate Preference | | | | | |
| rubble (rocky,gravel) | 71.25 | 30.26 | 67.70 | 74.79 | 17 |
| sand | 11.45 | 11.75 | 7.26 | 6.76 | 4 |
| silt | 0.94 | 0.11 | 0.20 | 0.06 | 7 |
| general | 16.36 | 42.88 | 24.84 | 18.39 | 15 |
| Tolerance | | | | | |
| high | 18.13 | 19.10 | 5.25 | 6.84 | 13 |
| medium | 11.94 | 29.21 | 23.85 | 17.36 | 13 |
| low | 69.92 | 36.69 | 70.91 | 75.80 | 17 |
| Temperature | | | | | |
| cold-water | 22.51 | 0.34 | 24.89 | 26.91 | 3 |
| cool-water | 10.11 | 42.05 | 24.83 | 16.55 | 12 |
| warm-water | 67.37 | 42.60 | 50.28 | 56.54 | 28 |
| Number of species | 35 | 32 | 30 | 39 | 43 |

*indicates value <0.01

Table 10. Results of MANOVA tests for significant variation ($p<0.05$) in the fish community (using species relative abundance data for each site) among strata for each season and among all seasons in the lower Muskegon River 2001-2002.

| Test | Summer 2001 | Fall 2001 | Spring 2002 | Summer 2002 | Seasons |
|---|---|---|---|---|---|
| Wilks' Lambda | | | | | |
| Value | 0.01 | 0.02 | 0.01 | 0.03 | 0.08 |
| Approx F | 1.78 | 1.49 | 1.69 | 1.32 | 9.82 |
| Num DF | 56.00 | 56.00 | 56.00 | 56.00 | 42.00 |
| Den DF | 48.85 | 48.85 | 41.07 | 48.85 | 300.38 |
| Probability | 0.02 | 0.08 | 0.04 | 0.16 | <0.01 |
| Pillai's Trace | | | | | |
| Value | 2.58 | 2.32 | 2.44 | 2.21 | 1.53 |
| Approx F | 1.95 | 1.49 | 1.45 | 1.32 | 7.65 |
| Num DF | 56.00 | 56.00 | 56.00 | 56.00 | 42.00 |
| Den DF | 60.00 | 60.00 | 52.00 | 60.00 | 309.00 |
| Probability | 0.01 | 0.07 | 0.09 | 0.15 | <0.01 |

Num DF = Numerator Degrees of Freedom
Den DF = Denominator Degrees of Freedom

Table 11. Results of MANOVA tests for significant variation (p<0.05) in physical habitat variables (temperature and current velocity only) among strata for each season and among all seasons in the lower Muskegon River 2001-2002.

| Test | Summer 2001 | Fall 2001 | Spring 2002 | Summer 2002 | Seasons |
|---|---|---|---|---|---|
| Wilks' Lambda | | | | | |
| Value | 0.21 | 0.42 | 0.17 | 0.04 | 0.04 |
| Approx F | 2.11 | 5.41 | 2.27 | 5.98 | 158.37 |
| Num DF | 20.00 | 20.00 | 20.00 | 20.00 | 6.00 |
| Den DF | 70.60 | 362.46 | 63.97 | 70.60 | 226.00 |
| Probability | 0.01 | <0.01 | 0.01 | <0.01 | <0.01 |
| | | | | | |
| Pillai's Trace | | | | | |
| Value | 1.06 | 0.69 | 1.19 | 1.27 | 1.21 |
| Approx F | 1.73 | 4.64 | 1.87 | 2.22 | 57.97 |
| Num DF | 20.00 | 20.00 | 20.00 | 20.00 | 6.00 |
| Den DF | 96.00 | 448.00 | 88.00 | 96.00 | 228.00 |
| Probability | 0.04 | <0.01 | 0.03 | 0.01 | <0.01 |

Num DF = Numerator Degrees of Freedom
Den DF = Denominator Degrees of Freedom

Table 12. Results of Hierarchical Cluster Analysis showing variance explained by individual clusters as well as cumulative variance ($R^2$). Values were calculated for each season using focus species relative abundance data in the lower Muskegon River 2001-2002.

| Season | Number of Clusters | Cluster Distance | Variance Explained | $R^2$ |
|---|---|---|---|---|
| Summer 2001 | | | | |
| | 1 | 11.09 | 0.20 | 0.20 |
| | 2 | 8.93 | 0.16 | 0.36 |
| | 3* | 6.86 | 0.12 | 0.48 |
| | 4 | 5.84 | 0.11 | 0.59 |
| | 5 | 4.78 | 0.09 | 0.68 |
| | 6 | 4.37 | 0.08 | 0.76 |
| | 7 | 3.22 | 0.06 | 0.81 |
| | 8 | 2.91 | 0.05 | 0.87 |
| | 9 | 2.41 | 0.04 | 0.91 |
| | 10 | 2.30 | 0.04 | 0.95 |
| | 11 | 1.70 | 0.03 | 0.98 |
| | 12 | 1.05 | 0.02 | 1.00 |
| | Total Sum of Squares | 55.47 | | |
| Fall 2001 | | | | |
| | 1 | 11.49 | 0.25 | 0.25 |
| | 2 | 9.41 | 0.20 | 0.45 |
| | 3* | 7.57 | 0.16 | 0.61 |
| | 4 | 4.36 | 0.09 | 0.71 |
| | 5 | 3.44 | 0.07 | 0.78 |
| | 6 | 2.94 | 0.06 | 0.85 |
| | 7 | 2.36 | 0.05 | 0.90 |
| | 8 | 1.75 | 0.04 | 0.93 |
| | 9 | 1.60 | 0.03 | 0.97 |
| | 10 | 1.11 | 0.02 | 0.99 |
| | 11 | 0.30 | 0.01 | 1.00 |
| | Total Sum of Squares | 46.34 | | |

*indicates number of clusters used for analysis.

Table 12. Continued.

| Season | Number of Clusters | Cluster Distance | Variance Explained | $R^2$ |
|---|---|---|---|---|
| Spring 2002 | | | | |
| | 1 | 12.49 | 0.26 | 0.26 |
| | 2 | 8.62 | 0.18 | 0.44 |
| | 3* | 6.60 | 0.14 | 0.58 |
| | 4 | 4.79 | 0.10 | 0.68 |
| | 5 | 3.97 | 0.08 | 0.77 |
| | 6 | 3.56 | 0.07 | 0.84 |
| | 7 | 2.01 | 0.04 | 0.88 |
| | 8 | 1.64 | 0.03 | 0.92 |
| | 9 | 1.38 | 0.03 | 0.95 |
| | 10 | 1.05 | 0.02 | 0.97 |
| | 11 | 0.97 | 0.02 | 0.99 |
| | 12 | 0.44 | 0.01 | 1.00 |
| | Total Sum of Squares | 47.52 | | |
| Summer 2002 | | | | |
| | 1 | 12.51 | 0.25 | 0.25 |
| | 2 | 8.90 | 0.18 | 0.43 |
| | 3* | 6.21 | 0.12 | 0.55 |
| | 4 | 5.93 | 0.12 | 0.67 |
| | 5 | 4.45 | 0.09 | 0.76 |
| | 6 | 4.06 | 0.08 | 0.84 |
| | 7 | 2.97 | 0.06 | 0.90 |
| | 8 | 1.54 | 0.03 | 0.93 |
| | 9 | 1.15 | 0.02 | 0.95 |
| | 10 | 0.99 | 0.02 | 0.97 |
| | 11 | 0.70 | 0.01 | 0.99 |
| | 12 | 0.66 | 0.01 | 1.00 |
| | Total Sum of Squares | 50.07 | | |

*indicates number of clusters used for analysis.

