An Assessment of the Current Distribution and Status of Freshwater Mussels (Unionidae) in the Muskegon River, Michigan

Prepared by:
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Michigan Natural Features Inventory
P.O. Box 30444
Lansing, MI 48909-7944

For:

Michigan Department of Environmental Quality, Coastal Zone Management Unit

November 2003

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Michigan DNR

MICHIGAN STATE UNIVERSITY EXTENSION

Michigan Natural Features Inventory

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INTRODUCTION

The consequences of human activities for North American rivers are apparent in many ways. Hydrologic regimes have been altered through the creation of impoundments, channelization and straightening of riverbeds, removal of vegetation, and urbanization (Poff et al. 1996). Changes in land cover, including deforestation and agricultural practices, have led to increased sediment, nutrient enrichment, chemical pollution, and modification of habitats in streams (Karr & Schlosser 1978, Clark et al. 1985, Richards & Host 1994, Roth et al. 1996). These local and landscape scale environmental changes have resulted in the serious threat of extinction for one-third of freshwater organisms (Heinz Center Report 2002).

Freshwater mussels (Mollusca: Unionidae) have been heavily impacted by the environmental degradation of rivers and streams (Bogan 1993, Williams & Neves 1995). Nearly half of native unionid species are extinct or listed as endangered, threatened, or special concern (Williams et al. 1993). In Michigan, there are 45 native unionid species, including 11 that are state-listed as endangered or threatened and eight that are considered of special concern. The decline of freshwater mussel populations, both in Michigan and across North America, has been attributed directly to increases in pollution and siltation, controls of natural flow regimes (e.g., impoundments), loss of fish hosts, and competition and fouling by exotic species (Bogan 1993). These threats are compounded by a lack of information on current distributions and population status, in part due to a historical lack of interest in unionids.

While some threats to freshwater mussels may be clear, conservation of mussels is not easy. Much remains to be known about the specific ecological requirements of most unionid species. In general, freshwater mussels need clean, well-oxygenated, flowing water and stable substrates (Strayer & Ralley 1993, Di Maio & Corkum 1995). However, detailed habitat requirements, like preferred substrate type, water velocity, and temperature, are largely unknown. Because mussels are largely sedentary, spending most of their lives buried in stream substrates, they cannot readily relocate if their habitat becomes degraded (Sibly & Calow 1986, Townsend 1989).

Several life history characteristics of unionids also complicate efforts to protect and manage these taxa. Mussels are long-lived, with many species attaining ages over 50 years (Bauer 1983, Heller 1990, Badra and Goforth 2001). Most species are also characterized by delayed maturity that can mask population declines. Thus, populations may be functionally extinct, with no young mussels present, before a decline is detected (Bogan 1993). Unionids also have a parasitic larval stage (i.e., glochidium) that requires a host, generally one or more fish species, for successful development (Kat 1984, Watters 1994). Consequently, loss of fish species can impede the successful reproduction of mussels (Kat & Davis 1984). Unfortunately, the identities of the host fishes for most mussel species remain unknown. Without knowing which fish species are critical for mussel communities, comprehensive and effective management to conserve these taxa cannot succeed.

Muskegon River Watershed, Michigan

In 1997, the Michigan Department of Natural Resources (MDNR), Fisheries Division, published the *Muskegon River Watershed Assessment* as a tool for the future study and management of the watershed (O'Neal 1997). Much of the information that follows about the basin is summarized from that report.

The Muskegon River watershed spans eight counties in north central Michigan (Figure 1). It is one of the largest rivers in Michigan, running over 200 miles long and draining over 2,300 square miles. The watershed has been greatly impacted by historical land use practices. Extensive logging took place throughout Michigan in the 1800's, during which the forests of the Muskegon River watershed were cleared and the river was used as a conduit for transporting logs. Today, much of the watershed has been reforested, and the extent of active anthropogenic land uses (primarily agriculture) in the watershed is moderate (i.e., <34% of the watershed area). Major developed areas in the watershed include Houghton Lake, Cadillac, Big Rapids, Newaygo and Muskegon.

Development has greatly influenced environmental quality in the Muskegon River watershed. There are over 200 listed environmental contamination sites in the watershed, including 10 that are on the national priority list (i.e., Superfund Sites). Chemical contaminants in the watershed include mercury, PCBs, chlordane, DDT, and DDE. These contaminants have led to public health advisories on fish consumption. Erosion and runoff have also increased nutrient enrichment and siltation above natural levels in the Muskegon River and its tributaries.

The natural hydrology of the Muskegon River has also been greatly altered, with 22% of the river currently impounded. While the majority of the Muskegon River is low gradient (<3 ft/mi), all of the high gradient (>10 ft/mi) and most of the moderate gradient reaches are impounded. Several large dams have been constructed on the river, four of which remain in operation (Figure 2). Reedsburg Dam, constructed in 1940 to create a wildlife flooding, is located in the headwaters. Rogers, Hardy, and Croton Dams are hydroelectric facilities with associated large impoundments located in the middle section of the river. Two other major dams on the river mainstem, Newaygo Dam and Big Rapids Dam, have been dismantled.

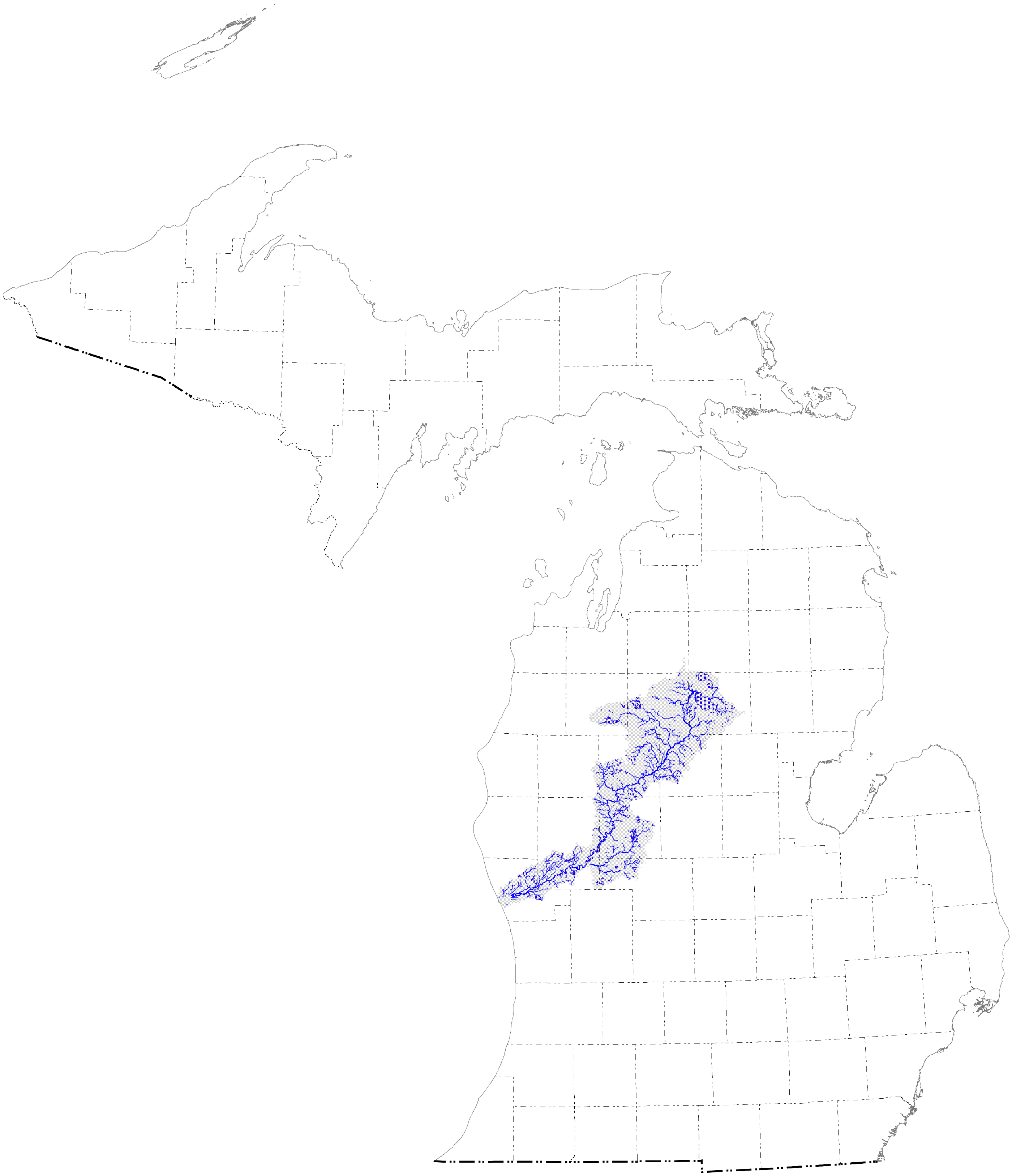

Figure 1. The Muskegon River watershed, Michigan.

The biota of the Muskegon River is intermediate between the coldwater assemblages typically found in northern Michigan and the warmwater assemblages of southern Michigan. The original fish community of the Muskegon River included 97 species (Bailey & Smith 1981). Five of the native species, Arctic grayling, lake herring, muskellunge, sauger, and white bass, are now considered to be extirpated from the basin. To date, about 112 fish species have been reported in the watershed, including five species listed as threatened and two species of special concern in the State of Michigan. Recent MDNR surveys reported 77 native fish species and 12 introduced species (O'Neal 1997).

Unionid status in the Muskegon River is less known. Noted malacologist Henry van der Schalie surveyed the mussel communities of many Michigan streams in the early to mid 1900's, including 24 sites in the Muskegon River watershed in a 1934 survey. He reported 18 unionid species from the Muskegon River, including the state-listed as endangered snuffbox mussel (*Epioblasma triquetra*) and four special concern mussel species: elktoe (*Alasmidonta marginata*), slippershell (*Alasmidonta viridis*), round pigtoe *(Pleurobema sintoxia*), and rainbow (*Villosa iris*) (van der Schalie 1941).

Muskegon River Initiative

As part of the Great Lakes Fishery Trust Muskegon River Initiative Program, Dr. R. Jan Stevenson (Michigan State University) and Dr. Michael Wiley (University of Michigan) initiated a project titled, *An Ecological Assessment of the Muskegon River Watershed to Solve and Prevent Environmental Problems* (Muskegon River Watershed Assessment Project, MRWAP). The project seeks to correlate changes in land use to indicators of ecological integrity, thereby developing quantified, predictive land use models. This comparative assessment of streams, lakes, and wetlands throughout the Muskegon River Watershed will aid in determining how sensitive these ecosystems are to human-generated disturbance. A major component of the project includes collecting field data describing fish, benthic macroinvertebrate, and periphyton communities at sites throughout the watershed. The group is also collecting geochemical and anthropogenic data for the watershed. These combined data will allow the MRWAP team to comprehensively investigate the impacts of human activities on the ecology of the Muskegon River watershed.

In the summer of 2002, Michigan Natural Features Inventory (MNFI) partnered with MRWAP to include an investigation of unionid community responses to human activities in the basin. This provided a unique opportunity to compare mussel distributions with basin environmental characteristics, including chemical (pH, conductivity, temperature), physical (land cover), and biological (fish and macroinvertebrate communities) factors. Using these data, we investigated responses of the mussel community to long-term, cumulative environmental changes in the watershed. We also evaluated the current status of the mussel community by using van der Schalie's 1934 survey as a baseline for comparison.

METHODS

Historical Data Compilation

An extensive literature and museum search was conducted to determine the historical distribution of mussels in the Muskegon River watershed. The primary source of historical mussel data was based on *Zoogeography of Naiads in the Grand and Muskegon Rivers of Michigan as Related to Glacial History* (van der Schalie 1941), in which data were reported for 24 sites in the Muskegon River watershed (Figure 3, Table 1). Historical data were also gathered from collections at the University of Michigan Museum of Zoology, Mollusk Division, and the Michigan State University Museum.

Current Mussel Distribution Surveys

We conducted freshwater mussel surveys from June through September, 2002. Mussel surveys were conducted at the MRWAP 2002 survey sites, supplemented with a few of the MRWAP 2001 sites. Locational descriptions, latitude, and longitude were provided by the MRWAP research partners and were used to define mussel survey sites. Mussel surveys were conducted at the nearest accessible stream area to the site described and locational information was verified using handheld GPS units (Garmin 12 XL). Sixty-one sites were surveyed, including 18 mainstem and 43 tributary sites (Figure 4, Tables 2 and 3).

Survey methods were flexible to accommodate the variable physical habitat conditions among sites (i.e., water depth, channel width, and substrates). At each site, timed surveys were conducted by searching for mussels along transects oriented parallel to stream flow. A band of approximately 0.8 m on either side of the transects (1.6 m total) was searched for each of 10 transects, providing a total search area of 128 m^2/site. For sites that were shallow (<1.0 m deep) and clear, transects were searched visually using glass bottom buckets while wading. Live mussels were marked with flags and processed following completion of each transect (Figure 5). For deeper or more turbid sites, SCUBA gear was used to allow surveyors to visually and tactilely search substrates within the transect areas (Figure 6). Mussels found during the search were placed in mesh bags carried by the divers and brought to the surface following completion of each transect. Processing of mussel samples included

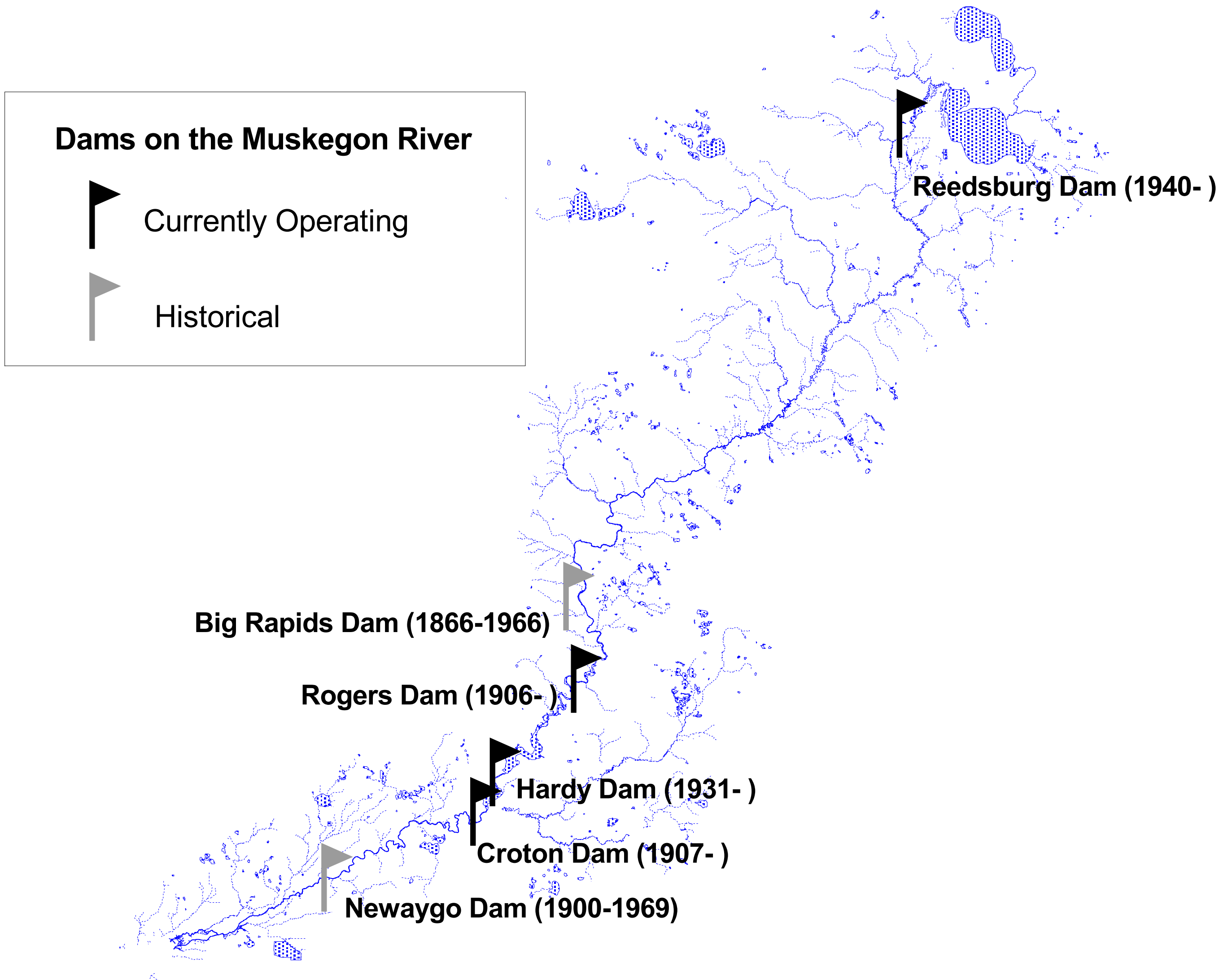

Figure 2. Current and historic locations of large dams on the Muskegon River, including dates of operation.

identification to species and length measurements (mm) along the longitudinal axis (i.e., anterior to posterior) with dial calipers for all individuals observed. After processing, all mussels were placed back into the substrate anterior end oriented down. Other species were noted when observed, especially other bivalves. Zebra mussel (*Dreissena polymorpha*) distribution was of particular interest, given that this species' negative effects on native mussel populations have been well documented (Ricciardi et al. 1998, Strayer 1999).

Mussel species richness values (MSR) were calculated for each site, tributary and mainstem river types, and the overall watershed. Site relative abundance measures were also calculated for each species. Density estimates were not calculated due to the general scarcity of live mussels in transects. Length measurements were combined for all sites to create length-frequency histograms for the most common species (i.e., species occurring at >8 sites).

Current vs. Historical Mussel Status

Fifteen of MNFI's 2002 sites were close enough to van der Schalie's 1934 sites to merit comparisons of data between the surveys (Figure 7, Table 4) (van der Schalie 1941). Because collection methods were unknown for the historical data, only species richness and relative abundance were calculated for the comparisons. Species richness and relative abundance measures were compared between van der Schalie's 1934 sites and MNFI's 2003 sites using a paired t-test.

Historical information was sought on environmental factors, such as water flow and water clarity, that are known to influence mussel populations so that we could assess changes in the mussel community. While general information concerning the watershed was found for several of these factors, only specific information regarding dam structures was identified. The 15 comparison sites

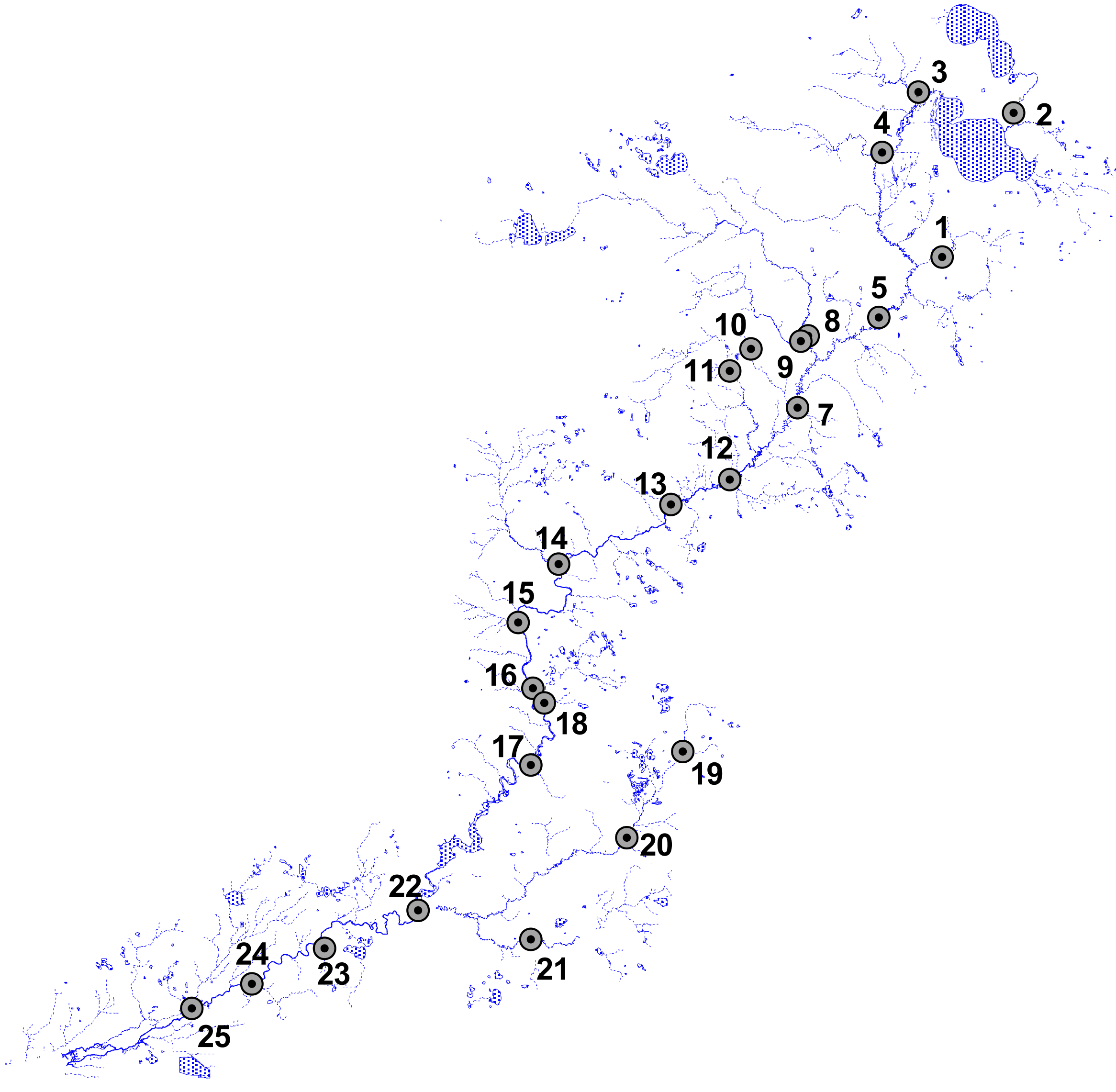

Figure 3. Historical (1934) mussel survey sites in the Muskegon River watershed reported by van der Schalie (1941).

were grouped into "always had a dam" (three sites), "dam added" (two sites), "dam removed" (two sites) and "no dam" (eight sites) classes and the change in mussel species richness (1934-2002) was evaluated using an analysis of variance (ANOVA) to determine whether changes in mussel communities were significantly related to dam locations in the Muskegon River.

Zebra mussel invasion of the watershed is another factor that may have caused changes in the mussel community. Therefore, changes in mussel community species richness were evaluated by comparing data from sites with and without zebra mussels using ANOVA. It was assumed that zebra mussels were not present in 1934 given that the introduction of this species was not detected in North America until the late 1980s.

Physicochemcial Habitat Measures and Analysis

Surveyors measured basic stream morphology features at each site. Channel depths were recorded along each transect, then averaged together to calculate mean site depth (cm). Wetted width was recorded every 10 m along the survey reach and was used to calculate a mean site width (m). Because wetted width and depth can vary depending on recent precipitation patterns, sites were grouped into more generalized depth and width classes for analysis. Width classes included narrow (<15 m), medium (15-30 m), and wide (> 30 m), and depth classes included shallow (<30 cm), medium (30-60 cm), and deep (>60 cm).

Substrates were visually assessed along each transect to provide estimates of percent composition by substrate types. Substrate typing followed the modified Wentworth classification of boulder (>256 mm diameter), cobble (64-256 mm diameter), pebble (32-64 mm diameter), gravel (4-32 mm diameter), sand (0.06-4 mm diameter), and clay/silt (<0.06 mm diameter) (Cummins 1962). To gain a perspective on substrate composition at each site, the substrate percentages were grouped into three classes.

Table 1. Historical (1934) mussel survey sites (VDS) in the Muskegon River watershed (van der Schalie 1941). Sites that were visited by MNFI during the summer of 2002 are indicated on the right.

VDS Site	Site Location	County	MNFI Site
1	Wolf Creek, 10 miles south of Houghton	Roscommon	
2	Between Higgins and Houghton Lake	Roscommon	27
3	Muskegon River, 3 miles below Houghton Lake	Roscommon	64
4	Muskegon River, 7 miles west of Houghton Lake	Missaukee	52
5	Muskegon River, ½ mile west of Leota	Clare	
7	Muskegon River, just west of Temple	Clare	54
8	Clam River, 7 miles east of Marion	Clare	70
9	West Branch Clam River, 5 miles east of Marion	Clare	18
10	Dishwash Creek, at Marion	Osceola	41
11	Middle Branch River, 2 miles south of Marion	Osceola	
12	Muskegon River, 11 miles south of Marion	Osceola	55
13	Muskegon River, 1 mile north east of Evart	Osceola	60
14	Muskegon River, below Hersey	Osceola	
15	Muskegon River, above Paris	Mecosta	
16	Muskegon River, at Big Rapids	Mecosta	59
17	Muskegon River, below Roger’s Dam	Mecosta	66
18	Ryan Creek, 2 miles southeast of Big Rapids	Mecosta	
19	East Branch Little Muskegon River, Mecosta	Mecosta	
20	Little Muskegon River, southwest of Altona	Mecosta	
21	Tamarack Creek at Howard City	Montcalm	1
22	Muskegon River, below Croton Dam	Newaygo	49
23	Muskegon River, 3 miles below Newaygo	Newaygo	50
24	Muskegon River, at Bridgeton	Newaygo	
25	Muskegon River, 10 miles northeast of Muskegon	Muskegon	51

The mixed substrate class was composed largely (>80%) of cobble, pebble, gravel, and sand in roughly equal parts. The small substrate class was dominated (>70%) by pebble, gravel, and sand. The soft substrate class was composed largely (>80%) of sand and silt.

ANOVA was used to determine whether MSR varied among width, depth, and substrate classes. A multiple analysis of variance (MANOVA) was used to determine whether individual species relative abundance measures differed among substrate types. An ANOVA was also used to determine whether species richness was different between stream types (i.e., tributary and mainstem).

Basic water chemistry data were collected at 57 sites. Sites were visited at the end of the field season (mid-October) over two consecutive days to maximize comparability of the data among sites. Temperature and dissolved oxygen were measured using a YSI 55 meter, and conductivity and pH were measured using an Oakton 10 Series meter. Correlation analysis was used to determine whether MSR was associated with temperature, dissolved oxygen, pH, and conductivity measurements for sites.

Fish Community Data and Analysis

MRWAP team members collected fish data at 52 of MNFI’s mussel survey sites during the summers of 2001 and 2002. The University of Michigan team, headed by Dr. Michael Wiley and Catherine Riseng, provided the data presented here. Sampling methodology varied between large river and tributary sites. For the tributary sites, surveys were conducted using a tow barge electroshocker along reaches varying between 50 and 200 m in length, depending on the width of the stream. The large river sites were sampled using two methods to achieve complete coverage. At each site, several 100 m edge reaches were sampled using a tow barge electroshocker and the central portion of the river was sampled with a boom shocker. At each site, two 10-minute electroshocking passes were conducted to complete the survey.

Regression analysis was used to determine whether MSR measures were related to fish species richness measures for the whole Muskegon River watershed and for tributary and mainstem stream types separately.

Table 2. Mussel survey sites in tributaries of the Muskegon River visited by MNFI during Summer 2002.

Site Number	Site Name	County	Substrate Class	Depth Class	Width Class
1	Tamarack Creek	Montcalm	Mixed	Medium	Narrow
2	Clam River	Missaukee	Mixed	Medium	Medium
3	Butterfield Creek	Missaukee	Soft	Medium	Narrow
4	Muskegon River, West Branch	Missaukee	Soft	Medium	Narrow
6	Butterfield Creek	Missaukee	Soft	Shallow	Narrow
7	Middle Branch River	Osceola	Mixed	Medium	Medium
8	Crocker Creek	Osceola	Soft	Shallow	Narrow
9	Hersey Creek, East Branch	Osceola	Soft	Medium	Narrow
10	Sand Creek	Newaygo	Small	Shallow	Narrow
12	Big Creek	Mecosta	Small	Shallow	Narrow
13	Handy Creek	Montcalm	Soft	Shallow	Narrow
14	Higginson Creek	Mecosta	Mixed	Shallow	Narrow
15	Thorn Creek	Osceola	Mixed	Shallow	Narrow
17	Middle Branch River, West Branch	Osceola	Mixed	Shallow	Narrow
18	Clam River, West Branch	Osceola	Mixed	Medium	Narrow
19	Stick Creek	Missaukee	Soft	Shallow	Narrow
20	Marks Creek	Missaukee	Soft	Medium	Narrow
21	Mosquito Creek	Muskegon	Small	Shallow	Narrow
22	Little Bear Creek	Muskegon	Soft	Shallow	Narrow
23	Little Whitefish Lake Creek	Montcalm	Soft	Medium	Narrow
24	Gilbert Creek	Mecosta	Soft	Medium	Narrow
25	Dye Creek	Mecosta	Soft	Medium	Narrow
26	Haymarsh Creek	Missaukee	Soft	Medium	Narrow
27	The Cut	Roscommon	Soft	Deep	Medium
28	Beebe Creek	Osceola	Soft	Shallow	Narrow
29	Olson Creek	Osceola	Soft	Shallow	Narrow
30	Hersey Creek	Osceola	Soft	Shallow	Narrow
31	Cold Spring Creek	Mecosta	Mixed	Shallow	Narrow
32	Quigley Creek	Mecosta	Soft	Medium	Narrow
33	Dalziel Creek	Mecosta	Small	Shallow	Narrow
34	Cat Creek	Osceola	Small	Shallow	Narrow
35	Blodgett Creek	Mecosta	Soft	Shallow	Narrow
36	Pogy Creek	Mecosta	Soft	Shallow	Narrow
37	Big Stone Creek	Osceola	Mixed	Shallow	Narrow
38	Sherlock Creek	Osceola	Soft	Shallow	Narrow
39	Lincoln Creek	Osceola	Mixed	Medium	Narrow
41	Dishwash Creek	Clare	Soft	Shallow	Narrow
43	Middle Branch Creek	Missaukee	Mixed	Medium	Narrow
44	Mosquito Creek	Missaukee	Soft	Shallow	Narrow
68	Green Creek	Muskegon	Soft	Shallow	Narrow
70	Clam River	Missaukee	Small	Medium	Narrow
71	Clam River	Missaukee	Mixed	Medium	Medium
72	Mitchell Creek	Mecosta	Mixed	Shallow	Narrow

Table 3. Mussel survey sites in the mainstem of the Muskegon River visited by MNFI during Summer 2002.

Site Number	Site Name	County	Substrate Class	Depth Class	Width Class
46	Muskegon River, near 120	Muskegon	Soft	Medium	Wide
47	Muskegon River, Sheridan Road	Muskegon	Soft	Medium	Wide
48	Muskegon River, Newaygo	Newaygo	Mixed	Medium	Wide
49	Muskegon River, below Croton	Newaygo	Mixed	Medium	Wide
50	Muskegon River, Felch Road	Newaygo	Small	Deep	Wide
51	Muskegon River, B-31	Newaygo	Soft	Deep	Wide
52	Muskegon River, M-55	Missaukee	Soft	Medium	Medium
53	Muskegon River, Cadillac Road	Missaukee	Soft	Medium	Medium
54	Muskegon River, Pine Road	Clare	Soft	Medium	Wide
55	Muskegon River, M-66	Osceola	Small	Medium	Wide
57	Muskegon River, Mill Iron	Muskegon	Soft	Deep	Wide
59	Muskegon River, Big Rapids	Newaygo	Mixed	Deep	Medium
60	Muskegon River, Evart	Osceola	Mixed	Deep	Wide
63	Muskegon River, US-27	Roscommon	Soft	Medium	Wide
64	Muskegon River, Dead Stream	Roscommon	Soft	Deep	Wide
65	Muskegon River, above Croton	Newaygo	Soft	Deep	Wide
66	Muskegon River, Brower Park	Mecosta	Mixed	Deep	Wide
67	Muskegon River, 185th Avenue	Mecosta	Soft	Deep	Medium

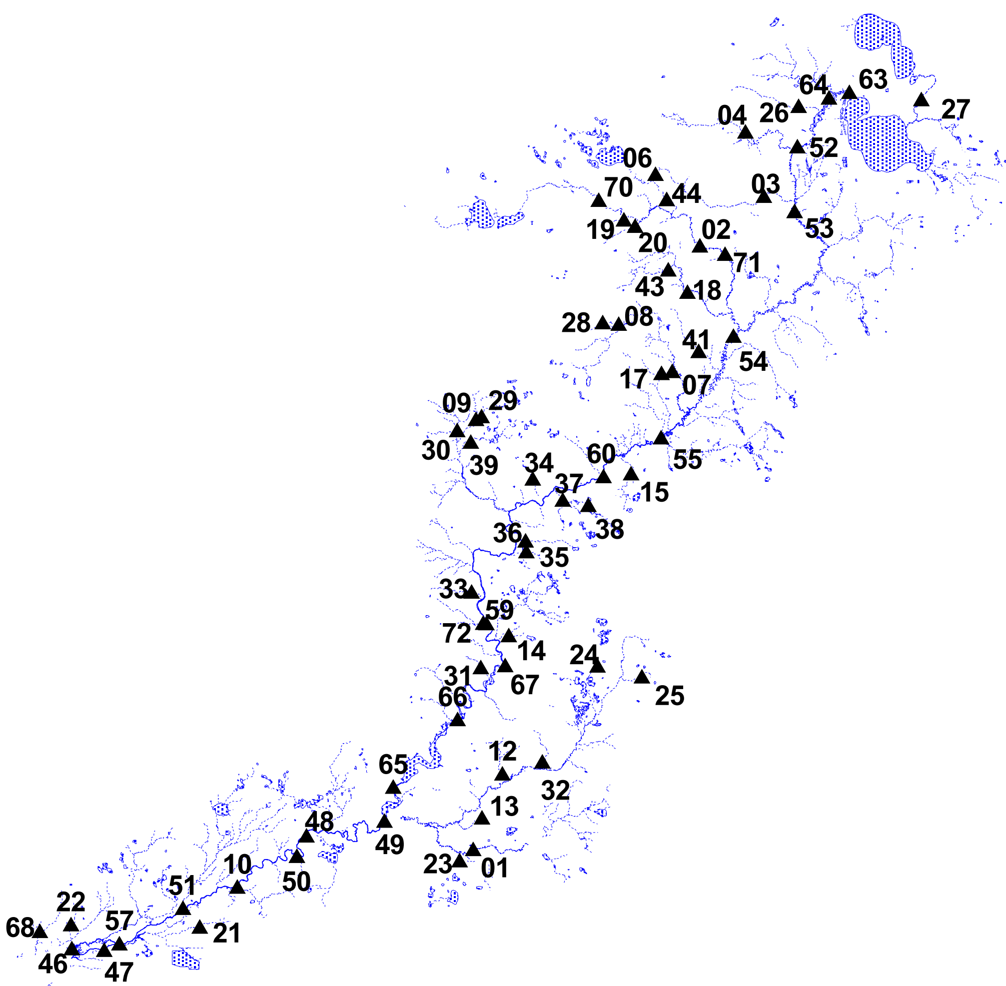

Figure 4. Mussel survey sites in the Muskegon River watershed visited by Michigan Natural Features Inventory (MNFI), Summer 2002.

Figure 5. MNFI staff surveying a clear, shallow reach of the Muskegon River with glass-bottom buckets, Summer 2002.

Figure 6. MNFI staff surveying a deep, murky reach of the Muskegon River using SCUBA equipment, Summer 2002.

Spatial Data and Analysis

Land cover data used in the spatial analyses were developed from 1978 MIRIS land covers updated to reflect conditions in 1995 using land transformation models (C. Riseng, pers. comm.). Nearstream buffers were the primary spatial units for analysis. Stream buffers were created in ArcView (ESRI 2003) representing 30, 60, 120, 240, and 480 m buffer areas around selected stream segments (e.g., the 30 m buffer class included 15 m lateral bands on both sides of the selected stream segments). The buffers were used as templates to extract the spatial extent of land covers in stream buffer areas using clipping procedures. Initial buffer delineations were chosen based on the common recommendation of preserving 30 m riparian buffers around streams in environmental planning (Petersen & Petersen 1992, Rabeni & Smale 1995). The larger buffer areas were delineated based on a geometric progression above the 30 m buffer size to detect potential relationships between mussel communities and buffer areas larger than the recommended 30 m minimum.

Buffer areas and associated land cover properties were quantified over four spatial scales (i.e., landscape contexts). Stream segments (i.e., lengths of stream between tributary confluences) were used as the basic units for defining landscape contexts. The local landscape contexts were defined as the stream segments encompassing the mussel sample sites (Figure 8). The stream segment immediately upstream (US1), two stream segments upstream (US2), and three stream segments upstream (US3) from each study site defined landscape contexts of progressively increasing scale (e.g., Figure 9a-c). Landscape contexts were nested, so the US2 landscape context included both the first and second segments upstream from a survey site and the US3 landscape context included the first, second, and third upstream segments from the site. Tributaries of upstream segments were included as part of the landscape contexts as the scale of the landscape contexts increased (Figure 9a-c). Environmental properties beyond the US3 context may have also influenced local biological and ecological properties of survey sites, although analyses of these potential associations were beyond the scope of this study. In a few cases where the entire upstream area from a survey site was described by the US1 or US2 context, the land cover data extracted for the largest landscape context available was used for all larger contexts in the statistical analyses.

The proportion of each buffer area encompassed by distinct land cover types was quantified for all landscape contexts using the GIS. Land cover types were combined into land cover groups according to expected similarity of influence on stream ecosystems, including forest (forest, brush, and plantations combined), wetlands (all wetland types combined), agricultural (row crop and pastures combined), and urban/residential. Other land cover types that represented minor contributions to the landscape were not included in these classifications (e.g., water bodies and grassland).

The buffer land cover data for all landscape contexts were used to determine whether MSR values were significantly related to land cover properties of buffers in the Muskegon River watershed. Principal components analysis (PCA) was used to compare mussel survey sites based on land cover characteristics for each of the four landscape contexts. Step-wise linear regression was used to determine whether MSR values were significantly related to the resulting synthetic variables from the PCA ordinations of sites based on the buffer land use data. For cases where tests to determine whether the assumptions of linear regression failed, the MSR data were transformed as the natural log of MSR+1.

RESULTS

Historical Data Compilation

Historic unionid community characteristics were reported for nine tributary and 15 mainstem sites of the Muskegon River (Figure 10) (van der Schalie 1941). Eighteen species were reported from the 1934 surveys (Tables 5 and 6), and the most frequently occurring (i.e., occurring at the most sites) species were *Lampsilis siliquoidea* (18 sites), *Strophitus undulatus* (17 sites), and *Fusconaia flava* (15 sites). Several species that are now considered rare in Michigan were reported live by van der Schalie (1941), including four special concern species (*A. marginata*, *A. viridis*, *P. sintoxia*, *V. iris*) and one state-listed as endangered species (*E. triquetra*). Historical MSR averaged six sp/site and ranged from one to 12 sp/site.

Historic data were also collected from the University of Michigan Museum of Zoology, Mollusk Division. Data were collected on the Michigan state-listed as special concern, threatened, and endangered species in the watershed. A total of 35 records were incorporated into the MNFI Biotics database as a result of this search, 21 of which were also reported by van der Schalie (1941).