Table 13. Results of Pair-wise correlation analysis of focus species for each season (significant correlations only) in the lower Muskegon River 2001-2002.

| Season | Species | Correlate | $R^2$ | Significance |
|---|---|---|---|---|
| Summer 2001 | SMB | RB | 0.76 | * |
| N=30 | WS | SPTS | 0.54 | * |
| | RBT | BNM | -0.51 | * |
| | MS | RH | 0.44 | 0.02 |
| | SMB | JD | 0.43 | 0.02 |
| | BNM | HHC | 0.41 | 0.02 |
| | WS | BNM | 0.40 | 0.03 |
| | LNG | RB | 0.37 | 0.04 |
| | Mean | | 0.48 | |
| | | | | |
| Fall 2001 | | | | |
| N=30 | SMB | RB | 0.56 | * |
| | JD | MS | 0.54 | * |
| | RH | RBD | 0.48 | 0.01 |
| | HHC | CS | -0.46 | 0.01 |
| | BNM | JD | 0.43 | 0.02 |
| | SPTS | HHC | -0.41 | 0.02 |
| | WS | RBD | 0.36 | 0.05 |
| | Mean | | 0.46 | |

*indicates <0.01

Table 13. Continued.

| Season | Species | Correlate | $R^2$ | Significance |
|---|---|---|---|---|
| Spring 2002 | | | | |
| N=28 | BNM | RBD | 0.56 | * |
| | CHK | CS | -0.44 | 0.02 |
| | MS | BNM | 0.54 | * |
| | | RBT | 0.52 | * |
| | | SMB | 0.41 | 0.03 |
| | | JD | 0.39 | 0.04 |
| | RBT | SMB | 0.47 | 0.01 |
| | | BNM | 0.42 | 0.02 |
| | RH | HHC | 0.45 | 0.02 |
| | SMB | JD | 0.61 | * |
| | WS | BNM | 0.67 | * |
| | | RBD | 0.62 | * |
| | Mean | | 0.51 | |
| Summer 2002 | | | | |
| N=30 | LNG | RB | 0.59 | * |
| | | CS | 0.55 | * |
| | RBT | CS | -0.52 | * |
| | | HHC | -0.41 | 0.03 |
| | | RBD | -0.39 | 0.03 |
| | RH | BNM | 0.44 | 0.01 |
| | WS | SMB | 0.69 | * |
| | | RH | 0.41 | 0.02 |
| | Mean | | 0.50 | |
| | Overall Mean | | 0.49 | |

*indicates <0.01

Table 14. Mean relative abundance values (± 1 SE) for each season and overall for focus species collected in the lower Muskegon River 2001-2002. Significant variation at spatial and temporal scales based on Kruskal-Wallis tests is also noted.

| | Summer 2001 | Fall 2001 | Spring 2002 | Summer 2002 | Overall |
|---|---|---|---|---|---|
| Species | Mean ± 1 SE | Mean ± 1 SE | Mean ± 1 SE | Mean ± 1 SE | Mean ± 1 SE |
| RBD† | 17.67 ± 3.36 | 3.28 ± 0.87 | 4.44 ± 1.55 | 10.17 ± 2.84 | 8.96 ± 1.30 |
| JD† | 12.23 ± 2.08 | 6.11 ± 1.08 | 5.30 ± 1.84 | 6.67 ± 2.21 | 7.62 ± 0.95 |
| CS† | 3.14 ± 1.21 | 15.29 ± 4.78 | 23.49 ± 5.28 | 10.56 ± 2.03 | 12.94 ± 1.94 |
| HHC† | 14.24 ± 3.21 | 36.31 ± 4.13 | 26.21 ± 3.91 | 16.19 ± 3.06 | 23.19 ± 1.95 |
| BNM | 2.77 ± 0.90 | 0.72 ± 0.18 | 1.06 ± 0.51 | 0.99 ± 0.28 | 1.39 ± 0.28 |
| SPTS† | 0.16 ± 0.16 | 16.99 ± 5.20 | 5.77 ± 2.41 | 1.00 ± 0.56 | 5.98 ± 1.56 |
| RB | 1.46 ± 2.95 | 2.48 ± 0.81 | 0.70 ± 0.24 | 1.41 ± 0.53 | 1.53 ± 0.29 |
| SMB† | 3.39 ± 0.81 | 6.28 ± 1.54 | 2.13 ± 0.60 | 1.49 ± 1.26 | 3.34 ± 0.51 |
| RH | 4.35 ± 2.17 | 2.64 ± 1.18 | 0.41 ± 0.21 | 8.77 ± 2.92 | 4.10 ± 1.02 |
| WS† | 5.75 ± 2.31 | 7.80 ± 2.36 | 1.73 ± 0.71 | 0.76 ± 0.27 | 4.05 ± 0.89 |
| RBT† | 30.26 ± 4.61 | 1.39 ± 0.55 | 1.40 ± 0.59 | 39.03 ± 5.02 | 18.30 ± 2.32 |
| CHK† | 0.03 ± 0.02 | <0.01 | 26.61 ± 3.87 | 0.03 ± 0.02 | 6.33 ± 1.38 |
| MS† | 3.33 ± 1.38 | 0.70 ± 0.19 | 0.76 ± 0.51 | 2.65 ± 0.63 | 1.88 ± 0.42 |
| LNG† | 1.23 ± 0.72 | <0.01 | x | 0.27 ± 0.29 | 0.38 ± 0.20 |

*indicates <0.01
†indicates significant variation (p<0.05) among seasons.
x indicates species not collected in season.

Table 15. Mean relative abundance values for each stratum for focus species collected in the lower Muskegon River 2001-2002.

| Season | Species | Stratum 1 | Stratum 2 | Stratum 3 | Stratum 4 | Stratum 5 |
|---|---|---|---|---|---|---|
| Summer 2001 | | | | | | |
| | RBD† | 9.81 | 8.83 | 23.01 | 18.78 | 53.28 |
| | JD | 10.24 | 16.24 | 20.28 | 8.92 | 2.33 |
| | CS | 0.66 | 3.69 | 0.76 | 17.45 | 3.97 |
| | HHC | 10.90 | 19.35 | 23.20 | 13.15 | 3.53 |
| | BNM | 4.37 | 1.66 | 1.58 | 6.64 | 0.09 |
| | SPTS | 0.42 | x | x | x | x |
| | RB | 0.81 | 1.30 | 5.37 | 0.48 | 0.22 |
| | SMB | 1.99 | 4.71 | 7.10 | 1.32 | 1.60 |
| | RH† | 11.62 | x | x | x | 0.66 |
| | WS | 13.06 | 2.02 | 1.43 | 1.69 | 0.36 |
| | RBT | 29.14 | 41.03 | 6.87 | 29.16 | 33.05 |
| | CHK† | x | x | x | 0.24 | 0.07 |
| | MS† | 6.98 | 1.17 | 2.09 | 1.79 | 0.18 |
| | LNG† | x | x | 8.32 | 0.42 | 0.68 |
| Fall 2001 | | | | | | |
| | RBD | 2.51 | 1.34 | 4.61 | 0.85 | 9.64 |
| | JD | 7.11 | 4.66 | 6.88 | 9.97 | 3.90 |
| | CS | 8.90 | 20.94 | 19.09 | 45.83 | 1.09 |
| | HHC | 34.97 | 40.49 | 27.52 | 20.74 | 47.14 |
| | BNM | 0.90 | 0.56 | 0.83 | 1.75 | x |
| | SPTS† | 30.98 | 18.78 | x | x | x |
| | RB | 0.86 | 1.46 | 3.85 | 4.26 | 6.97 |
| | SMB | 8.05 | 2.77 | 6.90 | 0.34 | 11.67 |
| | RH | 1.61 | 2.79 | 0.15 | x | 8.97 |
| | WS† | 2.08 | 2.84 | 30.12 | 15.25 | 8.67 |
| | RBT | 0.86 | 2.83 | x | x | 1.71 |
| | MS | 1.17 | 0.54 | 0.06 | 1.04 | 0.25 |

† indicates significant variation ($p<0.05$) at stratum-level for season.
x indicates species not collected in stratum.

Table 15.  Continued.

| Season | Species | Stratum 1 | Stratum 2 | Stratum 3 | Stratum 4 | Stratum 5 |
|---|---|---|---|---|---|---|
| Spring 2002 | | | | | | |
| | RBD | 6.13 | 1.40 | 7.11 | 3.47 | 4.09 |
| | JD† | 12.02 | 1.29 | 1.95 | 2.79 | 1.12 |
| | CS† | 2.59 | 53.03 | 13.89 | 7.53 | 34.23 |
| | HHC† | 21.40 | 22.44 | 46.61 | 56.98 | 10.00 |
| | BNM | 2.55 | 0.41 | 0.09 | 0.17 | 0.07 |
| | SPTS† | 15.53 | 0.79 | 0.01 | x | x |
| | RB | 0.63 | 0.97 | 0.85 | 0.69 | 0.22 |
| | SMB | 4.07 | 1.06 | 1.44 | 2.14 | 0.11 |
| | RH† | 0.09 | 0.23 | 2.17 | x | x |
| | WS | 3.42 | 0.32 | 1.26 | 1.10 | 1.10 |
| | RBT† | 3.53 | 0.48 | x | x | 0.02 |
| | CHK | 26.14 | 17.54 | 24.51 | 24.78 | 48.94 |
| | MS | 1.92 | 0.06 | 0.13 | 0.38 | 0.10 |
| Summer 2002 | | | | | | |
| | RBD† | 1.68 | 5.27 | 18.05 | 42.15 | 20.68 |
| | JD | 11.30 | 2.25 | 6.01 | 8.51 | 3.63 |
| | CS | 6.73 | 8.62 | 21.28 | 13.22 | 14.20 |
| | HHC | 7.08 | 21.14 | 31.97 | 10.90 | 16.80 |
| | BNM | 1.64 | 0.54 | 1.12 | 1.09 | 0.14 |
| | SPTS | 1.44 | 0.04 | x | x | 3.39 |
| | RB | 0.50 | 1.86 | 3.24 | 3.02 | 0.43 |
| | SMB | 0.54 | 5.54 | 1.19 | 0.18 | 0.89 |
| | RH | 19.36 | 3.54 | 0.57 | 2.01 | x |
| | WS | 0.55 | 1.24 | 0.28 | x | 0.43 |
| | RBT | 46.15 | 45.47 | 13.53 | 18.10 | 39.02 |
| | CHK | x | x | 0.11 | x | 0.08 |
| | MS | 3.04 | 4.49 | 0.47 | 0.84 | 0.34 |
| | LNG | x | x | 2.18 | x | x |

† indicates significant variation ($p<0.05$) at stratum-level for season.
x indicates species not collected in stratum.