Current Mussel Distribution Surveys

We surveyed 61 sites in the Muskegon River watershed, including 43 tributary reaches and 18 mainstem reaches (Figure 11). We observed an average of two mussel sp/site, with observations ranging from zero (34 sites) to eight (one site) sp/site. The majority of the sites with no live mussels present occurred lower in the watershed. Fourteen species were found live, and four additional species were observed as spent shells only (Tables 7 and 8). The most frequently occurring

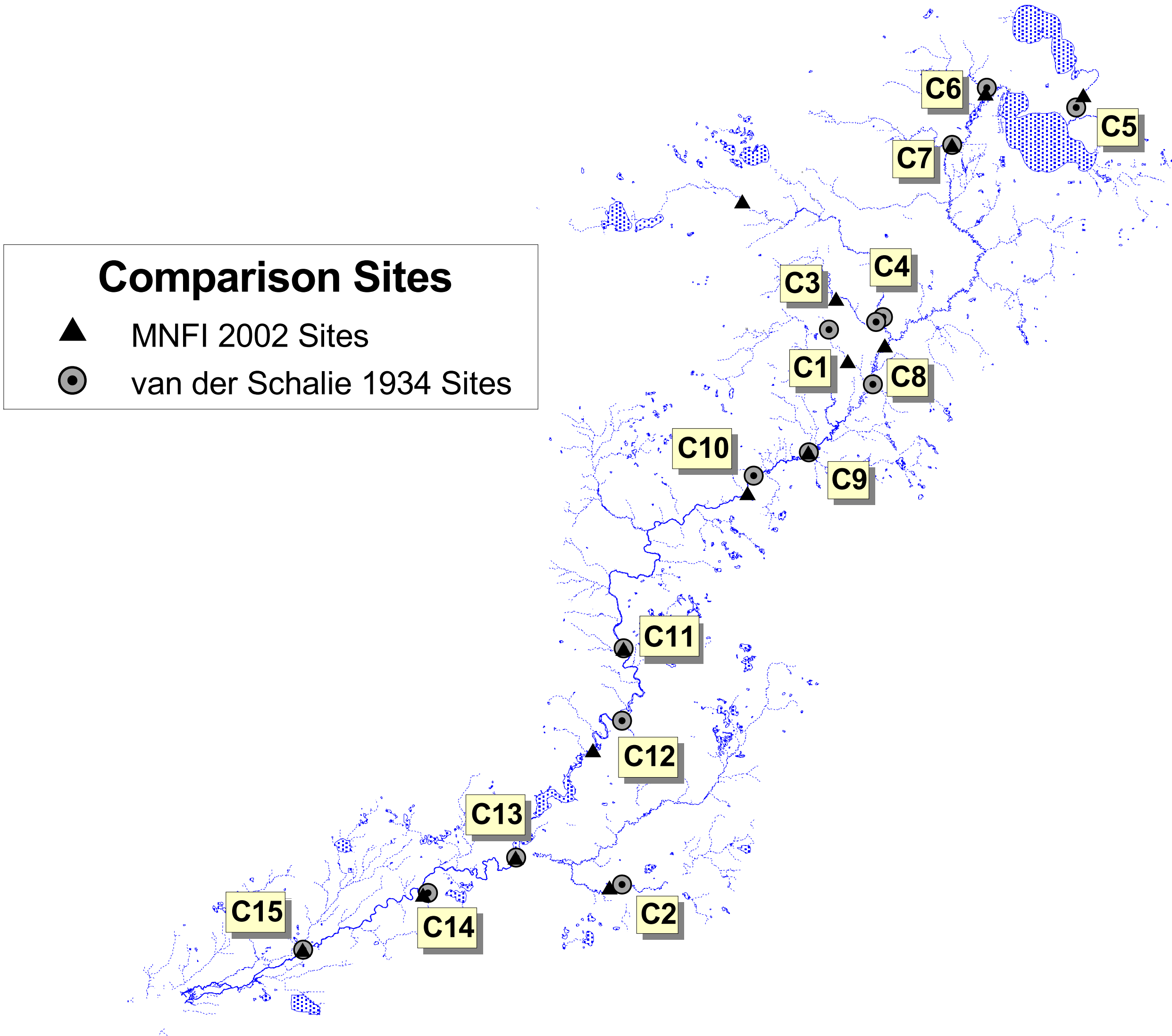

Figure 7. Sites used for comparison of historical (1934, van der Schalier 1941) and current (2002) mussel populations in the Muskegon River watershed.

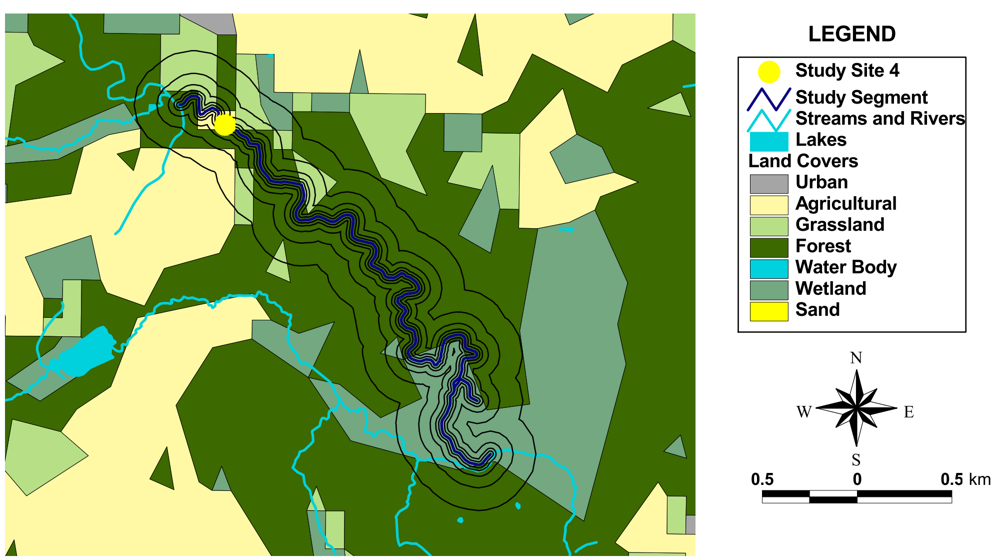

Figure 8. Example of a stream segment used for defining the local landscape context of a site (MNFI Site 4). The segment is defined at the upstream and downstream ends by tributary confluences, and the black lines represent buffers around the stream segment (i.e., 30, 60, 120, 240, and 480 m buffers).

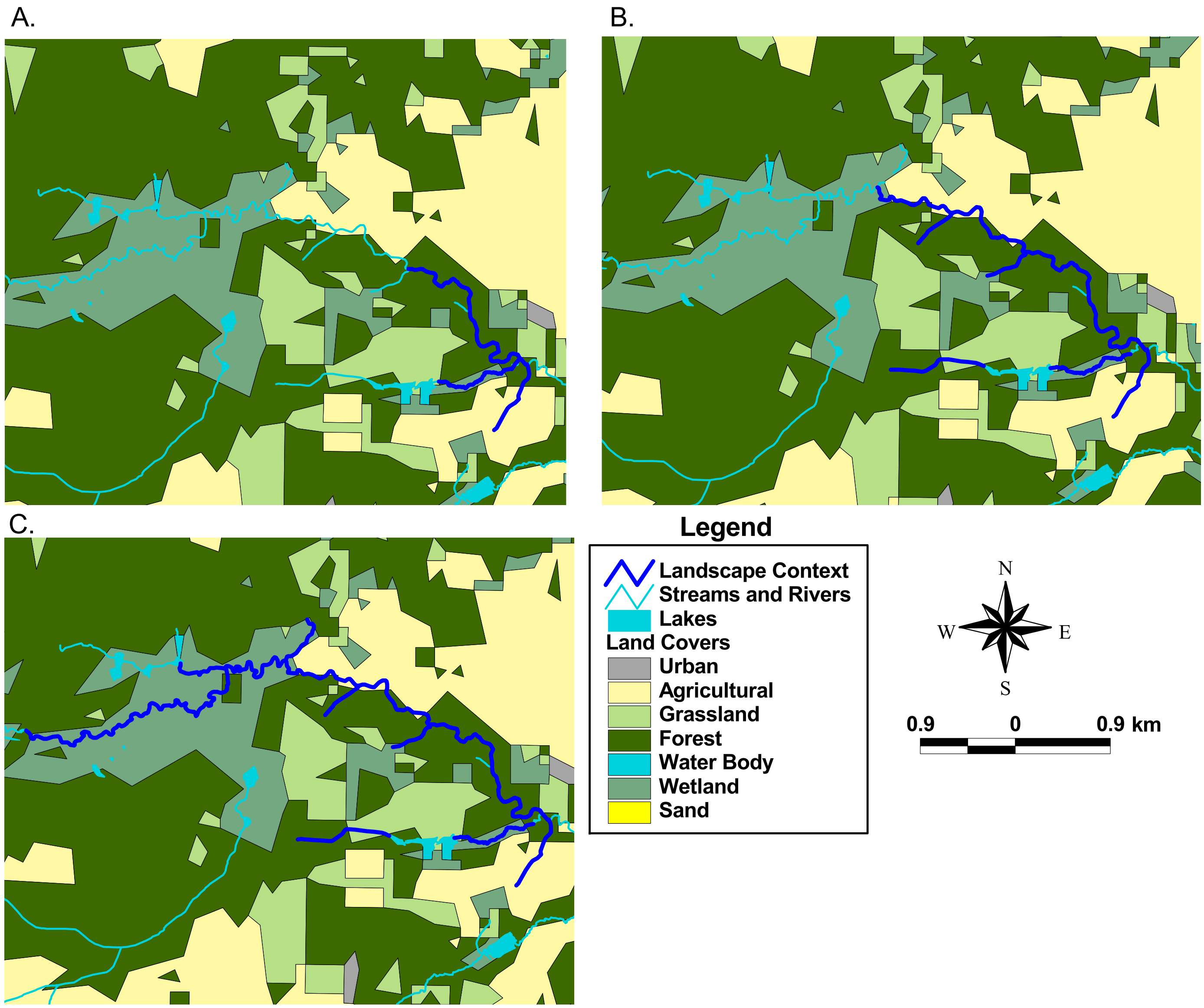

Figure 9. US1 (A), US2 (B), and US3 (C) landscape contexts used to describe land cover properties of buffered areas around and upstream from stream segments encompassing mussel survey sites in the Muskegon River watershed, Michigan.

species were *Actinonaias ligamentina* (11 sites), *Elliptio dilatata* (11 sites), *F. flava* (9 sites), and *L. siliquoidea* (8 sites). Three state-listed as special concern species (*A. marginata*, *A. viridis*, *V. iris*) were found live, and one state-listed as special concern species (*P. sintoxia*) and one state-listed as endangered species (*E. triquetra*) were observed as spent shells only.

Two other bivalves were found at the Muskegon River watershed mussel survey sites: native fingernail clams (Sphaeridae) and non-native zebra mussels (Dreissenidae). Presence/absence data were recorded for these taxa at all sites visited. Zebra mussel distribution was mapped for comparison with native mussel species population metrics (Figure 12). No live native mussels were found at sites with zebra mussels; hence, no zebra mussels were found attached to live unionids. Native MSR measures were not significantly different between sites with and without dreissenid mussels ($F_{(1, 59)} = 2.22$, $p > 0.14$).

Current vs. Historic Mussel Status

Both historical and current mussel data were available for 15 Muskegon River sites. Mean MSR was significantly lower in 2002 ($\bar{x} = 2.0$ sp/site) compared to 1934 ($\bar{x} = 6.1$ sp/site) ($t = 3.2$, $p < 0.007$, $n = 15$) (Figure 13). This trend was particularly prominent in the mainstem reaches of the watershed, where the majority of the sites surveyed in 2002 had no live mussels.

Of the 18 species reported live by van der Schalie (1941), only 13 were observed live in 2002. *E. triquetra*, *Lasmigona compressa*, *Ligumia recta*, and *P. sintoxia* were only found as spent shells during the 2002 surveys,

Table 4. Sites used for comparison of historical (VDS 1934, van der Schalie 1941) and current (MNFI 2002) mussel populations in the Muskegon River watershed.

Comparison Site Number	Site Name	VDS Site Number	MNFI Site Number
C1	Dishwash Creek	10	41
C2	Tamarack Creek	21	1
C3	Clam River, West Branch	9	18
C4	Clam River	8	71
C5	The Cut	2	27
C6	Muskegon River, Dead Stream	3	64
C7	Muskegon River, M-55	4	52
C8	Muskegon River, Pine Road	7	54
C9	Muskegon River, M-66	12	55
C10	Muskegon River, Evart	13	60
C11	Muskegon River, Big Rapids	16	59
C12	Muskegon River, Brower Park	17	66
C13	Muskegon River, below Croton	22	49
C14	Muskegon River, Felch Road	23	50
C15	Muskegon River, B31	25	51

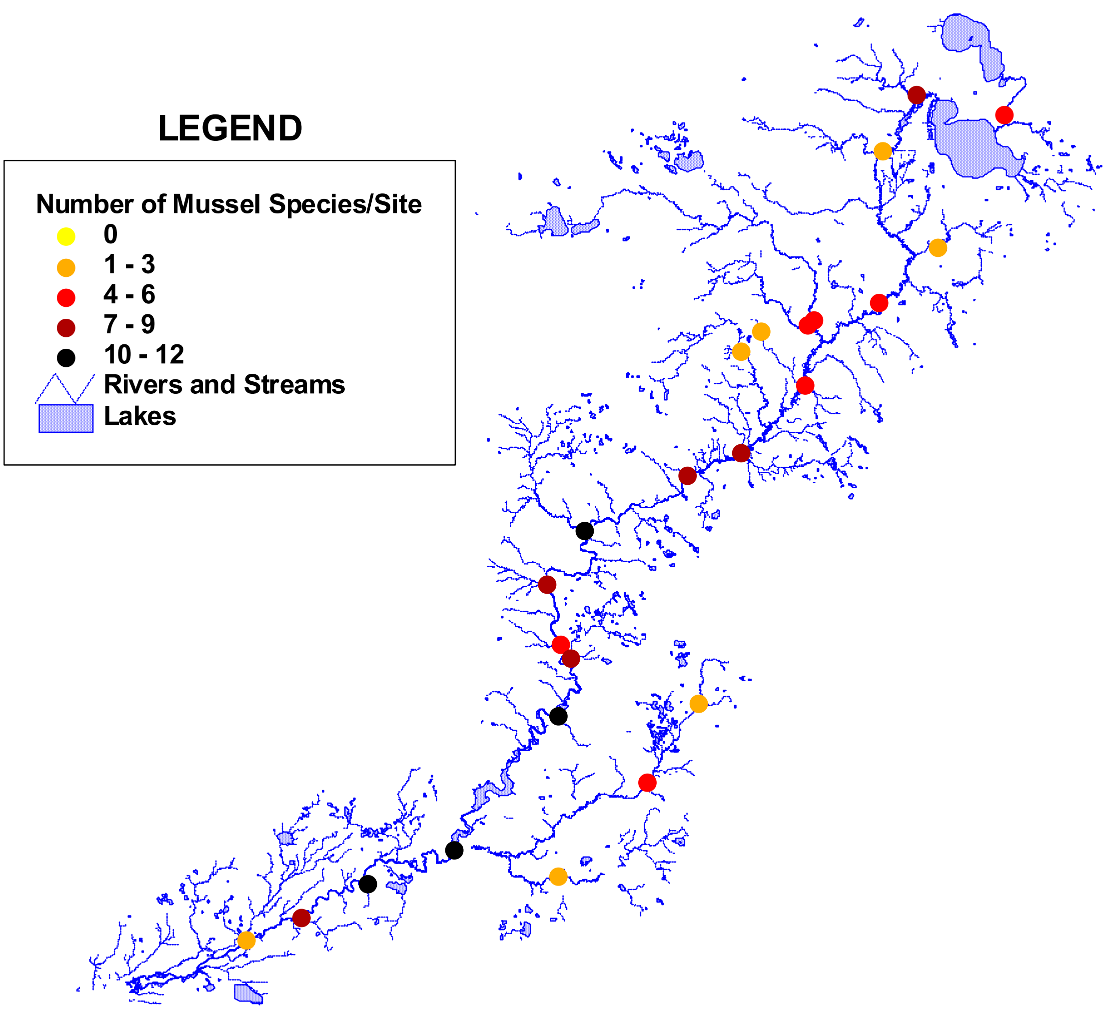

Figure 10. Historical (1934) mussel species richness in the Muskegon River watershed (van der Schalie 1941).

and *Potamilis alatus* was not observed at any survey sites in 2002 (Table 9). One species, *Ligumia nasuta*, was found in 2002 but not in 1934. There were no significant differences in the relative abundance of individual species between 1934 and 2002 (*Anodontoides ferruscianus* t=0.10, p>0.9; *A. ligamentina* t=1.22, p>0.2; *A. marginata* t=0.04, p>0.9; *A.viridis* t=2.03, p>0.06; *E.dilatata* t=0.08, p>0.9; *F. flava*.t=0.21, p>0.8; *Lasmigona costata* t=0.02, p>0.9; *Lampsilis ventricosa* t=1.83, p>0.08; *L. siliquoidea* t=1.64, p>0.1; *Pyganodon grandis* t=0.71, p>0.4; *S.undulatus* t=1.96, p>0.07; *V. iris* t=1.00, p>0.3;) (Figure 14).

No difference in the change in MSR between surveys was evident based on dam status ($F_{(3, 11)}$ =2.5, p>0.10) (Figure 15). However, sites with zebra mussels exhibited a greater loss of unionid species compared to sites without zebra mussels ($F_{(1, 13)}$ =13.0, p<0.004) (Figure 16).

Mussel-Physicochemical Habitat Analyses

MSR responses to varied habitat features of sites were evaluated using the stream morphology and substrate data. No significant differences were detected in MSR among stream depth classes ($F_{(2, 58)}$ =1.5, p>0.20) (Figure 17) or stream types ($F_{(1, 59)}$ =0.02, P>0.90) (Figure 18). MSR was significantly greater for the medium width class ($F_{(2, 58)}$ =7.6, p<0.002) (Figure 19). While there was no significant difference in MSR among substrate classes ($F_{(2, 58)}$ =2.4, p>0.10) (Figure 20), individual species relative abundance analysis with MANOVA revealed some significant differences. *A. marginata*, *A. viridis*, and *L. siliquoidea* showed significantly greater relative abundance at for the mixed substrate class ($F_{(2, 58)}$ =3.6, p<0.04; $F_{(2, 58)}$ =5.1, p<0.01; $F_{(2, 58)}$ =4.4, p<0.02, respectively) (Figures 21-23). No other species showed significant differences in relative abundance among substrate classes (*A. ligamentina* $F_{(2, 58)}$ =1.4, p>0.2; *A. ferussacianus* $F_{(2, 58)}$ =0.64, p>0.5; *E. dilatata* $F_{(2, 58)}$ =0.96, p>0.4; *F. flava* $F_{(2, 58)}$ =0.87, p>0.4; *L. ventricosa* $F_{(2, 58)}$ =0.36, p>0.7; *L. complanata* $F_{(2, 58)}$ =0.36, p>0.7; *L. costata* $F_{(2, 58)}$ =1.81, p>0.1; *L. nasuta* $F_{(2, 58)}$ =0.98, p>0.3; *P. grandis* $F_{(2, 58)}$ =0.59, p>0.5; *S. undulatus* $F_{(2, 58)}$ =0.01, p>0.9; *V. iris* $F_{(2, 58)}$ =0.68, p>0.5).

Correlation analyses to detect associations between MSR, temperature, dissolved oxygen, conductivity, and pH revealed negative correlations between MSR and temperature (n=57, R=0.3, p<0.03) (Figure 24). No other significant correlations between MSR and physicochemical measures were detected, although conductivity and pH (n=57, R>0.30) and temperature and pH (n=57, R>0.30) were correlated (Figures 25-26).

Mussel-Fish Community Analyses

Fish species richness was calculated and mapped using the data from surveys conducted by M. Wiley and C. Riseng (University of Michigan)(Figure 27). Regression analysis to determine whether MSR was related to fish species richness yielded no significant relationship at the watershed scale ($F_{(1, 51)}$ =1.1, p>0.3) (Figure 28). Regression analysis for data stratified by mainstem and tributary stream types indicated a non-significant relationship between MSR and fish species richness in the mainstem of the Muskegon River ($F_{(1, 16)}$ =0.6, p=0.5) and a significant positive relationship between MSR and fish species richness in tributary streams ($F_{(1, 33)}$ =9.5, p<0.005, R^2=0.22)(Figures 29-30).

Spatial Analysis Results

Local Buffer Land Cover Analysis

PCA ordination yielded no aggregation of sites based on local buffer land cover data (Figure 31). Three principal components with eigenvalues >1 resulted from this ordination, accounting for 91% of the variance. Principal component 1 (Local-1) explained 36% of the variance and primarily reflected the proportions of forest (negatively correlated) and agricultural (positively correlated) land uses within all local stream buffers (Table 10). Principal component 2 (Local-2) explained nearly as much variance as Local-1 (30%) and largely reflected the proportion of urban land uses (positively correlated) in local buffer areas. Local-2 also showed significant negative correlations with the proportion of forest land covers in local 30 m buffers (Table 10). The third principal component (Local-3) explained 25% of the variance and largely reflected the proportion of wetland land covers (positively correlated) in all of the local buffer areas. Local-3 also showed a significant negative correlation with the proportion of agricultural land use within all local buffer areas (Table 10).

Stepwise linear regression analysis using the three local principal components as independent variables and site MSR values as dependent variables yielded a significant linear relationship of MSR with Local-1 (Figure 32). The resulting model accounted for 46% of the variation ($F_{1, 47}$ = 39.4, p<0.001) in the MSR data and is represented by the equation:

$$MSR = 1.19(Local\text{-}1) + 1.12$$

A frequency histogram of the standardized residuals indicated that they were normally distributed, providing evidence to indicate that the assumptions of linear regression analysis were met. Both Local-2 and Local-3 were excluded as variables in the model during stepwise regression due to F-test significance levels >0.10.

US1 Buffer Land Cover Analysis

PCA ordination of the US1 buffer land cover data yielded no apparent aggregations of sites (Figure 33). Four principal components with eigenvalues >1 emerged

Table 5. Historical mussel survey results for tributaries of the Muskegon River reported by van der Schalie (VDS, 1941). The number of live individuals observed for each species is provided. Current State of Michigan listing status for relevant species is shown in parentheses (SC=special concern, E=endangered).

	VDS Site Number								
Species	1	8	9	10	11	18	19	21	20
Alasmidonta viridis (SC)	2	3	4		1	6		3	
Anodontoides ferussacianus		38	16		6	1	2		1
Elliptio dilatata						30			13
Fusconaia flava						20			1
Lampsilis siliquoidea	18	20	6	1	11	3			2
Lasmigona compressa		3	1	1			4	1	
Lasmigona costata						1		1	4
Pleurobema coccineum (SC)						6			
Strophitus undulatus		5				5			4
Villosa iris (SC)						4			
Total Number of Live Unionid Species	**2**	**5**	**4**	**2**	**3**	**9**	**2**	**3**	**6**

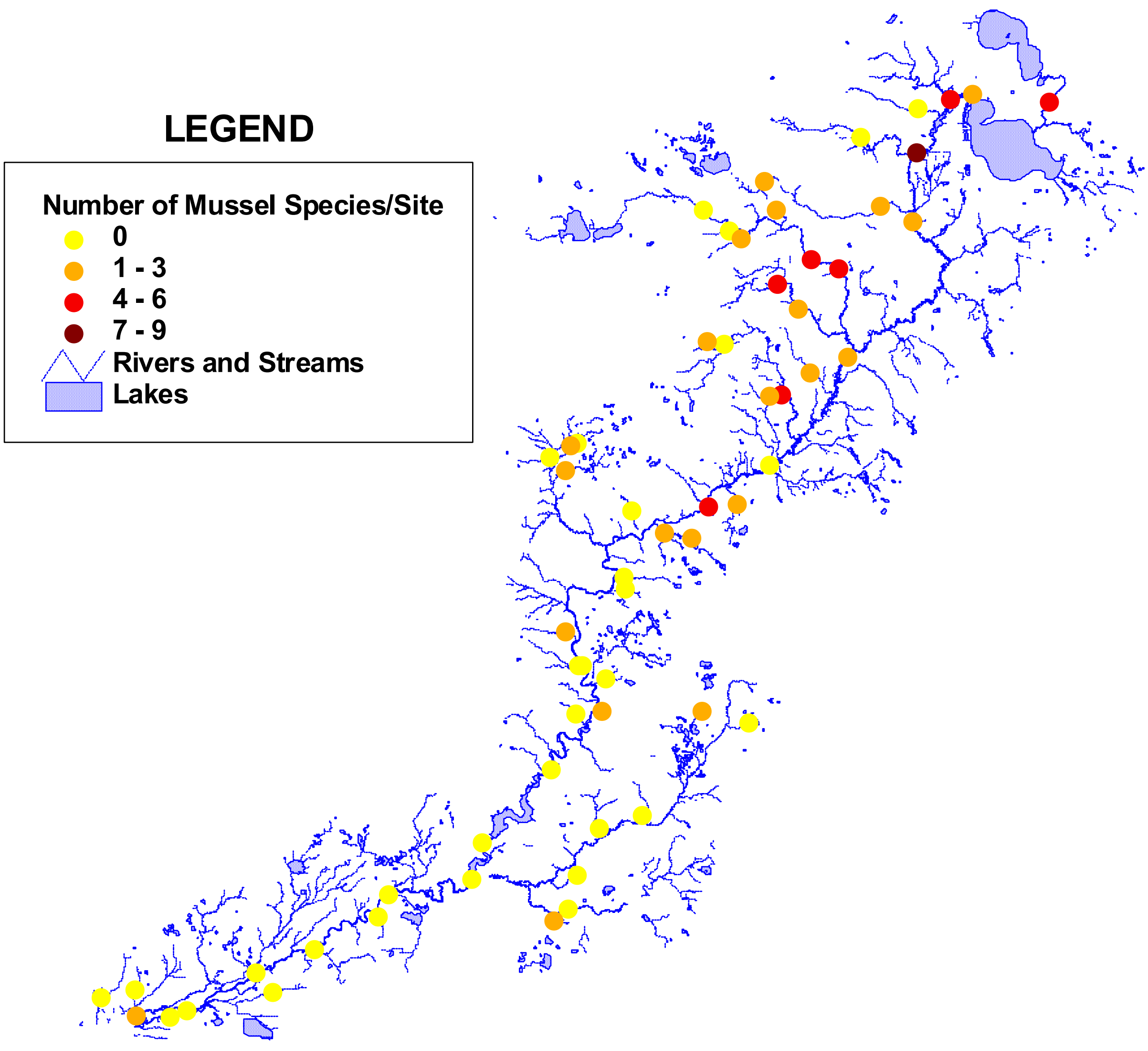

Figure 11. Current mussel species richness in the Muskegon River watershed reported by MNFI staff during Summer 2002.

Table 6. Historical (1934) mussel survey results for the mainstem of the Muskegon River reported by van der Schalie (VDS, 1941). The number of live individuals observed for each species is provided. Current State of Michigan listing status for relevant species is shown in parentheses (SC=special concern, E=endangered).

	VDS Site Number														
Species	2	3	4	5	7	12	13	14	15	16	17	22	23	24	25
Actinonaias ligamentina						16	8	6	13	2	5	4	31	5	1
Alasmidonta marginata (SC)								2			5	4		2	
Alasmidonta viridis (SC)						2	1	1							
Anodontoides ferussacianus				2								2			
Elliptio dilatata	33	71		3	7	20	75	49	55		3	2	8		1
Epioblasma triquetra (E)													6		
Fusconaia flava	2	2	1	10	2	5	10	6	9		1	1	27	1	
Lampsilis siliquoidea		46		77	45	31	57	25	25	17	3	15	5		
Lampsilis ventricosa	23	3				6			1		3	20	3		
Lasmigona costata		1				5	12	14	3	2	2	1			
Ligumia nasuta															
Ligumia recta		1			1	25	29	32	3		7	4	2		
Pleurobema coccineum (SC)				1				3			1	1	1	1	
*Potamilis alatus**														1	
Pyganodon grandis		38									1	1	2	1	
Strophitus undulatus	1	3		1	1	4	2	17	14	1	5	47	21	1	1
Villosa iris (SC)	30	5													
Total Number of Live Unionid Species	**5**	**9**	**1**	**6**	**5**	**9**	**8**	**10**	**8**	**4**	**11**	**12**	**10**	**7**	**3**

from the PCA ordination, explaining 94% of the total variance. Principal component 1 (US1-1) explained 38% of the total variance and principally reflected the proportion of forest land covers (negatively correlated) within all US1 buffers (Table 11). US1-1 also showed a significant positive correlation with the percentage of wetland land covers within all US1 buffer areas (Table 11). The second principal component (US1-2) accounted for 27% of the total variance and was positively correlated with the proportion of wetland land covers comprising US1 buffer areas. US1-2 was also significantly correlated with the proportion of nearly all buffer areas encompassed by urban land uses (Table 11). The third principal component (US1-3) explained 24% of the variance and reflected the proportion of wetland land covers (positively correlated) and urban land uses (negatively correlated) within all US1 buffer areas (Table 11). The fourth principal component (US1-4) accounted for 5% of the total variance and largely reflected the proportion of urban land uses comprising 120 m buffer areas (Table 11). Stepwise linear regression analysis yielded no statistically significant relationships between MSR values and the principle components for the US1 buffer land cover data (i.e., F-test significance levels for all variables was >0.10).

US2 Buffer Land Cover Analysis

PCA ordination of the US2 buffer land cover data resulted in four principal components with eignenvalues >1 that explained 97% of the variance. No discernable aggregation of sites was evident based on the ordination (Figure 34). Principal component one (US2-1) accounted for 38% of the total variance and principally reflected the proportion of agricultural land covers in all US2 buffer areas (R>0.79, p<0.001, Table 12). Principal component two (US2-2) explained 28% of the variance and primarily reflected the proportion of urban land uses comprising all US2 buffer areas (R>0.73, p<0.001, Table 12). Principal component three (US2-3) explained 25% of the total variance and primarily reflected the proportion of all buffer areas encompassed by wetlands (R>0.84, p<0.001, Table 12). Principal component four (US2-4) explained 6% of the variance and was not significantly correlated with the spatial extent of any land covers within US2 buffers.

Stepwise linear regression analysis of the four US2 principal components with MSR data yielded a significant relationship between MSR and US2-1. However, a frequency histogram of the standardized residuals indicated a non-normal distribution, indicating that the assumptions of linear regression were not met for this analysis. The MSR data were transformed as the natural log of MSR+1 in order to normalize the data. Stepwise linear regression of the transformed MSR data indicated a significant relationship between Ln(MSR+1) and US2-1. The resulting model accounted for 19% of the variation ($F_{1, 47}$ = 11.0, p<0.003, Figure 35) in the MSR data and is represented by the equation:

$$Ln(MSR+1) = 0.29(US2\text{-}1) + 0.50$$

A frequency histogram of the standardized residuals indicated that they were nearly normally distributed, providing evidence to suggest that the assumptions of linear regression analysis were met using the transformed data. US2-2, US2-3, and US2-4 were excluded as variables in the model during stepwise regression due to F-test significance levels >0.10.

US3 Buffer Land Cover Analysis

PCA ordination of the US3 buffer land cover data revealed four principal components with eigenvalues >1 although no aggregration was apparent based on the first two components (Figure 36). Principal component one (US3-1) accounted for 40% of the total variance and was most strongly correlated with the proportion of all buffer areas encompassed by agricultural land uses (R>0.78, p<0.001, Table 13). US3-1 was also significantly correlated with the proportion of forest (R>-0.57, p<0.001), wetland (R>0.46, p<0.002), and urban (R>-0.59, p<0.001) land cover types within the buffer areas. Principal component two (US3-2) explained 27% of the variance and largely reflected the spatial extent of forest and urban land covers in all buffer areas (R>0.65, p<0.001 and R>-0.71, p<0.001, respectively). Principal component three (US3-3) explained 24% of the variance and primarily reflected the proportion of buffer areas encompassed by wetland land covers (R>0.81, p<0.001). US3-3 was also correlated with the proportion of buffer areas dedicated to agricultural land uses (R>-0.44, p<0.002). Principal component four (US3-4) accounted for 7% of the variance and was not significantly correlated with land covers of any buffer classes of the US3 landscape context (R<0.32, p>0.03, Table 13).

Stepwise linear regression analysis using the four US3 buffer land cover principal components and Ln-transformed MSR values yielded a significant linear relationship of Ln(MSR+1) with US3-1 (Figure 37). The resulting model accounted for 19% of the variation ($F_{1, 48}$ = 10.9, p<0.003) in the MSR data and is represented by the equation:

$$Ln(MSR+1) = 0.29(US3\text{-}1) + 0.50$$

A frequency histogram of standardized residuals indicated that they were normally distributed, providing evidence to indicate that the assumptions of linear regression analysis were met. US3-2, US3-3, and US3-4 were excluded as variables in the model during stepwise regression due to F-test significance levels >0.10.

Table 7. Muskegon River watershed mussel survey results for tributary sites visited by MNFI in Summer 2002. Numbers reflect the number of live individuals found for each species. Current State of Michigan listing status for relevant species is provided in parentheses (SC=special concern, E=endangered). The presence of the exotic species *Dreissena polymorpha* and native spherid fingernail clams at a site is indicated by an "X."

	MNFI Site Number														
Species	1	2	3	4	6	7	8	9	10	12	13	14	15	17	18
Actinonaias ligamentina						1									
Alasmidonta marginata (SC)		S				1									
Alasmidonta viridis (SC)	S	2				S								1	1
Anodontoides ferussacianus			7		S	S		2					4	1	
Elliptio dilatata		2			S	6									
Epioblasma triquetra (E)															
Fusconaia flava		1			S	S									
Lampsilis siliquoidea			S										2	7	7
Lampsilis ventricosa															
Lasmigona complanata															
Lasmigona compressa															
Lasmigona costata															
Ligumia nasuta															
Ligumia recta															
Pleurobema coccineum (SC)					S	S									
Pyganodon grandis															
Strophitus undulatus		S				1							1		
Villosa iris (SC)															
Total Number of Live Unionid Species	**0**	**3**	**1**	**0**	**0**	**4**	**0**	**1**	**0**	**0**	**0**	**0**	**3**	**3**	**2**
Dreissena polymorpha															
Sphaeridae		X					X			X		X	X		

Table 7. *Cont.*

	MNFI Site Number														
Species	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Actinonaias ligamentina															
Alasmidonta marginata (SC)															
Alasmidonta viridis (SC)															
Anodontoides ferussacianus		9							1	7					1
Elliptio dilatata									16						
Epioblasma triquetra (E)															
Fusconaia flava					1				2						
Lampsilis siliquoidea									S						4
Lampsilis ventricosa															
Lasmigona complanata															
Lasmigona compressa															
Lasmigona costata															
Ligumia nasuta									3						
Ligumia recta															
Pleurobema coccineum (SC)															
Pyganodon grandis		3							1						
Strophitus undulatus															1
Villosa iris (SC)						1			5						
Total Number of Live Unionid Species	**0**	**2**	**0**	**0**	**1**	**1**	**0**	**0**	**6**	**1**	**0**	**0**	**0**	**0**	**3**
Dreissena polymorpha															
Sphaeridae						X		X		X	X				X

Table 7. *Cont.*

	MNFI Site Number												
Species	34	35	36	37	38	39	41	43	44	68	70	71	72
Actinonaias ligamentina									S				
Alasmidonta marginata (SC)												2	
Alasmidonta viridis (SC)								1				S	
Anodontoides ferussacianus					S		1	2				S	
Elliptio dilatata				S	30	48		29	23				
Epioblasma triquetra (E)													
Fusconaia flava					S	60		5	2			S	
Lampsilis siliquoidea				1	S			10	S			5	
Lampsilis ventricosa													
Lasmigona complanata													
Lasmigona compressa					S								
Lasmigona costata												5	
Ligumia nasuta													
Ligumia recta													
Pleurobema coccineum (SC)													
Pyganodon grandis				1				S	S				
Strophitus undulatus				S								1	
Villosa iris (SC)													
Total Number of Live Unionid Species	**0**	**0**	**0**	**2**	**1**	**2**	**1**	**5**	**2**	**0**	**0**	**4**	**0**
Dreissena polymorpha													
Sphaeridae	X	X	X						X				

Table 8. Muskegon River watershed mussel survey results for mainstem sites visited by MNFI in Summer 2002. Numbers reflect the number of live individuals found for each species. Current State of Michigan listing status for relevant species is provided in parentheses (SC=special concern, E=endangered). The presence of the exotic species *Dreissena polymorpha* and native spherid fingernail clams at a site is indicated by an "X."

	MNFI Site Number																	
Species	46	47	48	49	50	51	52	53	54	55	57	59	60	63	64	65	66	67
Actinonaias ligamentina					S					S			11					
Alasmidonta marginata (SC)									S				1					
Anodontoides ferussacianus							1											
Elliptio dilatata					S		3	1	S	S		S	16		36			
Epioblasma triquetra (E)					S													
Fusconaia flava					S	S	22	S	1	S	S		S		3			
Lampsilis siliquoidea			S				5		S	S			S					S
Lampsilis ventricosa	S				S		2						S	S	S			S
Lasmigona complanata	1		S		S													
Lasmigona costata					S		1						2					
Ligumia nasuta														2	1			
Ligumia recta			S		S								S					
Pyganodon grandis															2		S	
Strophitus undulatus			S		S		5		S									
Villosa iris (SC)							1											
Total Number of Unionid Species **Live**	**1**	**0**	**0**	**0**	**0**	**0**	**8**	**1**	**1**	**0**	**0**	**0**	**4**	**1**	**4**	**0**	**0**	**0**
Dreissena polymorpha		**X**	**X**	**X**	**X**											**X**	**X**	
Sphaeridae		**X**										**X**						**X**

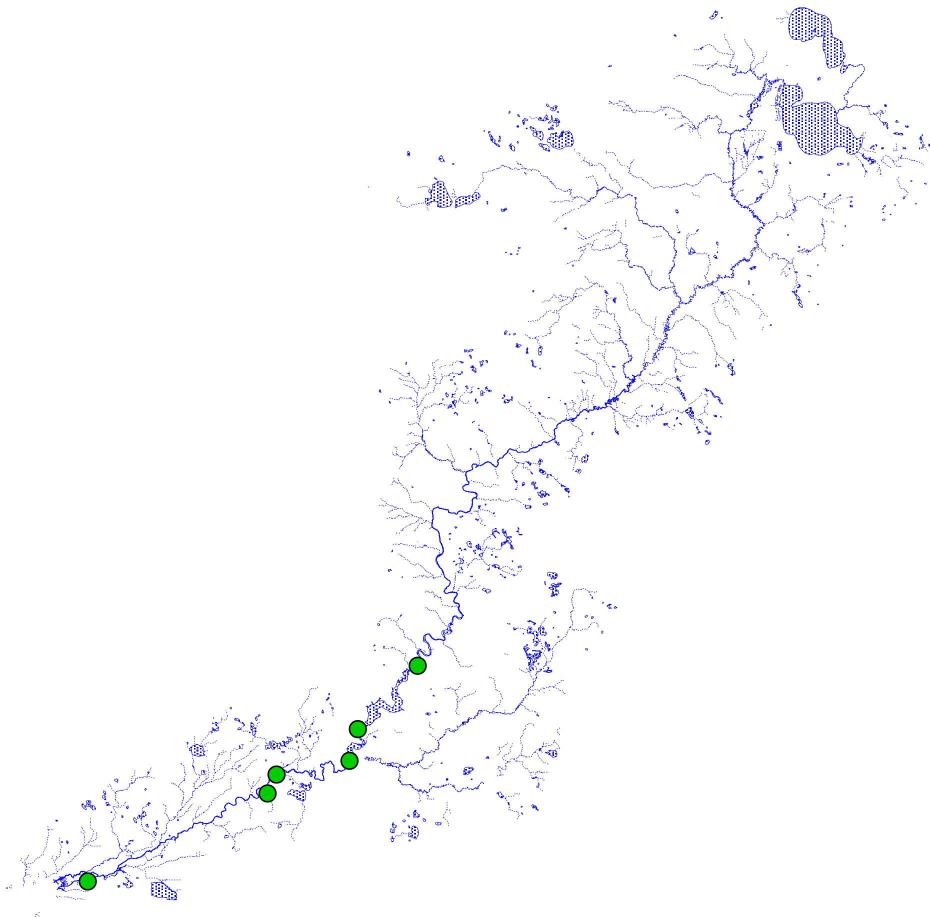

Figure 12. Locations (indicated by green dots) at which zebra mussels (Dreissenidae) were observed during MNFI native mussel surveys in the Muskegon River watershed during summer 2002.