Table 16. Mean values (± 1 SE) of physical habitat variables by stratum and season for the lower Muskegon River 2001-2002. Temperature (°C) and current velocity (m $sec^{-1}$) were measured at all sites for all seasons; percent hard substrate, % woody debris, and % vegetation were measured at all sites once for the study or in previous studies (Godby et al. 2007). Significance of variation among strata and seasons was determined using Kruskal-Wallis tests.

| Season | Habitat Variable | Stratum 1 | | Stratum 2 | | Stratum 3 | | Stratum 4 | | Stratum 5 | | Overall | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Summer 2001 | | Mean | ± 1 SE | Mean | ± 1 SE | Mean | ± 1 SE | Mean | ± 1 SE | Mean | ± 1 SE | Mean | ± 1 SE |
| | Temperature*† | 21.9 | 0.3 | 22.8 | 0.3 | 24.3 | 0.5 | 23.1 | 0.1 | 22.6 | 0.2 | 22.7 | 0.2 |
| | Current Velocity*† | 0.19 | 0.04 | 0.27 | 0.04 | 0.16 | 0.04 | 0.14 | 0.09 | 0.36 | 0.05 | 0.23 | 0.02 |
| Fall 2001 | | | | | | | | | | | | | |
| | Temperature*† | 10.4 | 0.3 | 9.2 | 0.3 | 10.6 | 0.3 | 10.8 | 0.8 | 13.5 | 0.0 | 10.5 | 0.3 |
| | Current Velocity† | 0.38 | 0.24 | 0.26 | 0.04 | 0.28 | 0.07 | 0.18 | 0.09 | 0.51 | 0.07 | 0.34 | 0.17 |
| Spring 2002 | | | | | | | | | | | | | |
| | Temperature*† | 12.5 | 0.5 | 14.0 | 0.0 | 15.5 | 0.3 | 15.5 | 0.5 | 14.3 | 0.3 | 13.8 | 0.3 |
| | Current Velocity† | 0.57 | 0.14 | 0.77 | 0.14 | 0.46 | 0.06 | 0.39 | 0.25 | 1.01 | 0.12 | 0.66 | 0.07 |
| Summer 2002 | | | | | | | | | | | | | |
| | Temperature*† | 21.4 | 0.0 | 21.8 | 0.0 | 23.3 | 0.2 | 23.2 | 0.1 | 21.2 | 0.2 | 21.9 | 0.1 |
| | Current Velocity*† | 0.21 | 0.05 | 0.29 | 0.05 | 0.18 | 0.02 | 0.15 | 0.10 | 0.39 | 0.05 | 0.24 | 0.03 |
| Summer 2000 | | | | | | | | | | | | | |
| | % Hard Substrate* | 66.27 | 5.59 | 55.00 | 8.62 | 32.00 | 10.90 | 36.50 | 1.50 | 68.50 | 6.51 | 56.63 | 4.23 |
| | % Woody Debris* | 2.82 | 1.17 | 3.11 | 1.70 | 12.00 | 3.54 | 9.00 | 9.00 | 0.00 | 0.00 | 4.17 | 1.10 |
| Fall 2002 | | | | | | | | | | | | | |
| | % Vegetation | 35.25 | 6.25 | 31.49 | 11.00 | 30.83 | 9.92 | 27.50 | 14.20 | 8.00 | 2.13 | 29.38 | 4.41 |

*indicates significant variation ($p<0.05$) among strata.
†indicates significant variation ($p<0.05$) among seasons.

Table 17. List of species and number of individuals collected by boom-electrofishing sampling at two sites in the lower Muskegon River, summer 2002 (Riseng et al. 2006).

| Common Name | Family | Scientific Name | Site 1 | Site 2 |
|---|---|---|---|---|
| Bowfin | Amiidae | *Amia calva* | 1 | x |
| Quillback Carpsucker | Catostomidae | *Carpiodes cyprinus* | x | 3 |
| White Sucker | Catostomidae | *Catostomus commersoni* | 30 | 4 |
| Northern Hogsucker | Catostomidae | *Hypentelium nigricans* | 7 | 17 |
| Silver Redhorse | Catostomidae | *Moxostoma anisurum* | 2 | x |
| Black Redhorse | Catostomidae | *Moxostoma duquesnei* | x | 1 |
| Golden Redhorse | Catostomidae | *Moxostoma erythrurum* | 20 | 56 |
| Shorthead redhorse | Catostomidae | *Moxostoma macrolepidotum* | 94 | 140 |
| Rockbass | Centrarchidae | *Ambloplites rupestris* | 2 | 2 |
| Smallmouth Bass | Centrarchidae | *Micropterus dolomieu* | 5 | 9 |
| Common Carp | Cyprinidae | *Cyprinus carpio* | 3 | x |
| Common Shiner | Cyprinidae | *Luxilus cornutus* | 13 | x |
| Hornyhead Chub | Cyprinidae | *Nocomis biguttatus* | 1 | 3 |
| River Chub | Cyprinidae | *Nocomis micropogon* | 3 | x |
| Rosyface Shiner | Cyprinidae | *Notropis rubellus* | x | 2 |
| Longnose Dace | Cyprinidae | *Rhinichthys cataractae* | x | 4 |
| Rainbow Darter | Pericdae | *Etheostoma caeruleum* | x | 1 |
| Yellow Perch | Pericdae | *Perca flavescens* | 1 | x |
| Walleye | Pericdae | *Sander vitreus* | 2 | 3 |
| Rainbow Trout | Salmonidae | *Oncorhynchus mykiss* | 18 | 23 |
| Brown trout | Salmonidae | *Salmo trutta* | 10 | 3 |

x indicates species not collected at site.

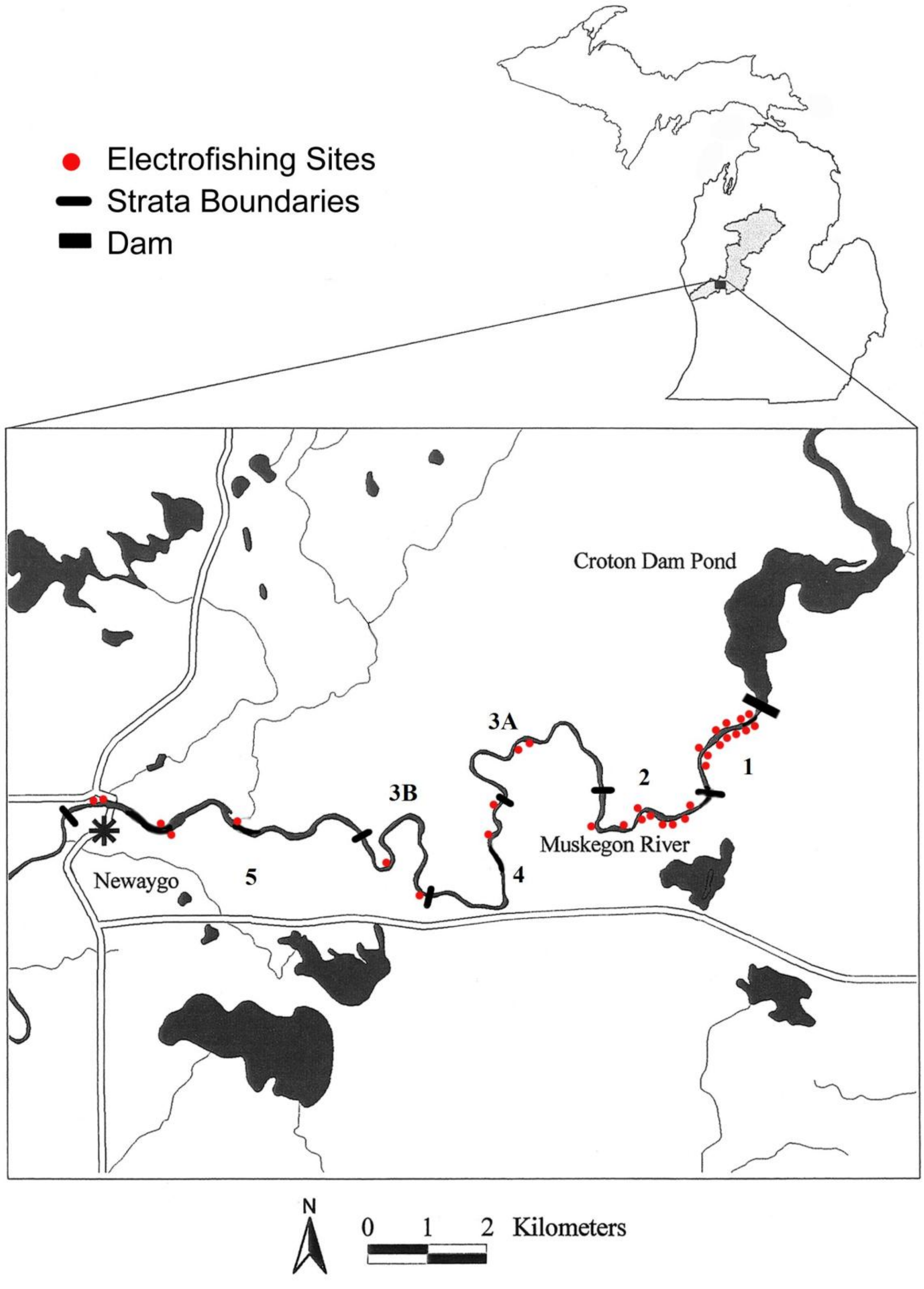


Figure 1. Map of the study area in the Muskegon River, Michigan, showing locations of 5 study strata and 30 fish and physical habitat sampling sites.

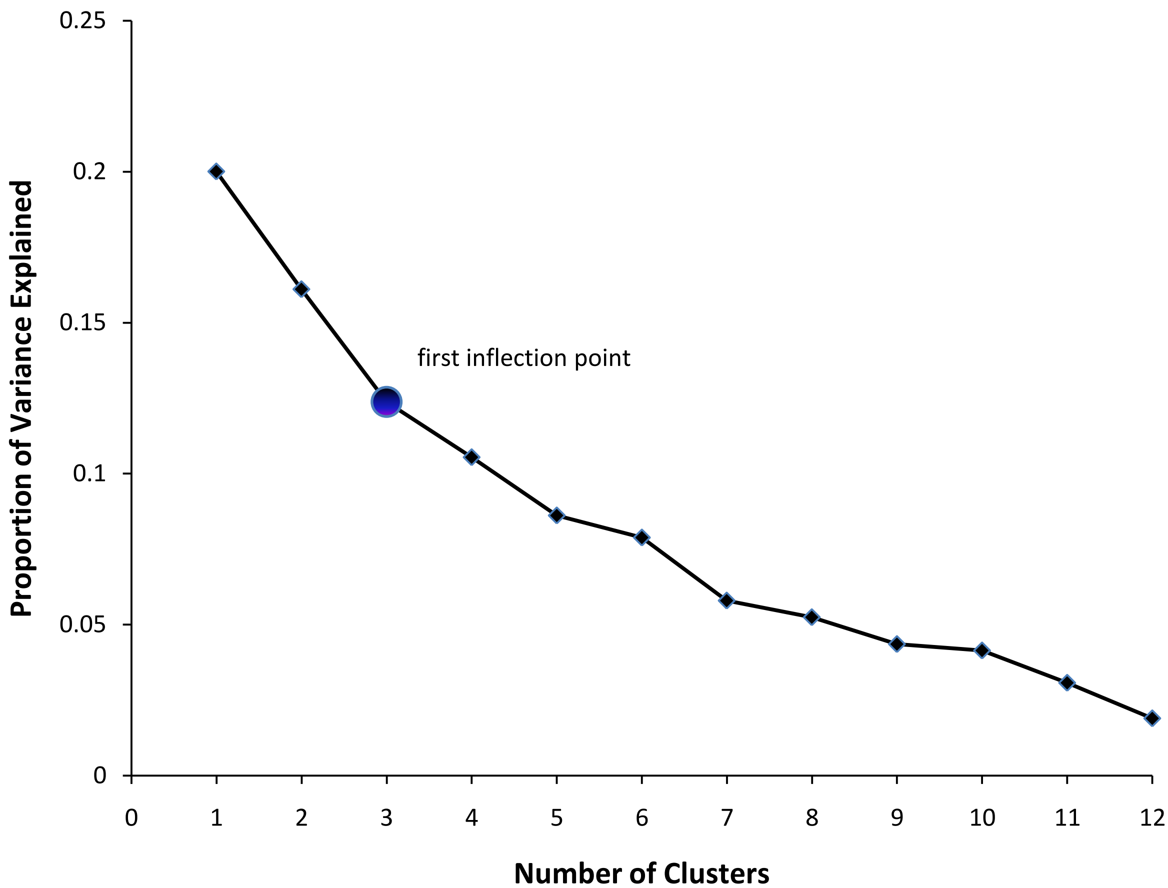


Figure 2. Profile curve indicating number of clusters and proportion of variance explained for hierarchical cluster analysis of focus species relative abundance in the lower Muskegon River, Summer 2001. $R^2$ = 0.48 for first 3 clusters.

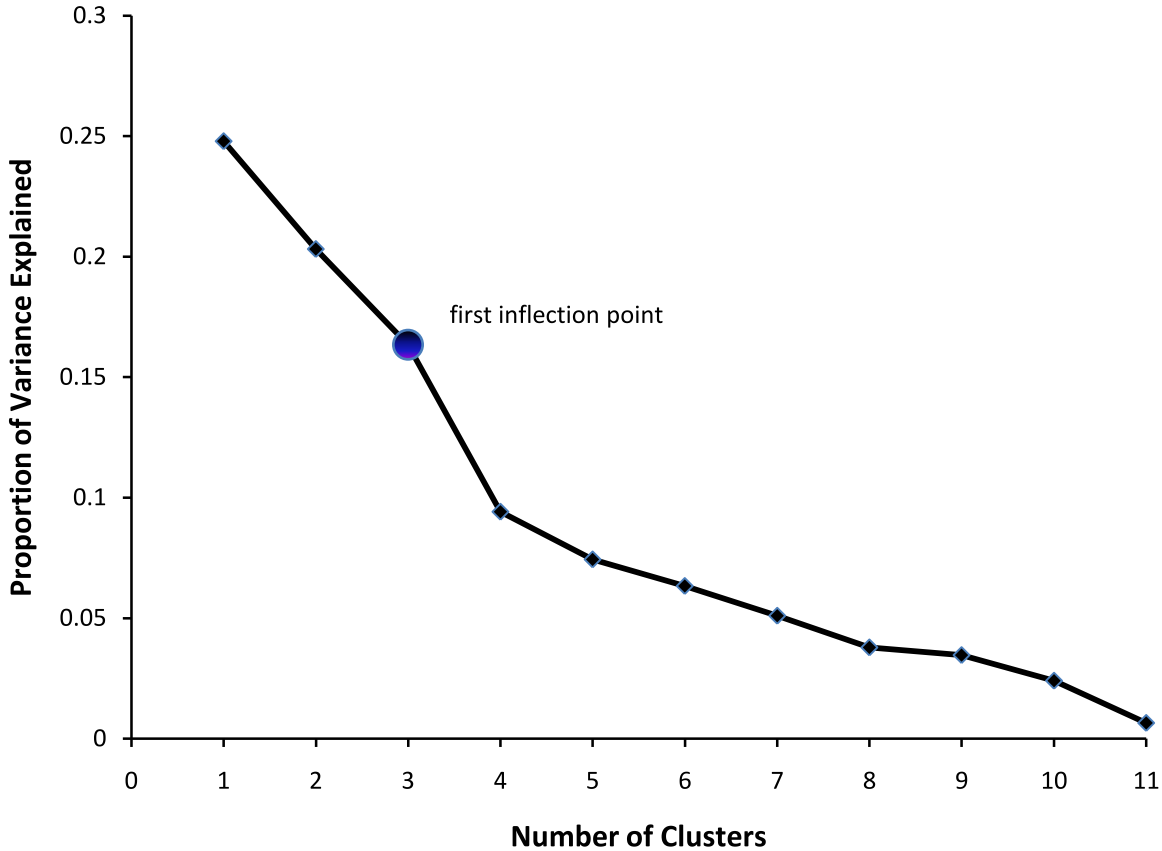


Figure 3. Profile curve indicating number of clusters and proportion of variance explained for hierarchical cluster analysis of focus species relative abundance in the lower Muskegon River, Fall 2001. $R^2$ = 0.61 for first 3 clusters.