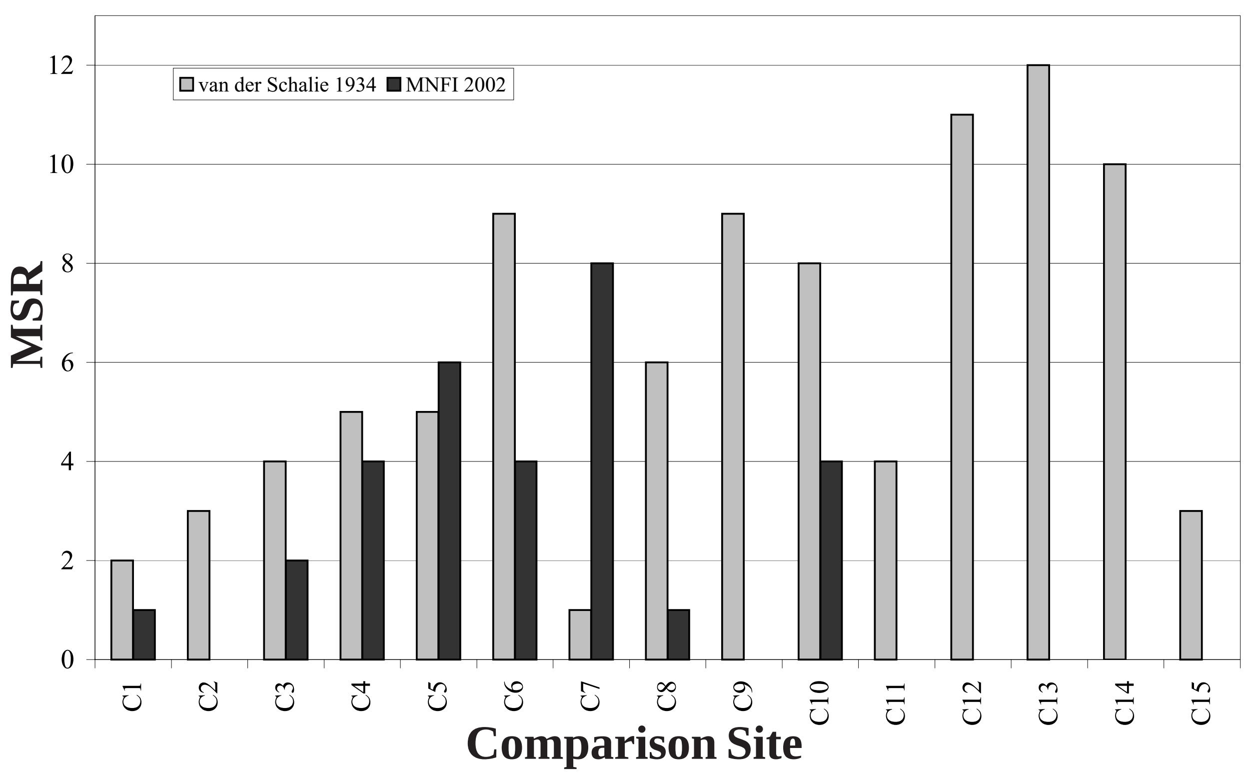

Figure 13. Comparisons of mussel species richness (MSR) measures for sites in the Muskegon River watershed based on historical (1934; van der Schalie 1941) and current (2002) unionid surveys.

Table 9. Comparison of historical (1934; van der Schalie 1941) and current (2002) mussel species survey data in the Muskegon River watershed. An "X" indicates the presence of live individuals and an "S" indicates the presence of spent shells only. Current conservation status for relevant species is provided in parentheses (SC=special concern and E=endangered).

	Survey Site																													
	C1		C2		C3		C4		C5		C6		C7		C8		C9		C10		C11		C12		C13		C14		C15	
Species	1934	2002	1934	2002	1934	2002	1934	2002	1934	2002	1934	2002	1934	2002	1934	2002	1934	2002	1934	2002	1934	2002	1934	2002	1934	2002	1934	2002	1934	2002
Actinonaias ligamentina																	X	S	X	X	X		X		X		X	S	X	
Alasmidonta marginata (SC)								X								S				X			X		X					
Alasmidonta viridis (SC)			X	S	X	X	X	S									X		X											
Anodontoides ferussacianus		X			X		X	S		X				X											X					
Elliptio dilatata									X	X	X	X		X	X	S	X	S	X	X		S	X		X		X	S	X	
Epioblasma triquetra (E)																											X	S		
Fusconaia flava								S	X	X	X	X	X	X	X	X	X	S	X	S			X		X		X	S		S
Lampsilis siliquoidea	X				X	X	X	X		S	X			X	X	S	X	S	X	S	X		X		X		X			
Lampsilis ventricosa									X		X	S		X			X			S			X		X		X	S		
Lasmigona complanata																												S		
Lasmigona compressa	X		X		X		X																							
Lasmigona costata			X					X			X			X			X		X	X	X		X		X			S		
Ligumia nasuta										X		X																		
Ligumia recta											X				X		X		X	S			X		X		X	S		
Pleurobema sintoxia (SC)																							X		X		X			
*Potamilis alatus**																														
Pyganodon grandis										X	X	X											X		X		X			
Strophitus undulatus							X	X	X		X			X	X	S	X		X		X		X		X		X	S	X	
Villosa iris (SC)									X	X	X			X																
Total Number of Live Unionid Species	**2**	**1**	**3**	**0**	**4**	**2**	**5**	**4**	**5**	**6**	**9**	**4**	**1**	**8**	**5**	**1**	**9**	**0**	**8**	**4**	**4**	**0**	**11**	**0**	**12**	**0**	**10**	**0**	**3**	**0**

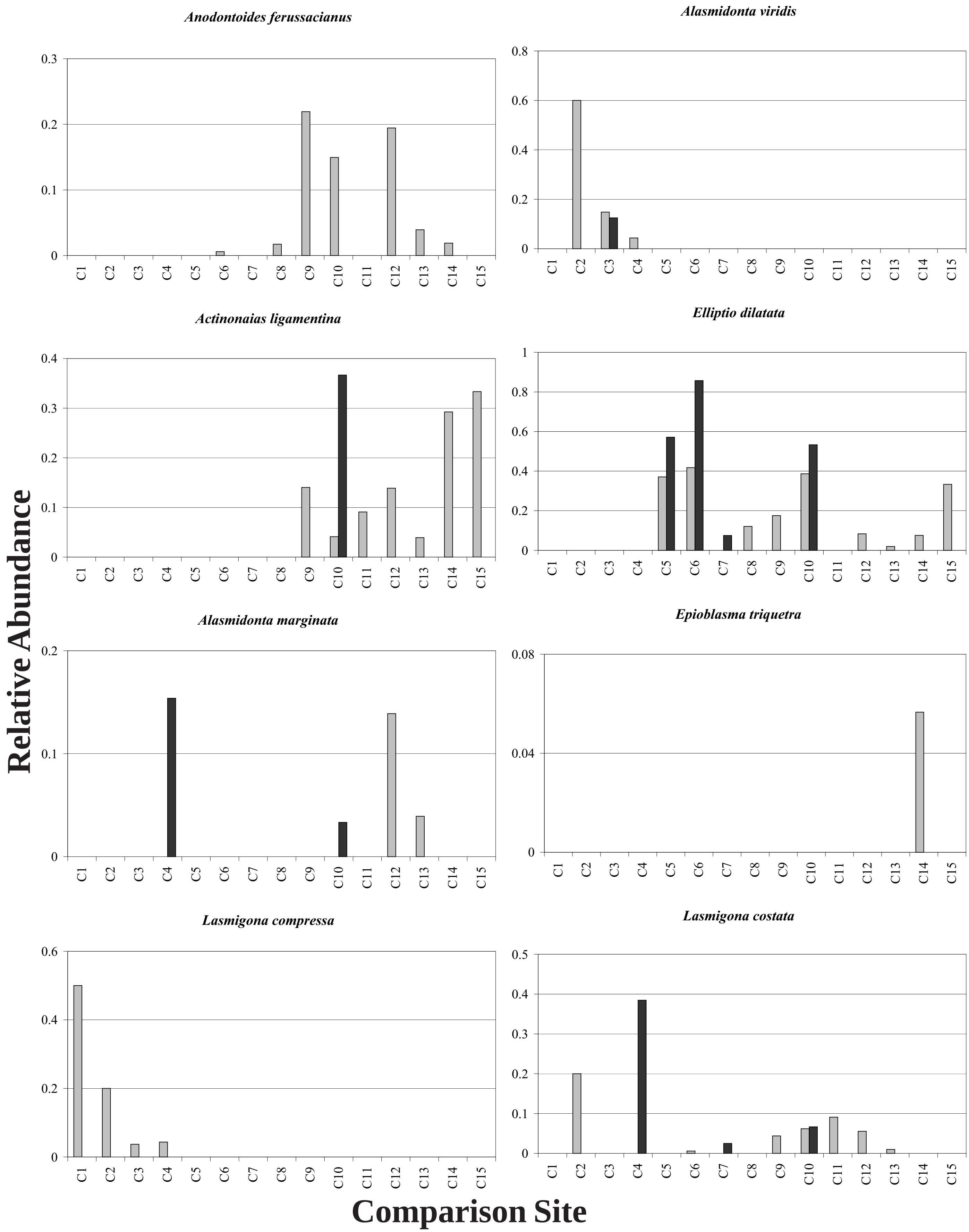

Figure 14. Comparisons of individual species relative abundance measures for Muskegon River watershed reaches surveyed in 1934 (van der Schalie 1941) and 2002.

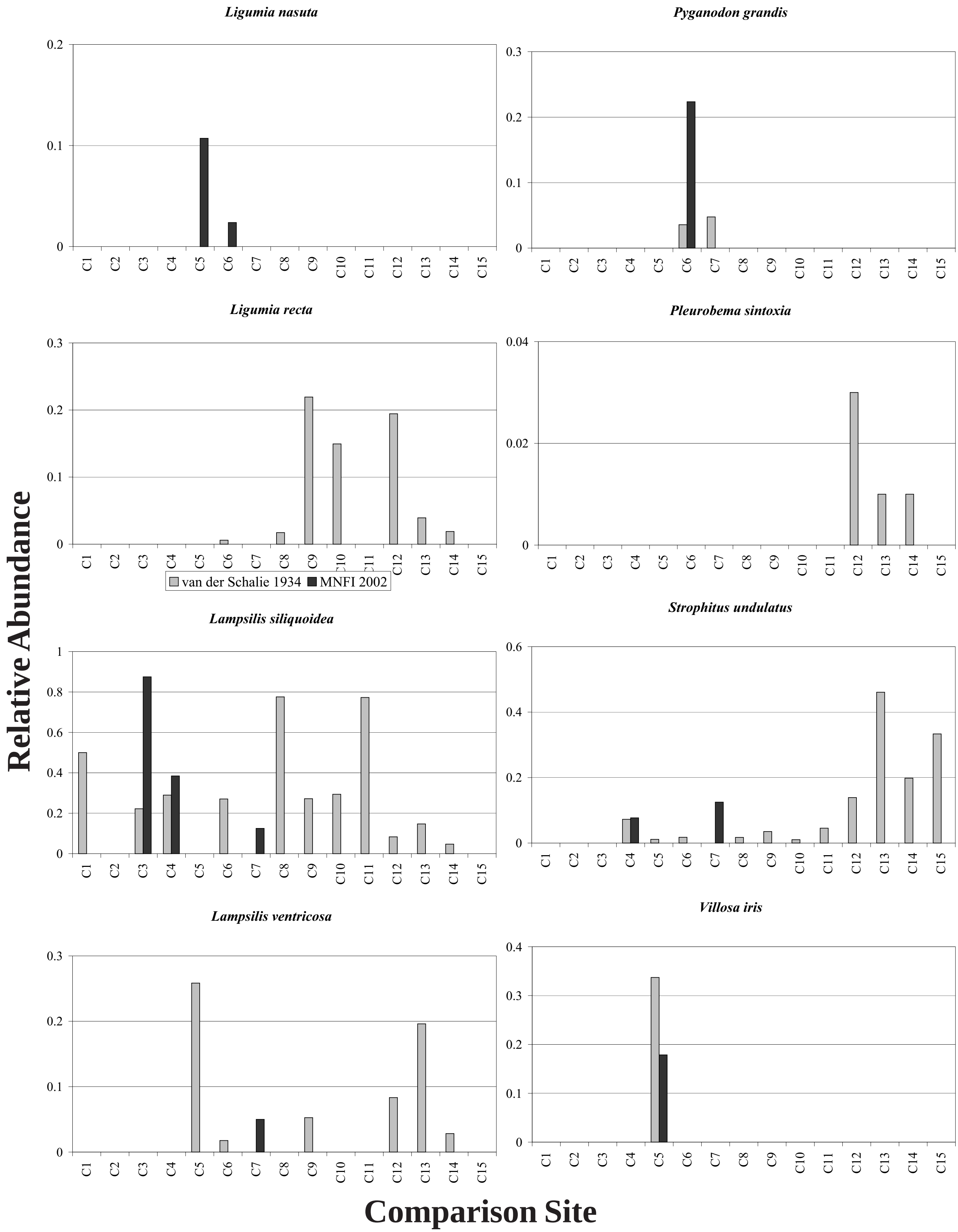

Figure 14. *Cont.*

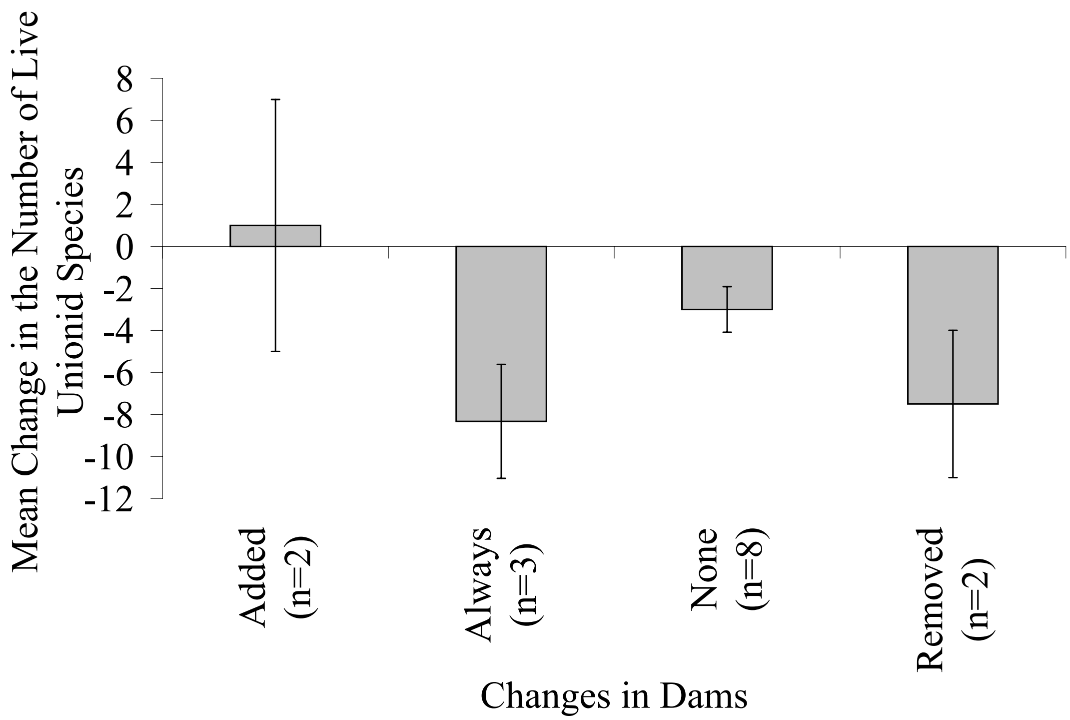

Figure 15. Comparisons of mean changes in unionid species richness for comparison sites (i.e., between 1934 and 2002) based on changes in the status of dams in the Muskegon River watershed. Dam categories include dam added between surveys (added), dam present at the time of both surveys (always), no dam present at the time of either survey (none), and dam removed between the 1934 and 2002 surveys (removed).

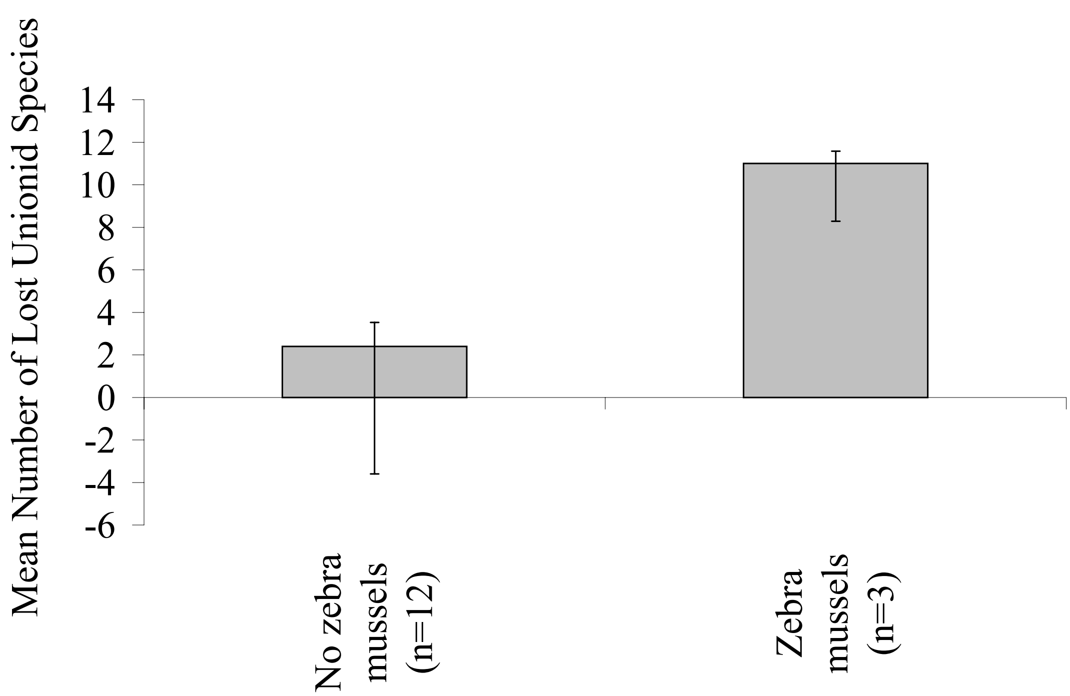

Figure 16. Comparison of the mean changes in Muskegon River watershed unionid species richness between 1934 and 2002 based on the status of zebra mussel invasion (i.e., present vs. absent) at sites.

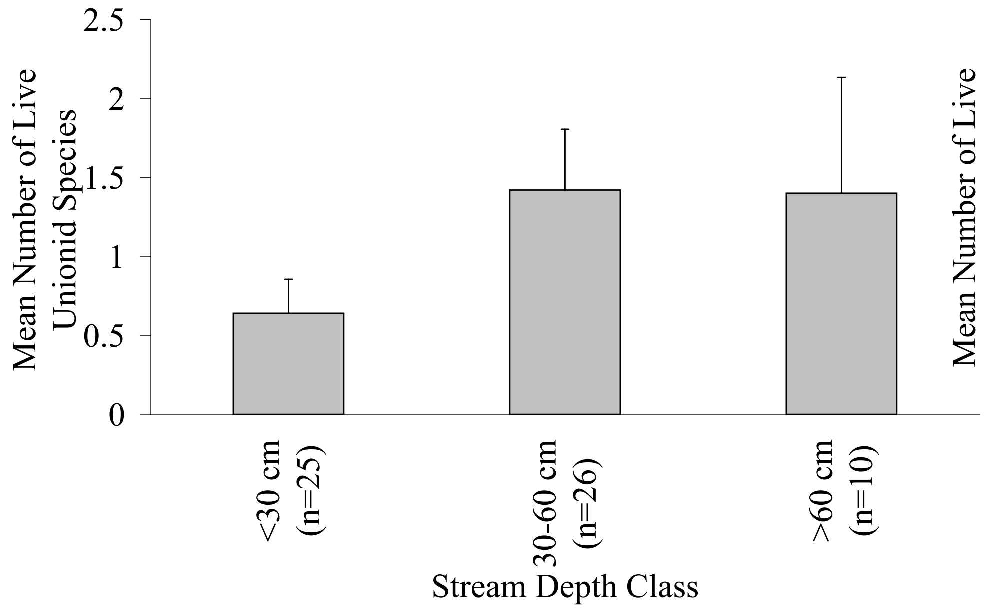

Figure 17. Comparison of mean 2002 Muskegon River unionid species richness among stream depth classes.