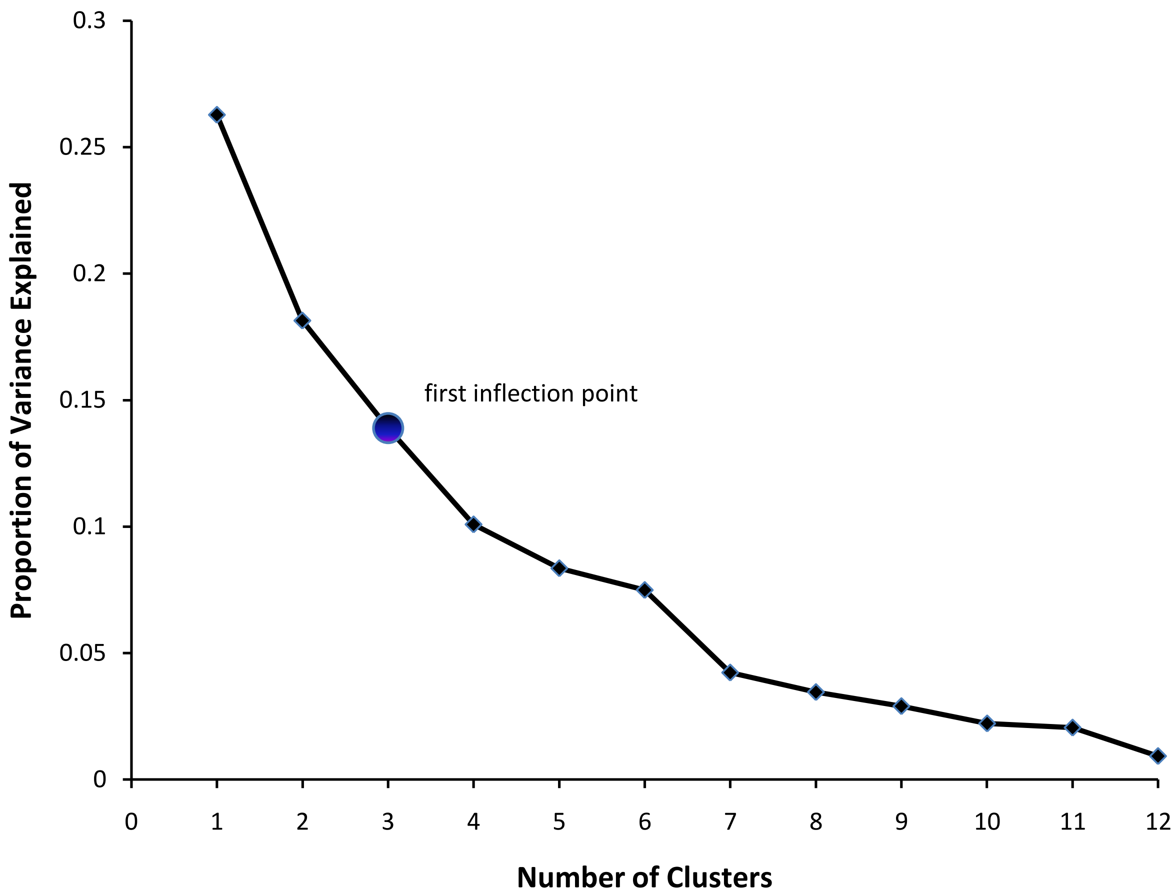


Figure 4. Profile curve indicating number of clusters and proportion of variance explained for hierarchical cluster analysis of focus species relative abundance in the lower Muskegon River, Spring 2002. $R^2 = 0.58$ for first 3 clusters.

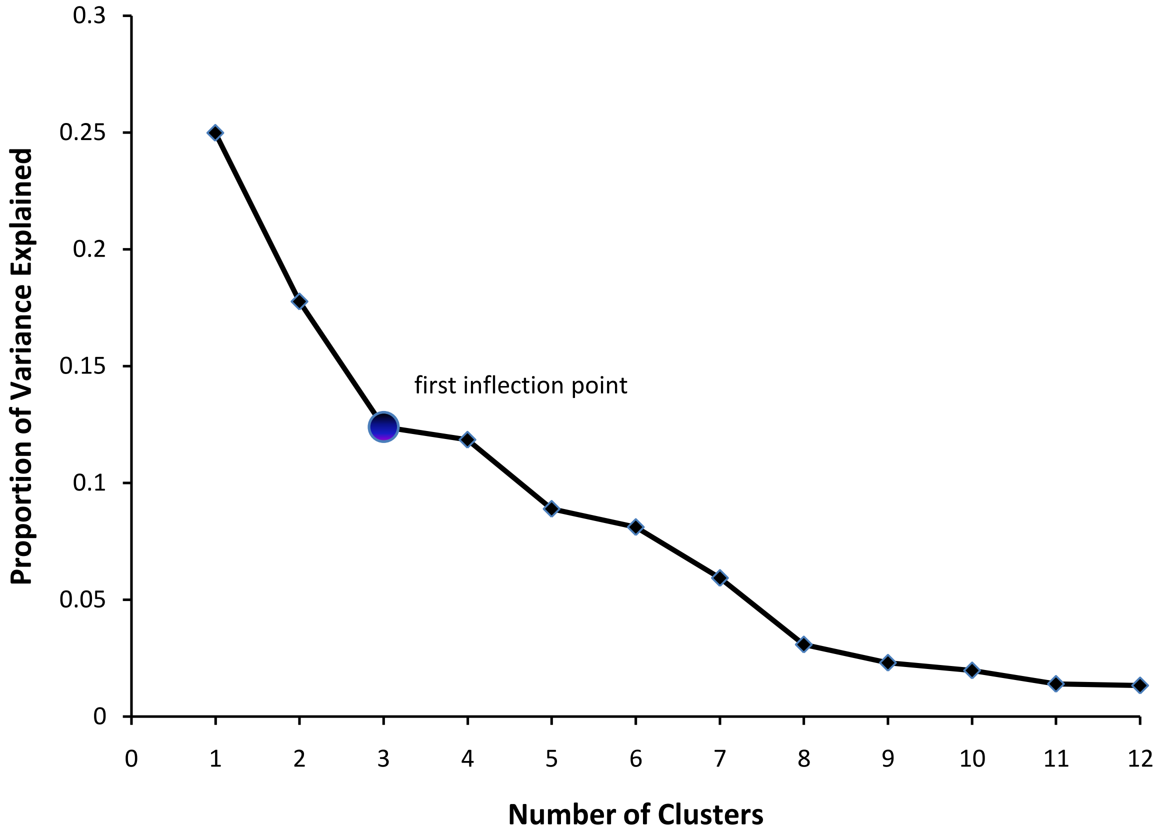


Figure 5. Profile curve indicating number of clusters and proportion of variance explained for hierarchical cluster analysis of focus species relative abundance in the lower Muskegon River, Summer 2002. $R^2 = 0.55$ for first 3 clusters.

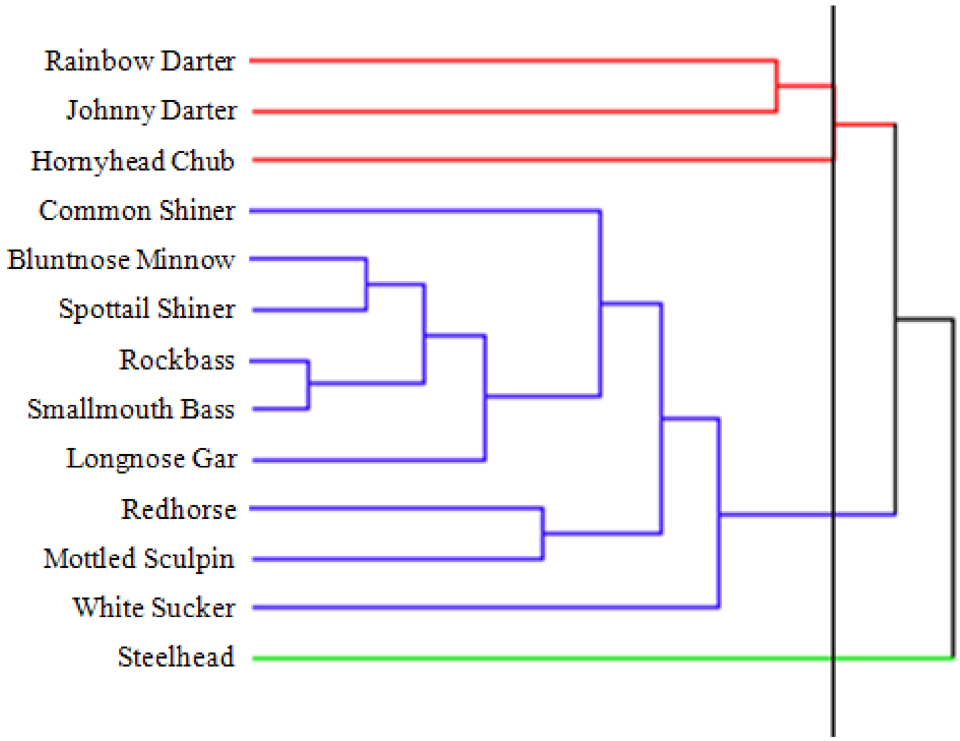


Figure 6. Dendrogram of hierarchical cluster analysis of focus species relative abundance in the lower Muskegon River, Summer 2001. Vertical line indicates cut-point for 3 clusters explaining 48% of the variation in relative density.

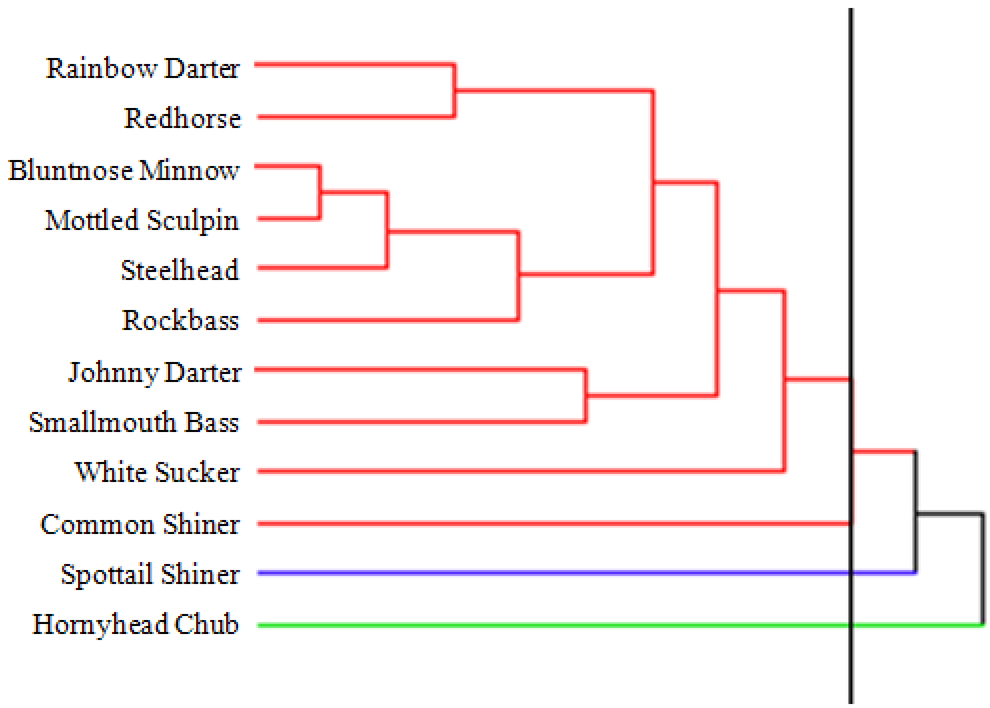


Figure 7. Dendrogram of hierarchical cluster analysis results of focus species relative abundance in the lower Muskegon River, Fall 2001. Vertical line shows cut-point for 3 clusters explaining 61% of the variation in relative density.

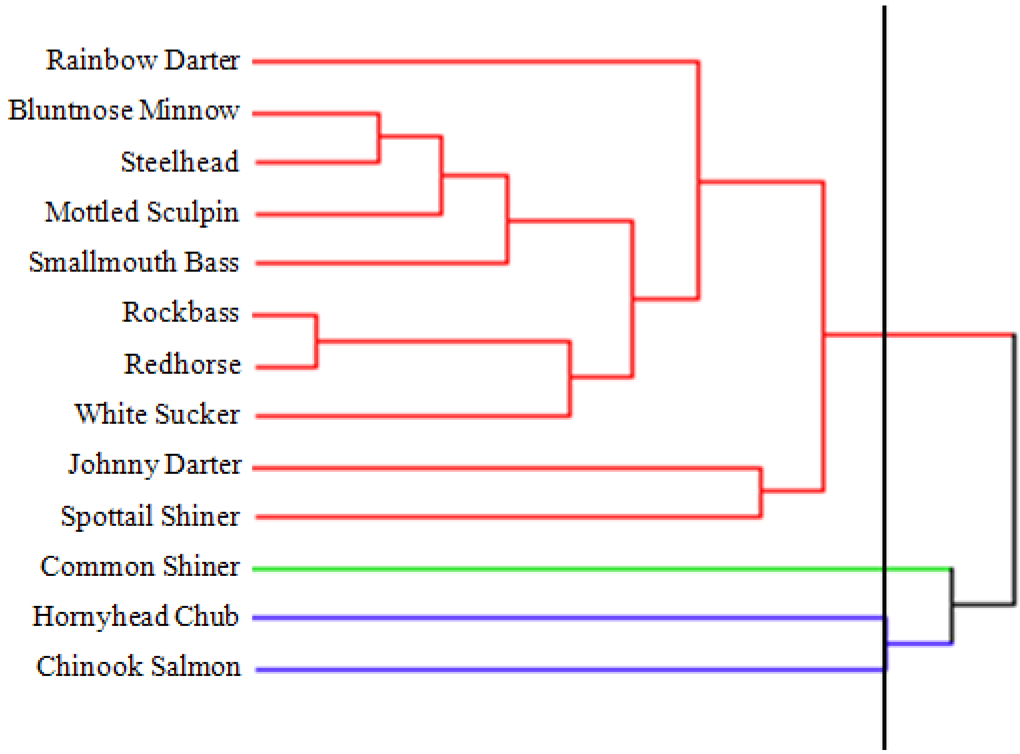


Figure 8. Dendrogram of hierarchical cluster analysis results of focus species relative abundance in the lower Muskegon River, Spring 2002. Vertical indicates cut-point for 3 clusters explaining 58% of the variation in relative density.

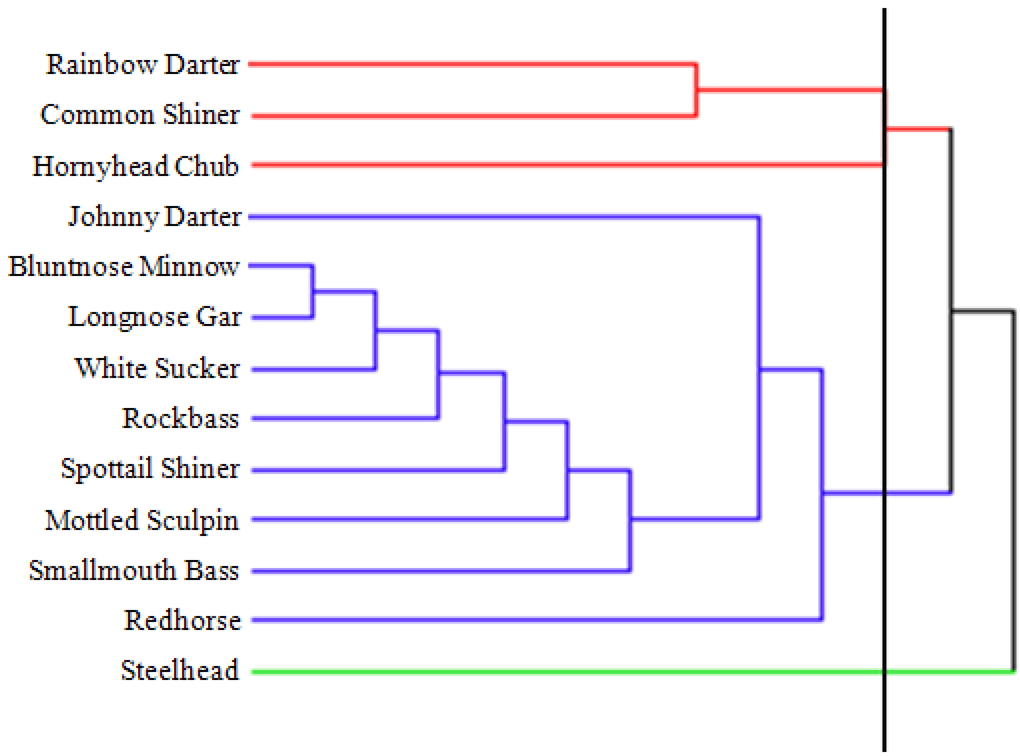


Figure 9. Dendrogram of hierarchical cluster analysis results of focus species relative abundance in the lower Muskegon River, Summer 2002. Vertical line indicates cut-point for 3 clusters explaining 55% of the variation in relative density.