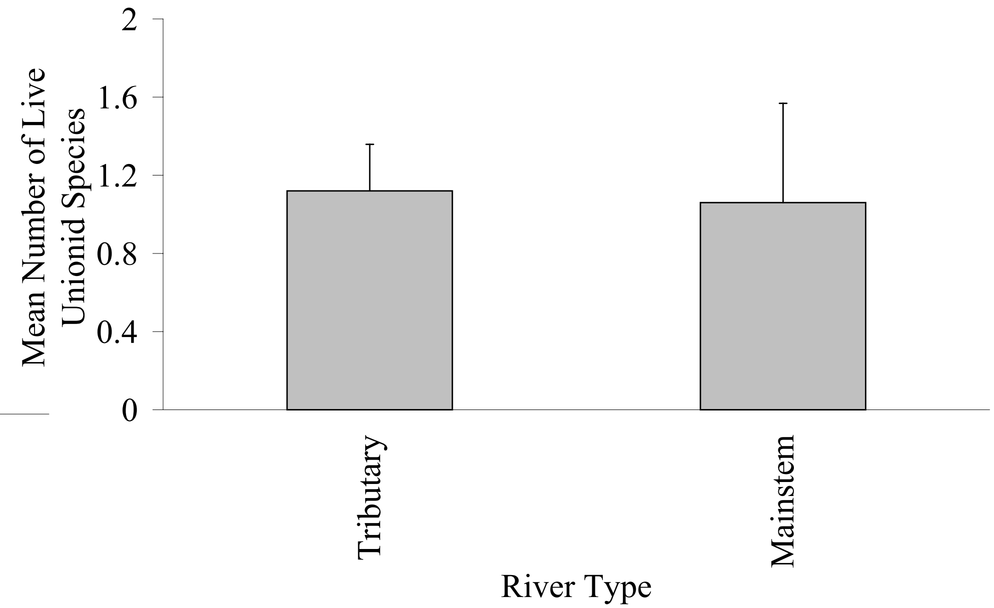

Figure 18. Comparison of mean 2002 Muskegon River unionid species richness between river classes.

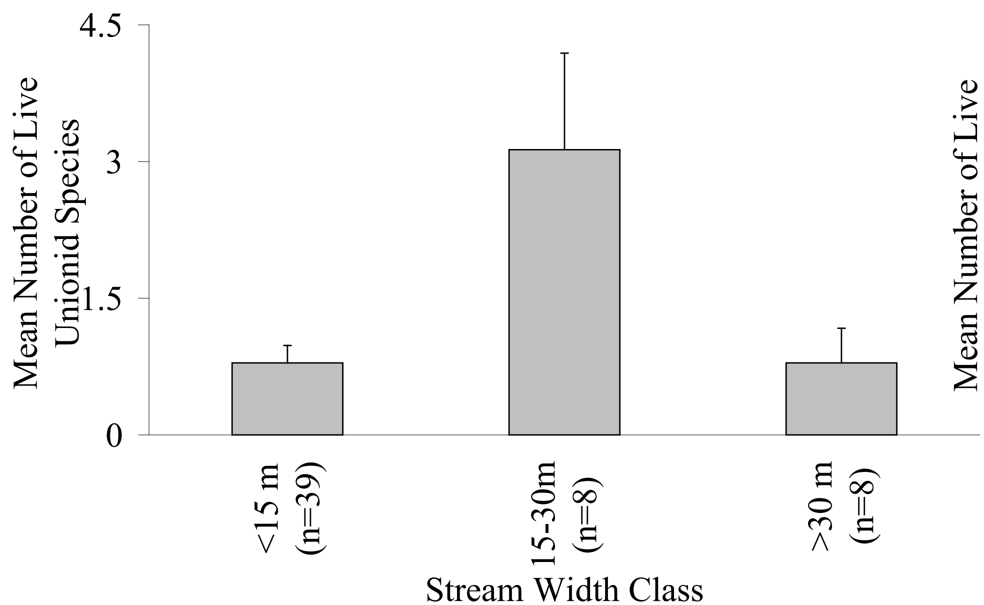

Figure 19. Comparison of mean 2002 Muskegon River unionid species richness among stream width classes.

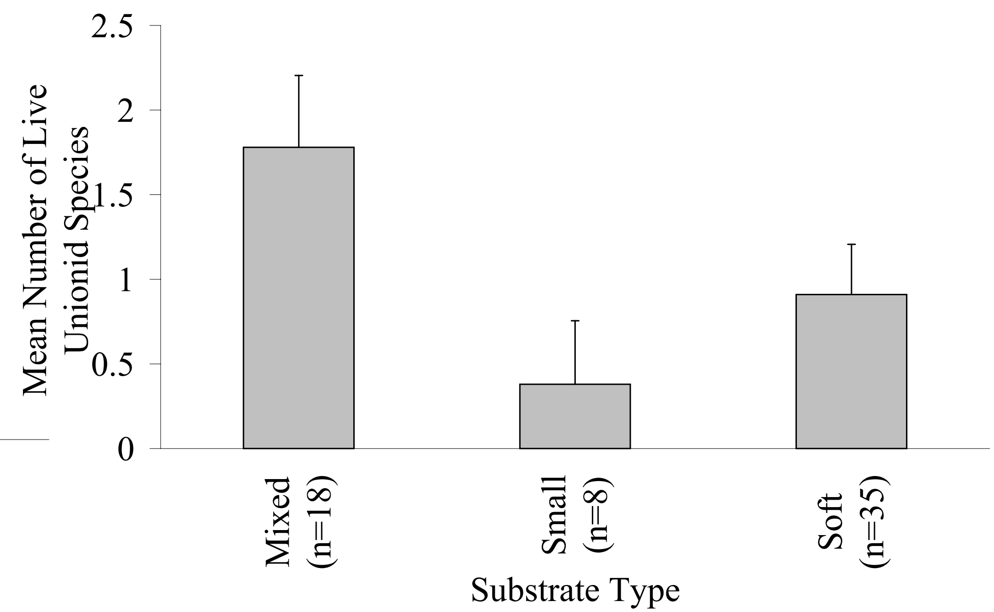

Figure 20. Comparison of mean 2002 Muskegon River unionid species richness among substrate classes.

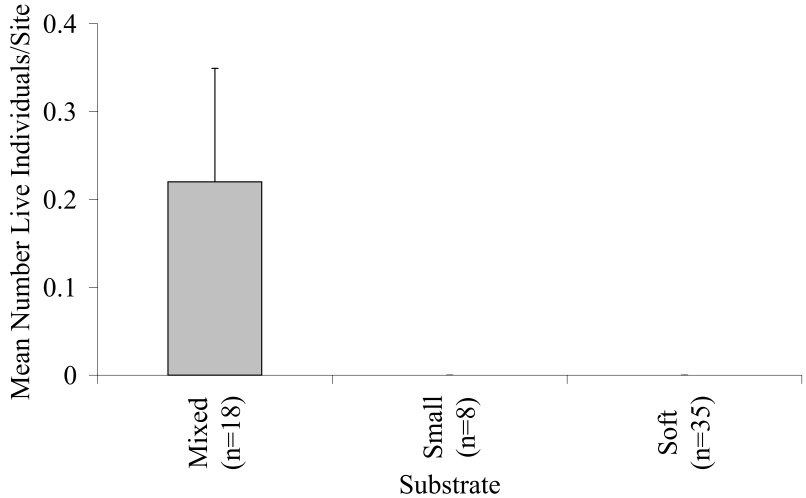

Figure 21. Comparison of mean *Alasmidonta marginata* relative abundance measures among substrate classes in the Muskegon River watershed based on surveys conducted in 2002.

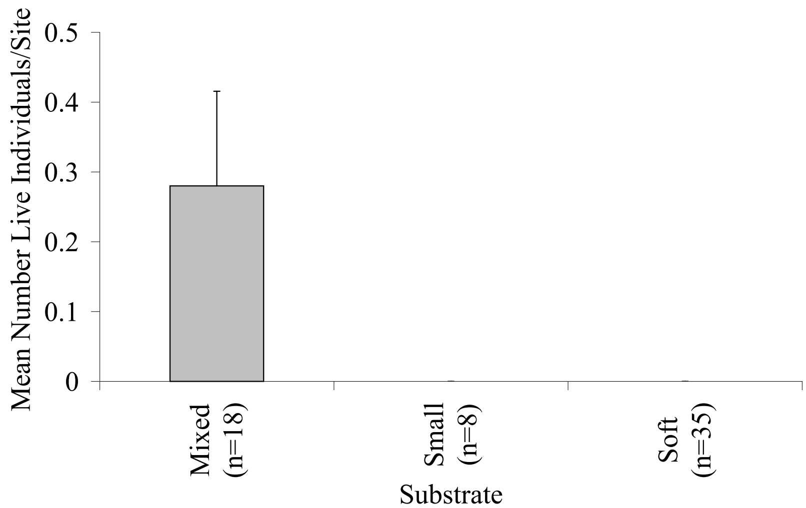

Figure 22. Comparison of mean *Alasmidonta viridis* relative abundance measures among substrate classes in the Muskegon River watershed based on surveys conducted in 2002.

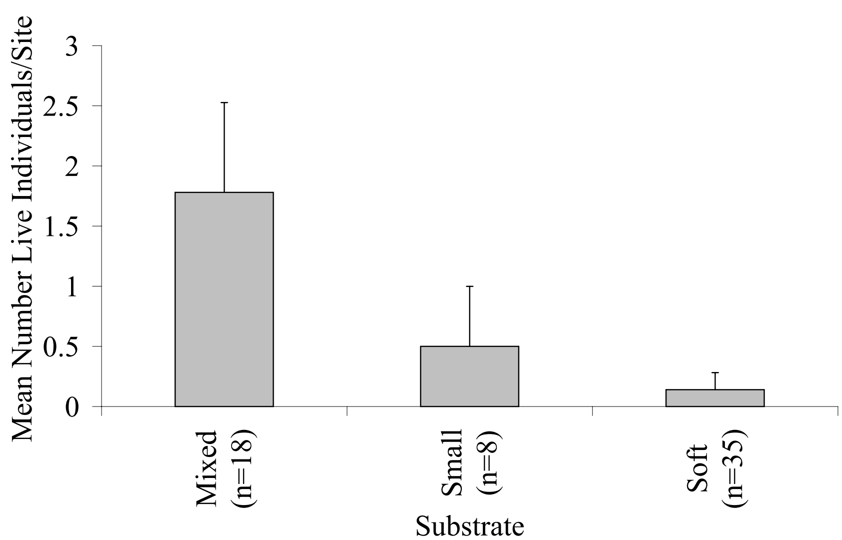

Figure 23. Comparison of mean *Lampsilis siliquoidea* relative abundance measures among substrate classes in the Muskegon River watershed based on surveys conducted in 2002.

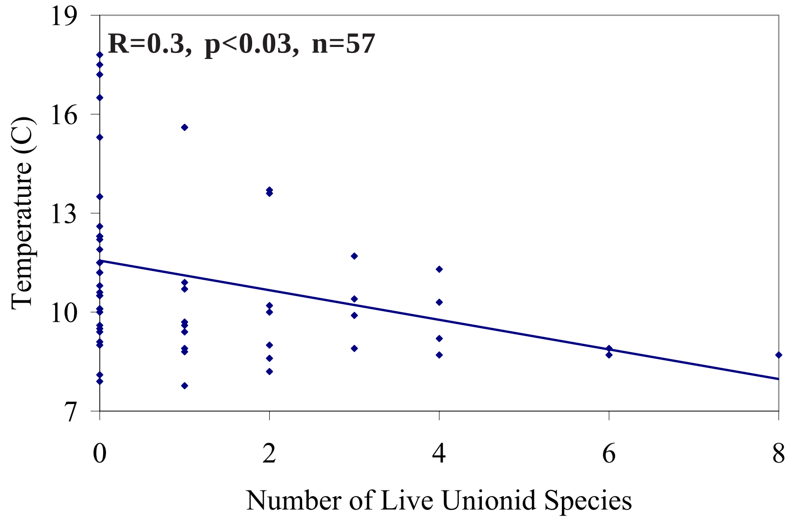

Figure 24. Correlation between unionid species richness and temperature data for the Muskegon River watershed based on surveys conducted in 2002.

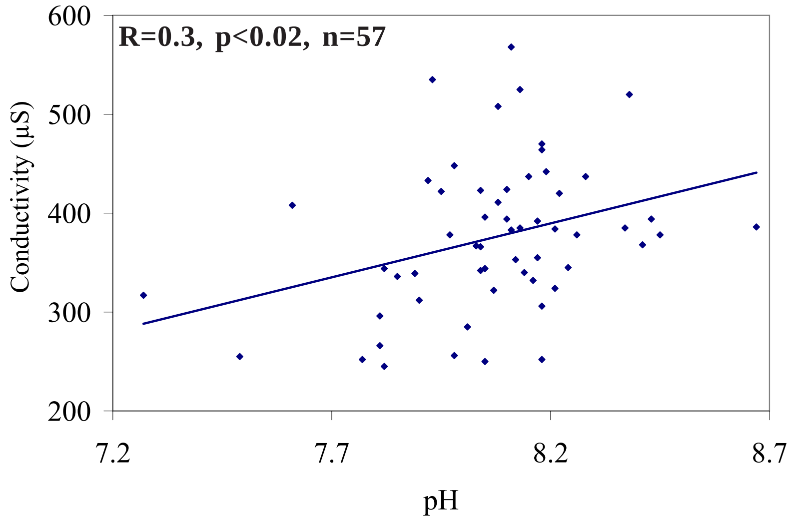

Figure 25. Correlation between conductivity and pH measures taken at sites in the Muskegon River watershed as part of freshwater mussel surveys conducted in 2002.

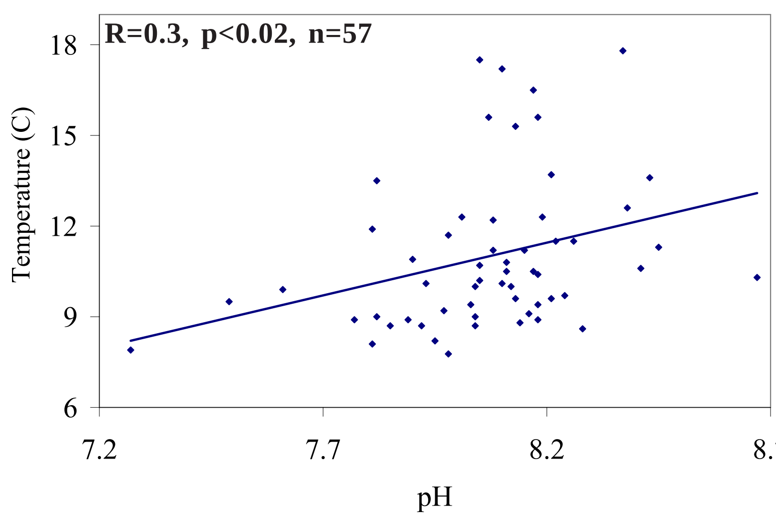

Figure 26. Correlation between pH and temperature measures taken at sites in the Muskegon River watershed as part of freshwater mussel surveys conducted in 2002.

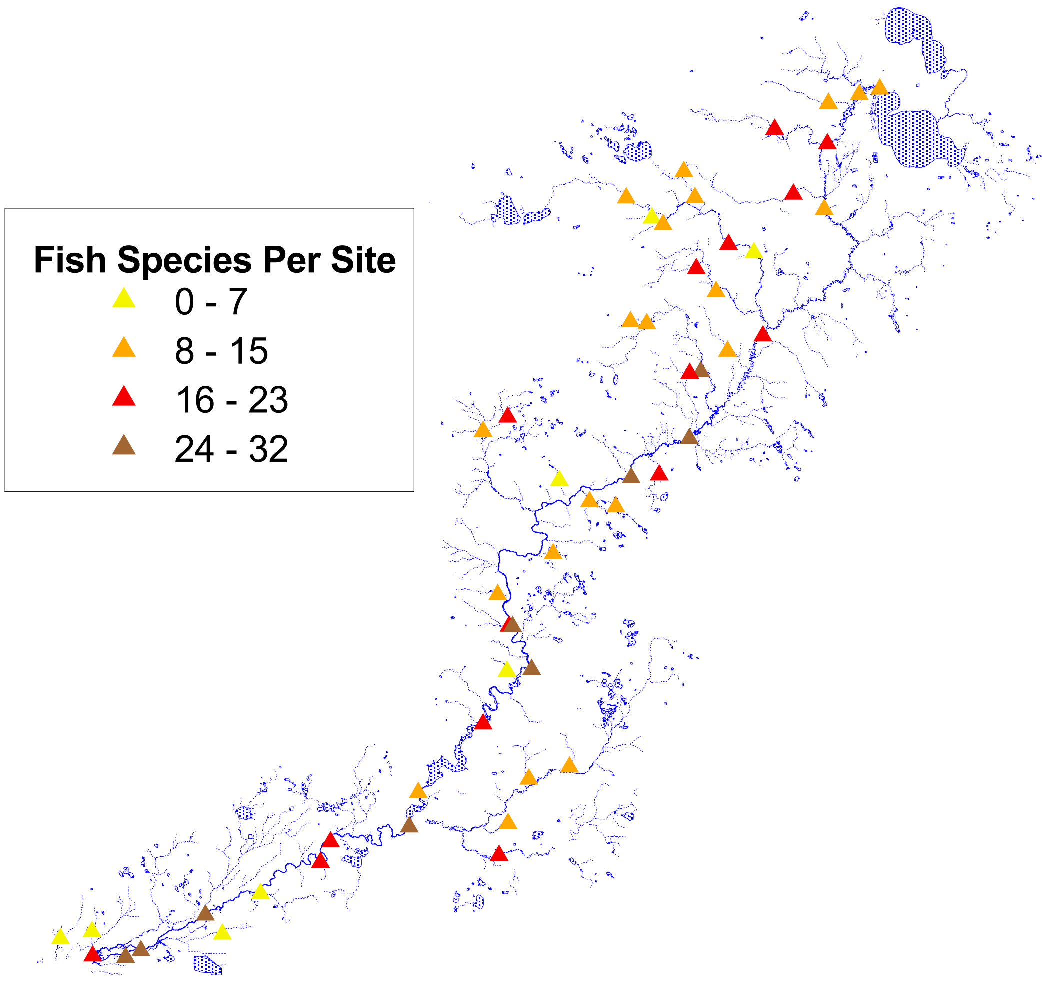

Figure 27. Current fish species richness in the Muskegon River watershed based on field surveys conducted by M. Wiley and C. Riseng (University of Michigan) during summer 2002.

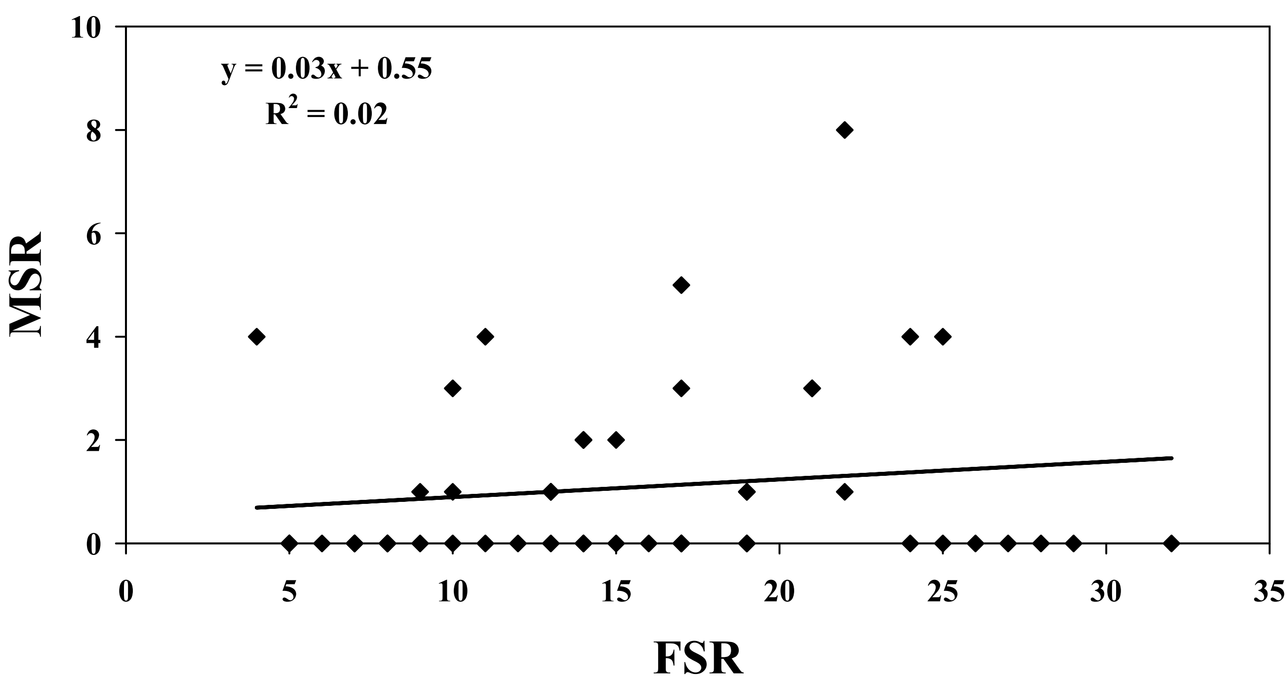

Figure 28. Relationship of mussel species richness (MSR) and fish species richness (FSR) based on surveys conducted at tributary and main stem sites of the Muskegon River watershed, Michigan (2002).

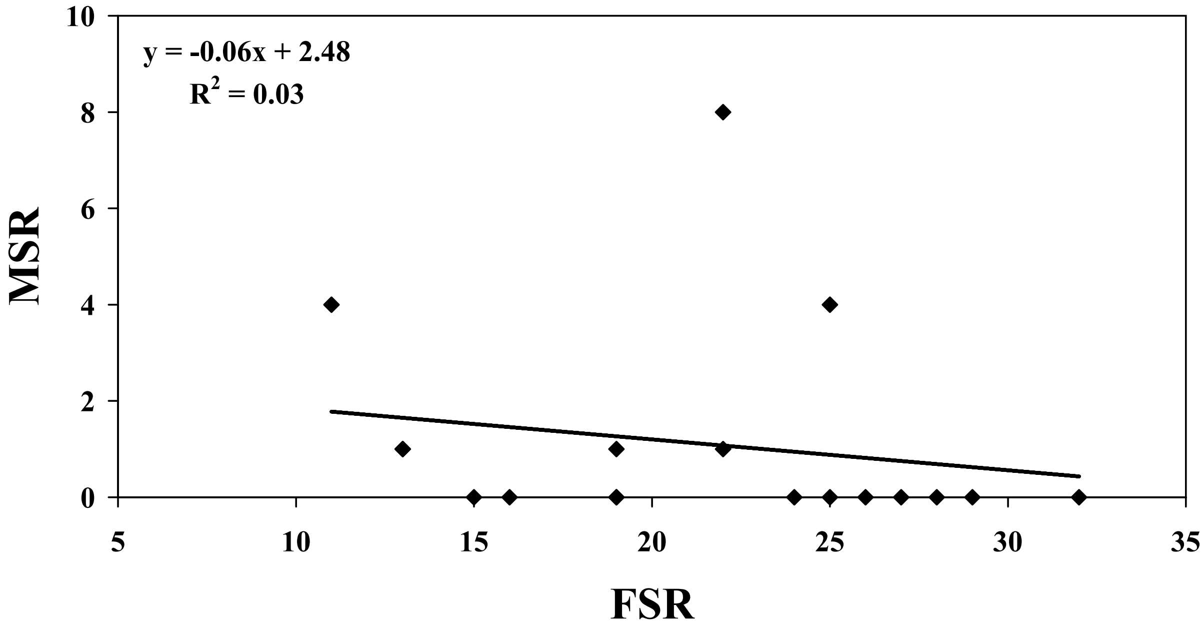

Figure 29. Relationship of mussel species richness (MSR) with fish species richness (FSR) based on surveys of main stem sites in the Muskegon River watershed, Michigan (2002).

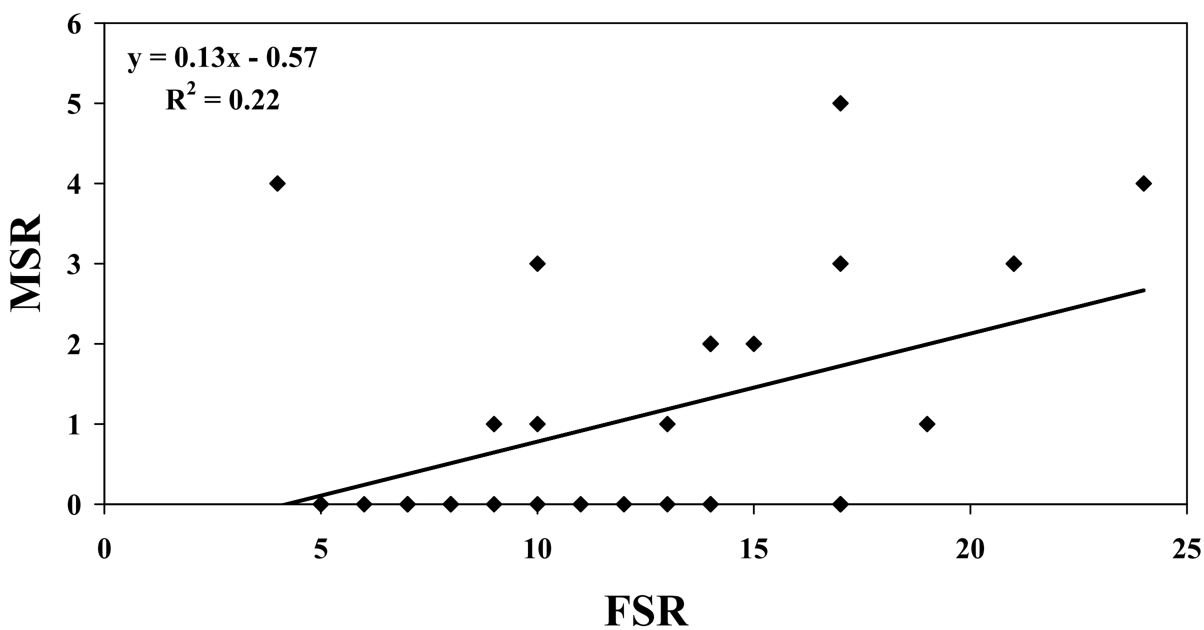

Figure 30. Relationship of mussel species richness (MSR) with fish species richness (FSR) based on surveys of tributary sites in the Muskegon River watershed, Michigan (2002).

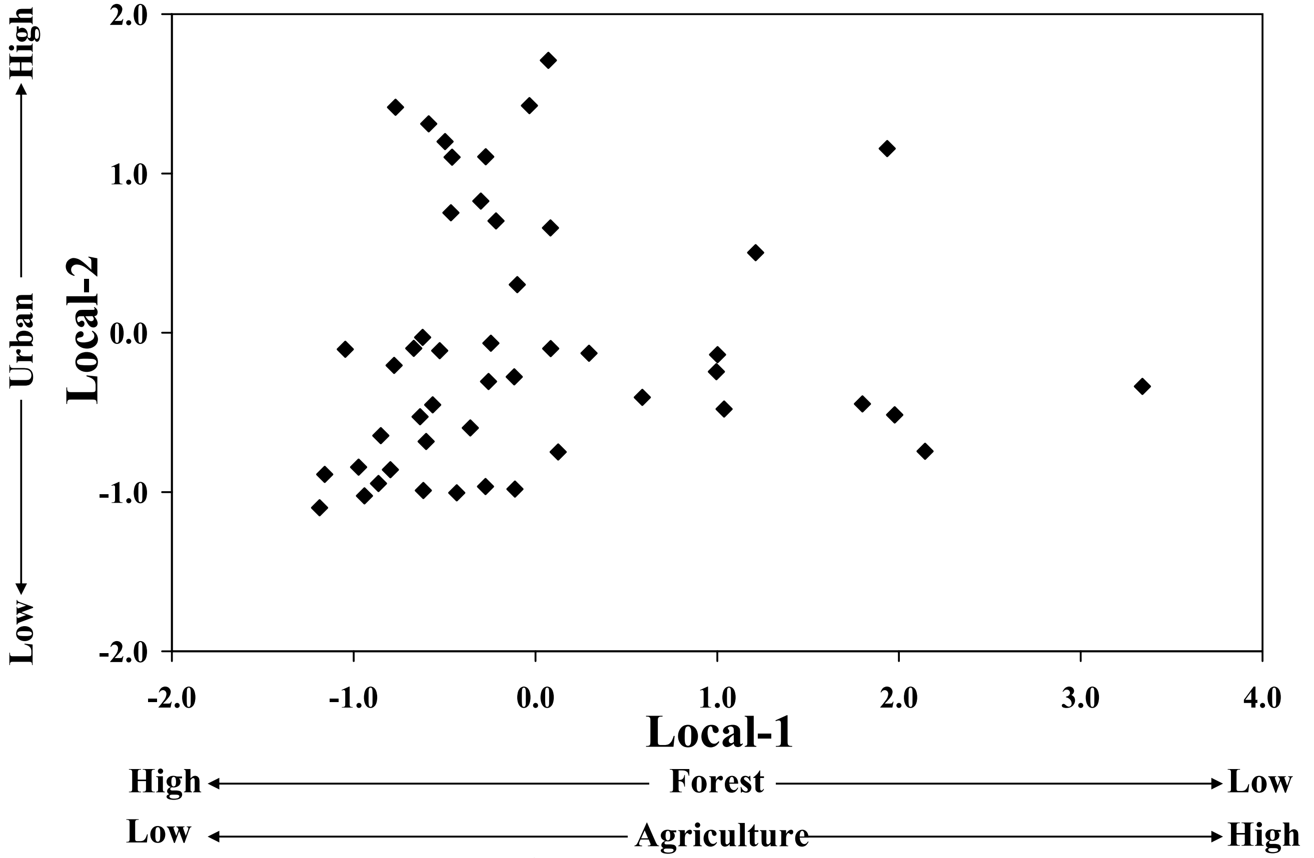

Figure 31. Principal component ordinations of Muskegon River mussel survey sites based on the percentages of land cover types within 30, 60, 120, 240, and 480 m buffers around local stream segments encompassing study sites.

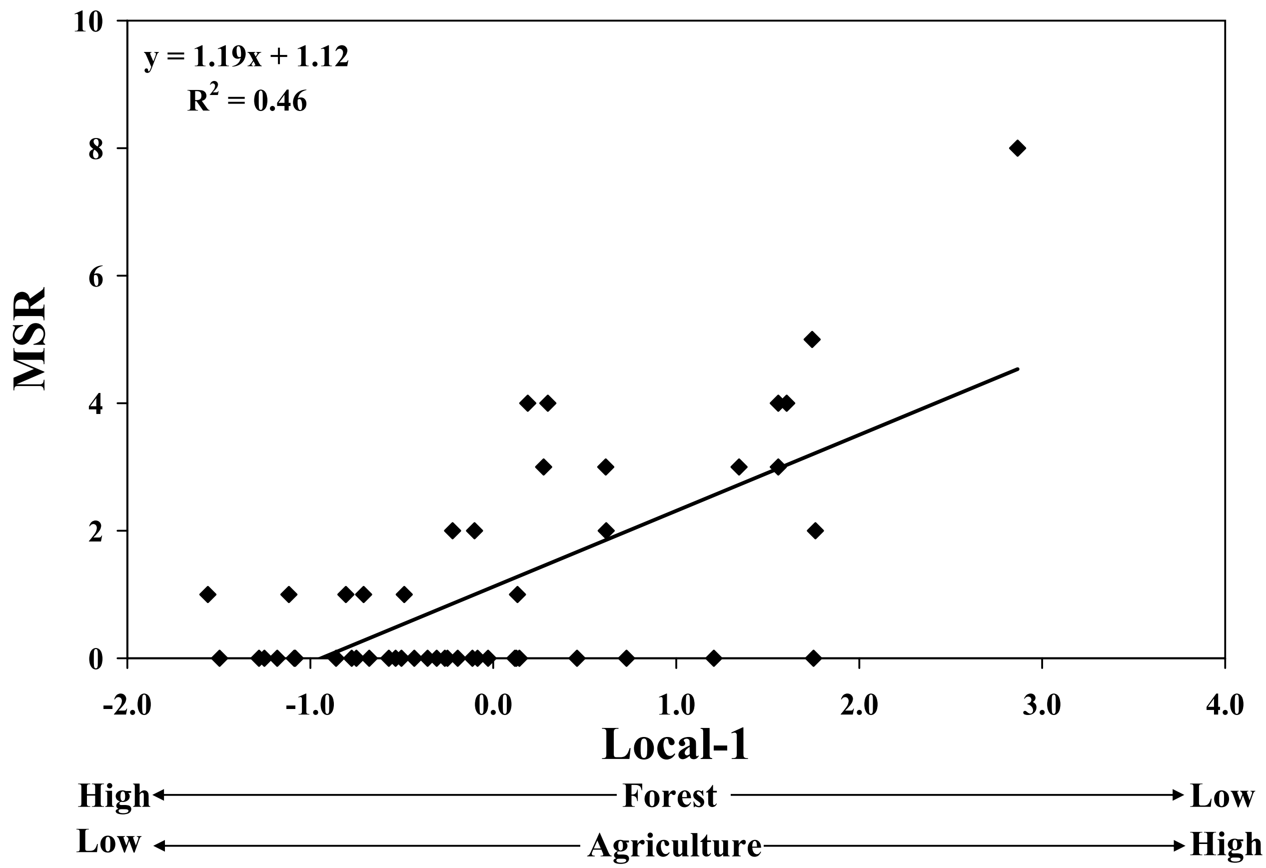

Figure 32. Relationship of mussel species richness (MSR) with principal component one (Local-1) derived from PCA ordination of local buffer land cover data.

Table 10. Correlations of local land cover properties with principal components from the PCA of local land cover data for unionid mussel survey sites in the Muskegon River watershed, Michigan. Pearson correlation coefficients (R) and statistical significance values (p) are provided for each buffer land cover component (n=50). Significant correlations (p<0.005) are highlighted in gray. The percentage of the variance in the data explained by each component is also provided.

		Principal Component					
		Local-1		Local-2		Local-3	
Land Cover Class	Buffer Width (m)	R	p	R	p	R	p
Forest	30	-0.81	<0.001	-0.43	0.002	-0.25	0.08
	60	-0.83	<0.001	-0.40	0.005	-0.25	0.08
	120	-0.84	<0.001	-0.40	0.005	-0.26	0.07
	240	-0.86	<0.001	-0.37	0.008	-0.26	0.07
	480	-0.85	<0.001	-0.33	0.02	-0.17	0.23
Wetland	30	0.20	0.17	-0.19	0.19	0.76	<0.001
	60	0.26	0.07	-0.38	0.008	0.86	<0.001
	120	0.27	0.06	-0.38	0.006	0.86	<0.001
	240	0.25	0.08	-0.39	0.005	0.86	<0.001
	480	0.21	0.15	-0.39	0.006	0.85	<0.001
Agricultural	30	0.81	<0.001	-0.15	0.30	-0.49	<0.001
	60	0.82	<0.001	-0.16	0.28	-0.48	<0.001
	120	0.83	<0.001	-0.17	0.23	-0.48	<0.001
	240	0.84	<0.001	-0.20	0.18	-0.47	0.001
	480	0.83	<0.001	-0.22	0.12	-0.43	0.002
Urban	30	-0.06	0.67	0.88	<0.001	0.12	0.43
	60	-0.06	0.69	0.96	<0.001	0.12	0.40
	120	-0.08	0.59	0.97	<0.001	0.13	0.39
	240	-0.11	0.45	0.97	<0.001	0.12	0.40
	480	-0.15	0.30	0.92	<0.001	0.13	0.38
%Variance Explained		36		30		25	

Table 11. Correlations of US1 buffer land cover properties with principal components from the PCA of US1 buffer land cover data for unionid mussel survey sites in the Muskegon River watershed, Michigan. Pearson correlation coefficients (R) and statistical significance values (p) are provided for each buffer land cover component (n=50). Significant correlations (p<0.005) are highlighted in gray. The percentage of the variance in the data explained by each component is also provided.

		Principal Component							
		US1-1		US1-2		US1-3		US1-4	
Land Cover Class	Buffer Width (m)	R	p	R	p	R	p	R	p
Forest	30	-0.92	<0.001	0.10	0.48	0.11	0.46	0.15	0.29
	60	-0.94	<0.001	0.11	0.46	0.16	0.29	0.14	0.32
	120	-0.95	<0.001	0.10	0.51	0.18	0.21	0.14	0.34
	240	-0.94	<0.001	0.05	0.76	0.21	0.14	0.13	0.38
	480	-0.90	<0.001	-0.04	0.76	0.26	0.07	0.13	0.39
Wetland	30	0.63	<0.001	-0.08	0.57	0.72	<0.001	0.12	0.42
	60	0.63	<0.001	-0.07	0.64	0.74	<0.001	0.09	0.53
	120	0.63	<0.001	-0.08	0.59	0.75	<0.001	0.09	0.53
	240	0.64	<0.001	-0.09	0.52	0.75	<0.001	0.08	0.61
	480	0.64	<0.001	-0.12	0.41	0.72	<0.001	0.07	0.63
Agricultural	30	0.36	0.01	0.83	<0.001	-0.34	0.02	0.1	0.51
	60	0.37	0.009	0.85	<0.001	-0.32	0.02	0.08	0.57
	120	0.52	<0.001	0.53	<0.001	-0.57	<0.001	-0.03	0.85
	240	0.36	0.01	0.87	<0.001	-0.29	0.04	0.06	0.7
	480	0.37	0.009	0.86	<0.001	-0.22	0.13	0.05	0.71
Urban	30	0.34	0.02	-0.73	<0.001	-0.53	<0.001	0.12	0.4
	60	0.34	0.02	-0.73	<0.001	-0.54	<0.001	0.12	0.42
	120	0.14	0.33	0.07	0.66	-0.17	0.23	0.93	<0.001
	240	0.34	0.02	-0.73	<0.001	-0.55	<0.001	0.1	0.48
	480	0.30	0.04	-0.71	<0.001	-0.57	<0.001	0.07	0.66
%Variance Explained		38		27		24		5	

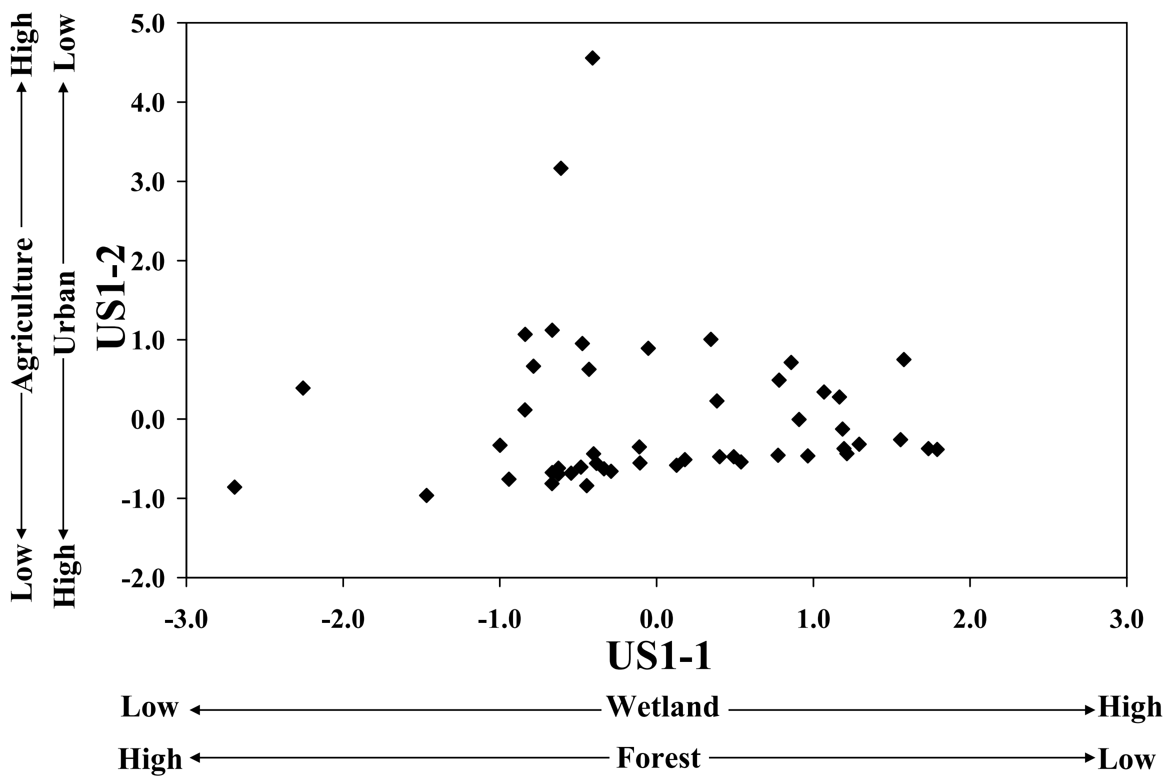

Figure 33. Principal component ordinations of Muskegon River mussel survey sites based on the percentages of land cover types within 30, 60, 120, 240, and 480 m buffers around US1 stream segments located upstream of study sites.