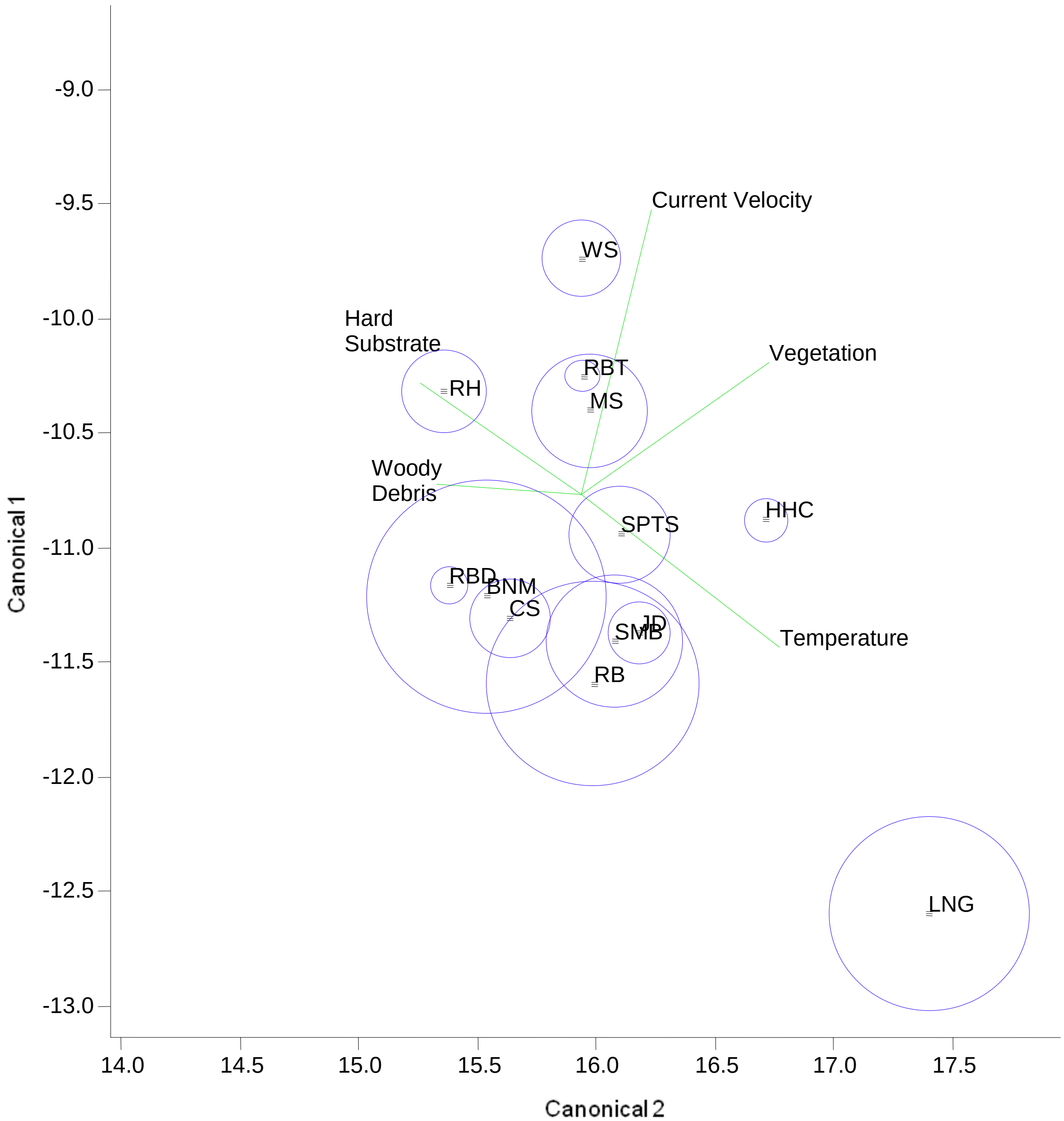


Figure 10. Canonical Correspondence Analysis (CCA) centroid plots for relative density of focus species and physical habitat factors, lower Muskegon River, Summer 2001. CCA indicated that physical habitat variables explained 53% of variation in species densities. Species abbreviations: RBD (Rainbow Darter), JD (Johnny Darter), CS (Common Shiner), HHC (Hornyhead Chub), BNM (Bluntnose Minnow), SPTS (Spottail Shiner), RB (Rockbass), SMB (Smallmouth Bass), RH (Redhorse), WS (White Sucker), RBT (Steelhead), CHK (Chinook Salmon), MS (Mottled Sculpin), LNG (Longnose Gar).

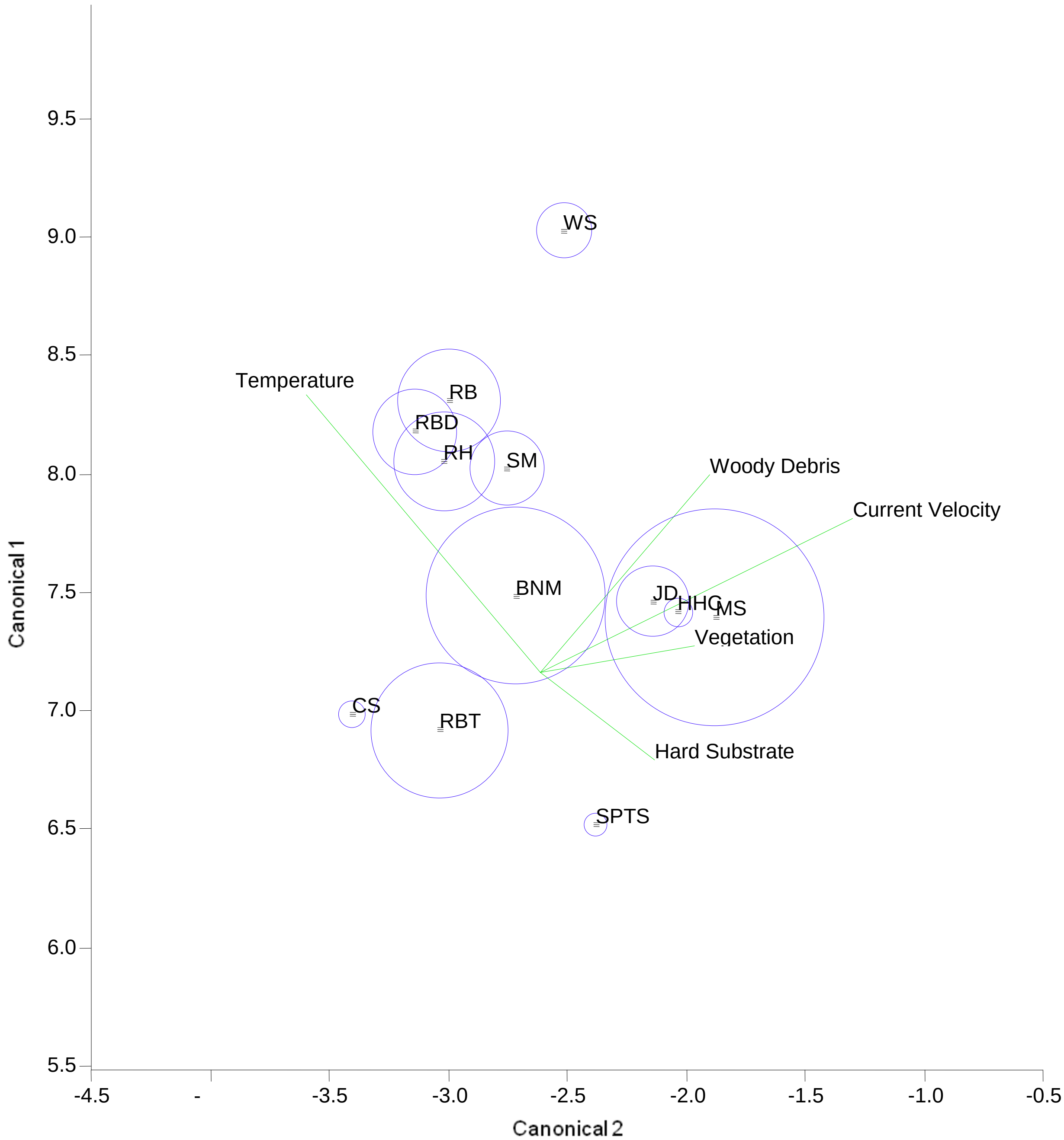


Figure 11. Canonical Correspondence Analysis (CCA) centroid plot for relative density of each focus species and physical habitat factors, lower Muskegon River, Fall 2001. CCA indicated that physical habitat variables explained 60% of variation in species densities. Refer to Figure 10 caption for species abbreviations.

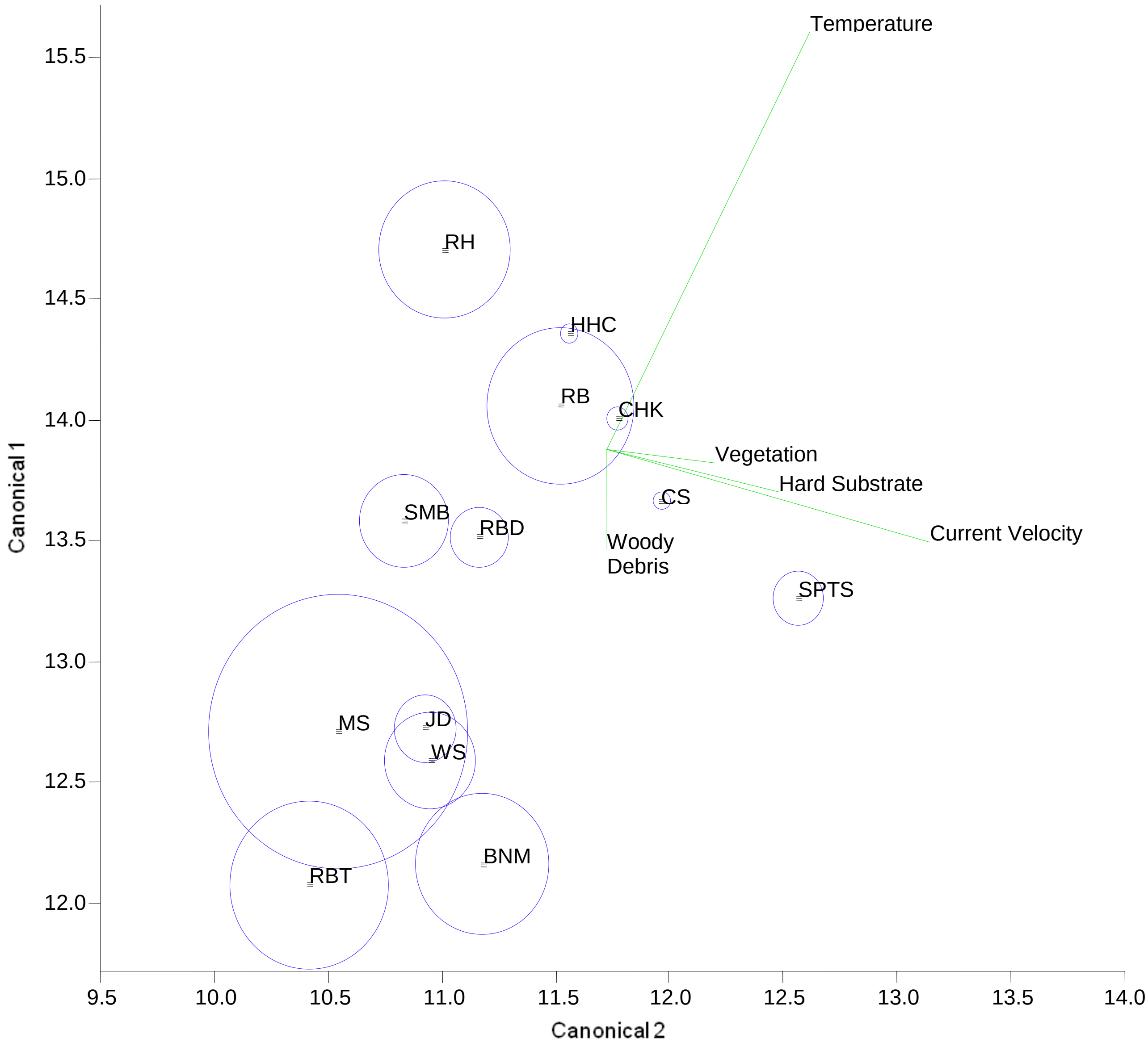


Figure 12. Canonical Correspondence Analysis (CCA) centroid plot for relative density of each focus species and physical habitat factors, lower Muskegon River, Spring 2002. CCA indicated that physical habitat variables explained 34% of variation in species densities. Refer to Figure 10 caption for species abbreviations.

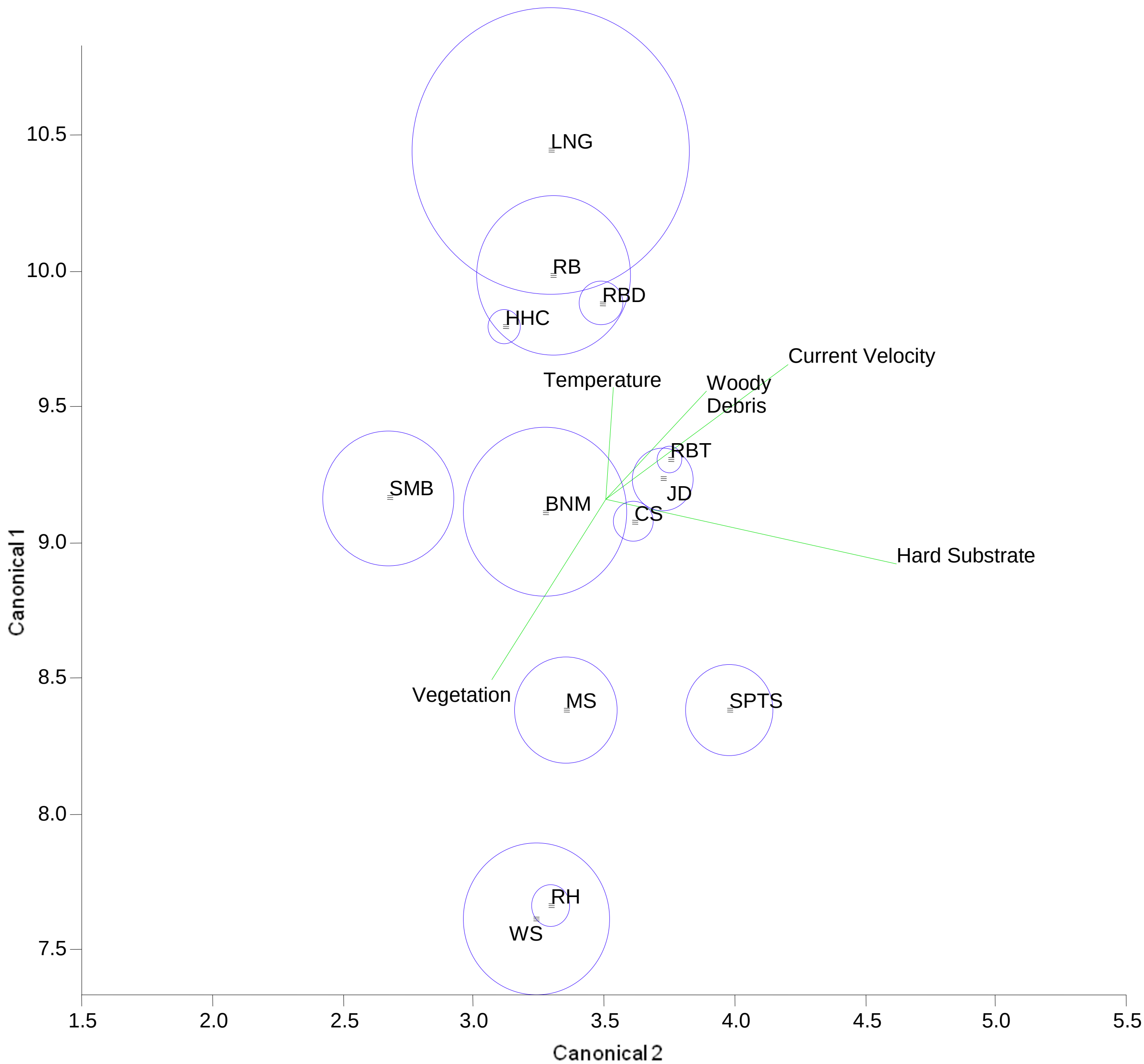


Figure 13. Canonical Correspondence Analysis (CCA) centroid plot for relative density of each focus species and physical habitat factors, lower Muskegon River, Summer 2002. CCA indicated that physical habitat variables explained 44% of variation in species densities. Refer to Figure 10 caption for species abbreviations.