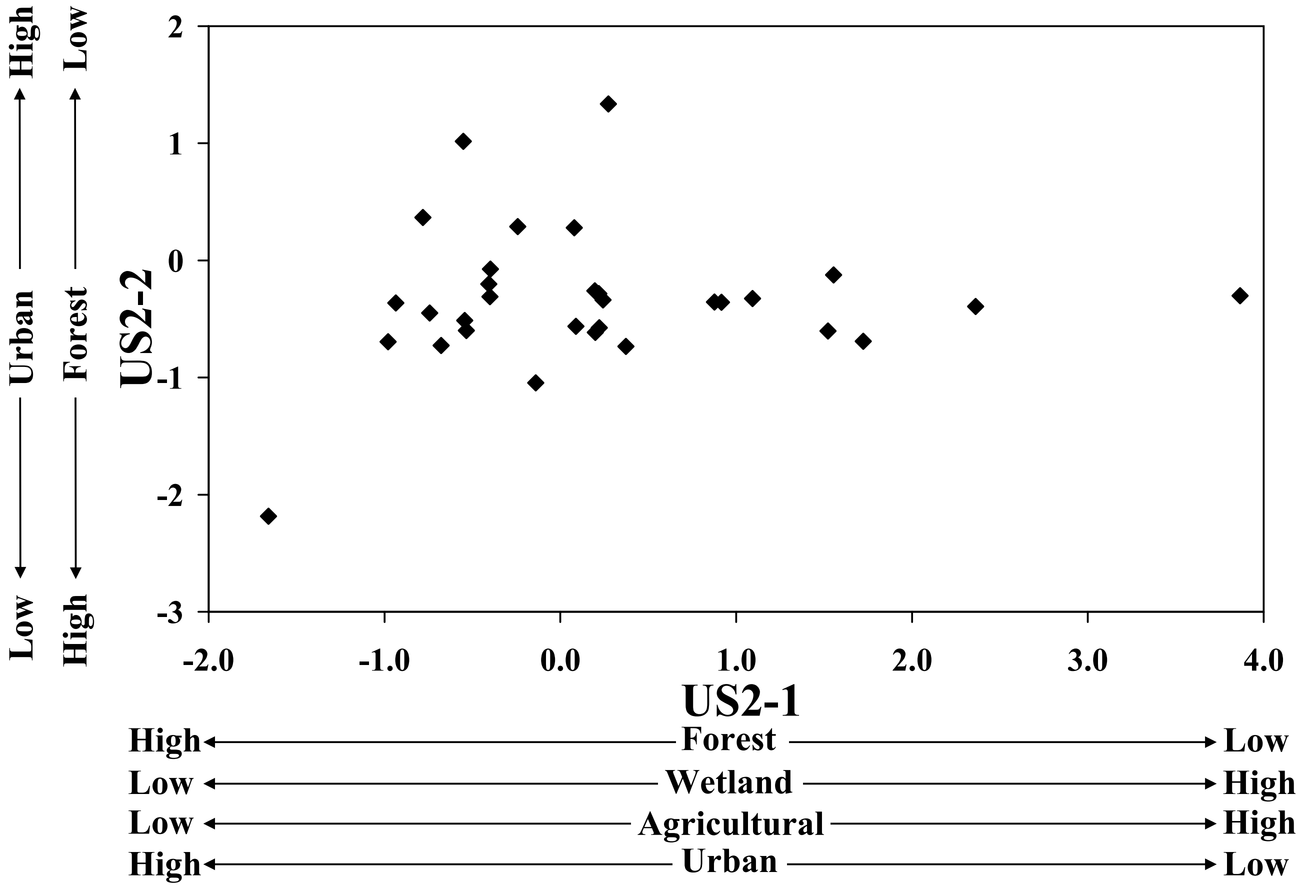

Figure 34. Principal component ordinations of Muskegon River mussel survey sites based on the percentages of land cover types within 30, 60, 120, 240, and 480 m buffers around US2 stream segments located upstream of study sites.

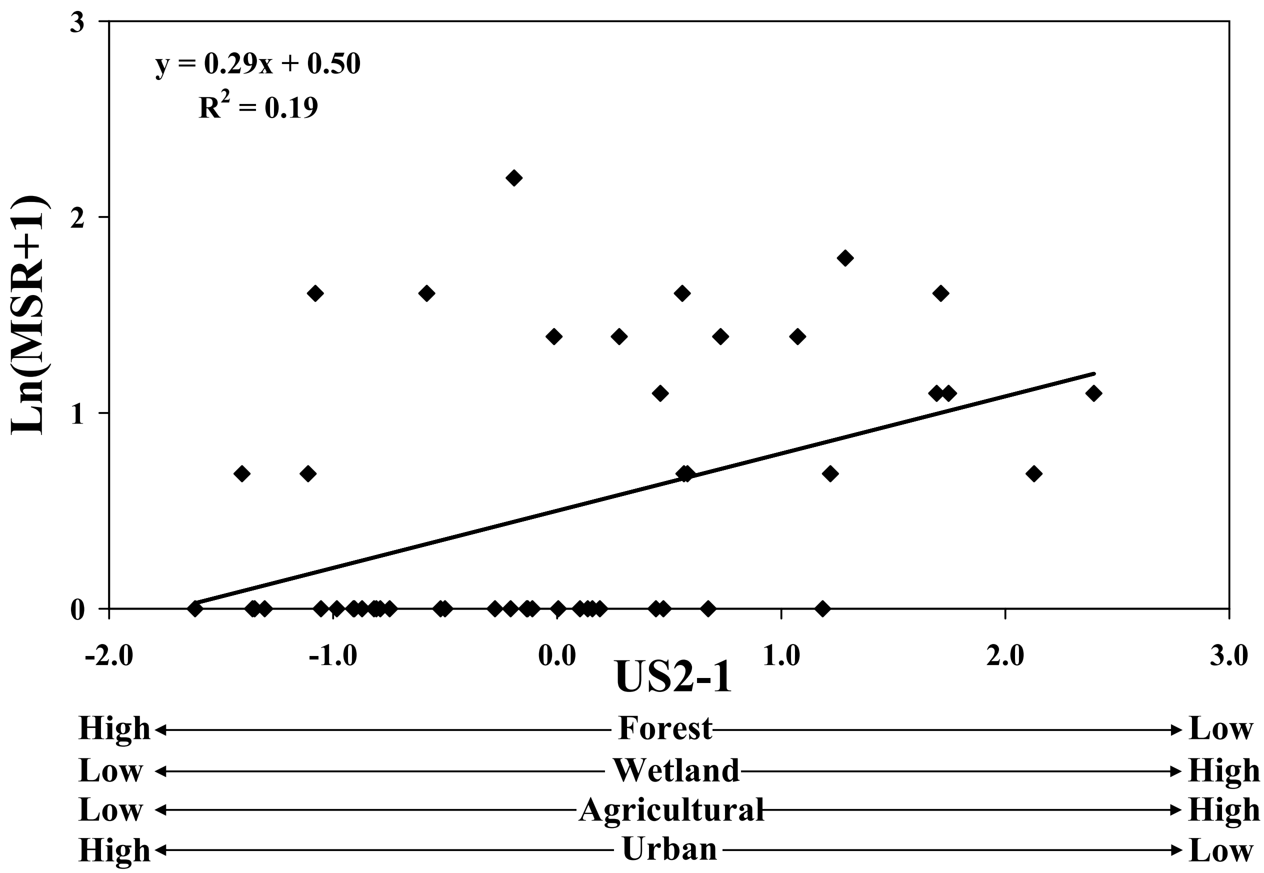

Figure 35. Relationship of Ln(MSR+1) with principal component 1 (US2-1) derived from PCA ordination of US2 buffer land cover data.

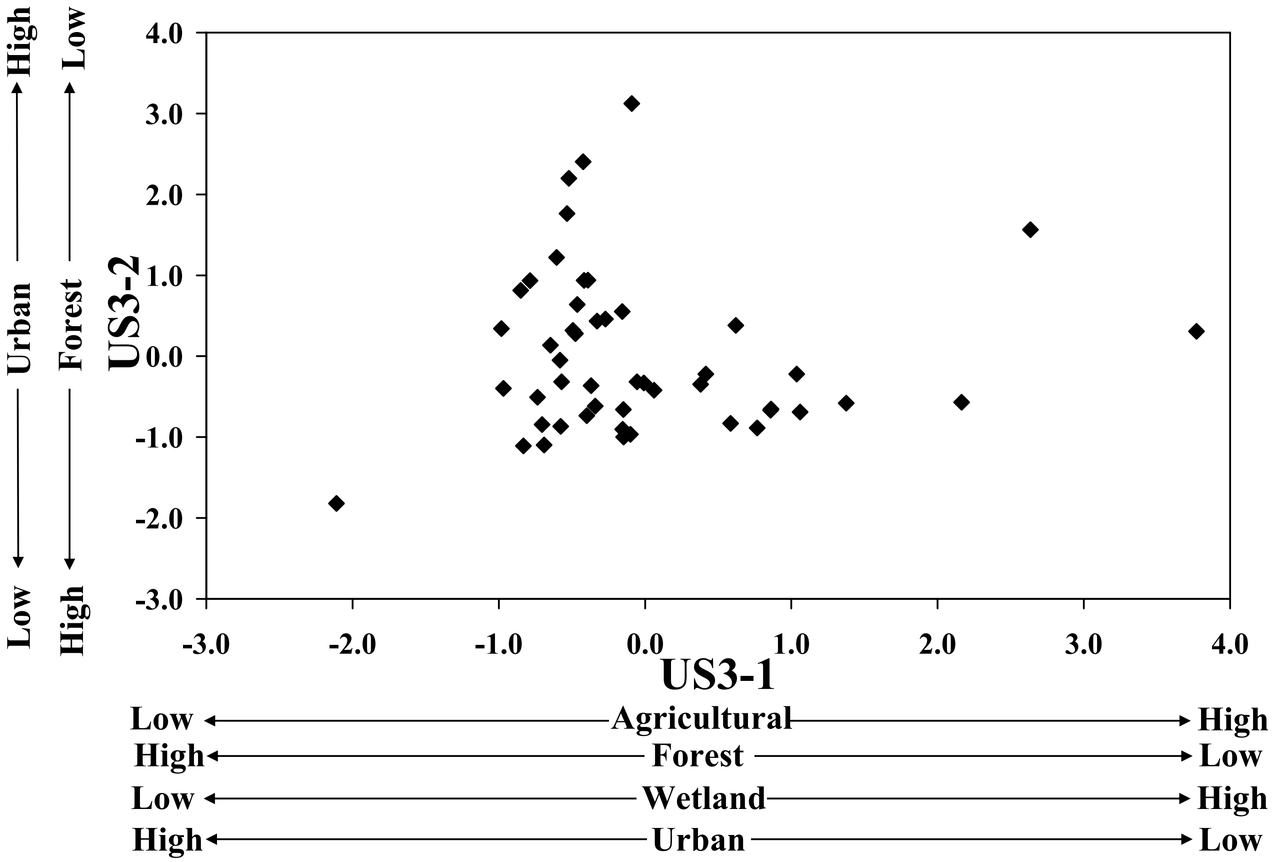

Figure 36. Principal component ordinations of Muskegon River mussel survey sites based on the percentages of land cover types within 30, 60, 120, 240, and 480 m buffers around US3 stream segments located upstream of study sites.

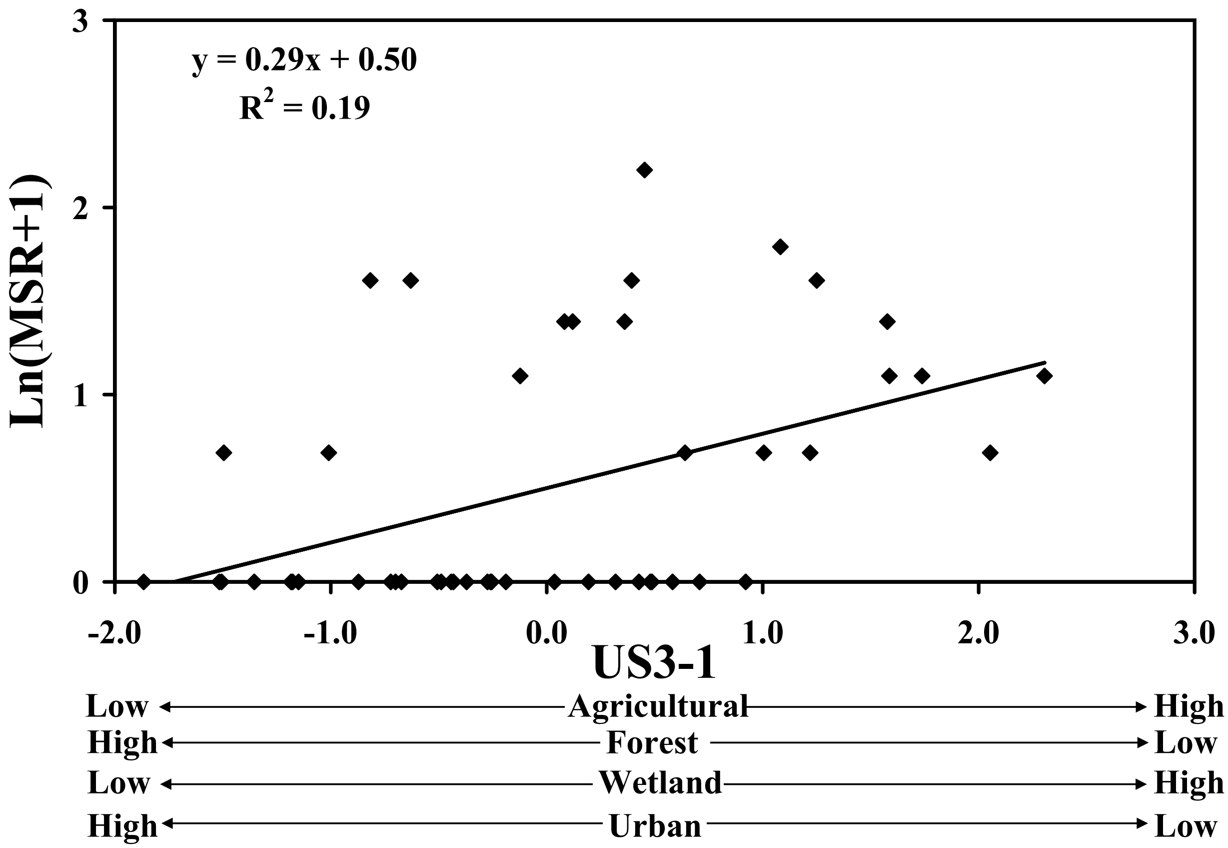

Figure 37. Relationship of Ln(MSR+1) with principal component 1 (US3-1) derived from PCA ordination of US3 buffer land cover data.

Table 12. Correlations of US2 buffer land cover properties with principal components from the PCA ordinations of US2 buffer land cover data for unionid mussel survey sites in the Muskegon River watershed, Michigan. Pearson correlation coefficients (R) and statistical significance values (p) are provided for each buffer land cover component (n=50). Significant correlations (p<0.005) are highlighted in gray. The percentage of the variance in the data explained for each component is also provided.

		Principal Component							
		US2-1		US2-2		US2-3		US2-4	
Land Cover Class	Buffer Width (m)	R	p	R	p	R	p	R	p
Forest	30	-0.56	<0.001	-0.75	<0.001	0.04	0.79	0.30	0.03
	60	-0.55	<0.001	-0.77	<0.001	0.05	0.75	0.29	0.05
	120	-0.56	<0.001	-0.77	<0.001	0.05	0.72	0.28	0.05
	240	-0.60	<0.001	-0.74	<0.001	0.07	0.63	0.26	0.08
	480	-0.61	<0.001	-0.69	<0.001	0.09	0.52	0.23	0.11
Wetland	30	0.45	0.001	0.11	0.45	0.86	<0.001	0.18	0.22
	60	0.45	0.001	0.09	0.56	0.87	<0.001	0.18	0.23
	120	0.45	0.001	0.09	0.56	0.87	<0.001	0.18	0.22
	240	0.46	0.001	0.09	0.53	0.86	<0.001	0.17	0.24
	480	0.46	0.001	0.12	0.41	0.84	<0.001	0.16	0.28
Agricultural	30	0.79	<0.001	-0.03	0.82	-0.53	<0.001	0.29	0.04
	60	0.79	<0.001	-0.03	0.83	-0.52	<0.001	0.29	0.04
	120	0.80	<0.001	-0.03	0.86	-0.52	<0.001	0.29	0.05
	240	0.81	<0.001	-0.05	0.75	-0.50	<0.001	0.29	0.05
	480	0.84	<0.001	-0.05	0.71	-0.42	0.003	0.29	0.04
Urban	30	-0.60	<0.001	0.75	<0.001	-0.07	0.61	0.25	0.08
	60	-0.58	<0.001	0.76	<0.001	-0.07	0.63	0.25	0.08
	120	-0.59	<0.001	0.76	<0.001	-0.07	0.63	0.26	0.07
	240	-0.59	<0.001	0.76	<0.001	-0.08	0.60	0.27	0.06
	480	-0.60	<0.001	0.73	<0.001	-0.10	0.49	0.27	0.06
%Variance Explained		38		28		25		6	

Table 13. Correlations of US3 buffer land cover properties with principal components from the PCA of US3 buffer land cover data for unionid mussel survey sites in the Muskegon River watershed, Michigan. Pearson correlation coefficients (R) and statistical significance values (p) are provided for each buffer land cover component (n=50). Significant correlations (p<0.005) are highlighted in gray. The percentage of variance in the data explained for each component is also provided.

		Principal Component							
		US3-1		US3-2		US3-3		US3-4	
Land Cover Class	Buffer Width (m)	R	p	R	p	R	p	R	p
Forest	30	-0.58	<0.001	0.71	<0.001	-0.20	0.17	0.30	0.04
	60	-0.59	<0.001	0.71	<0.001	-0.20	0.18	0.30	0.04
	120	-0.61	<0.001	0.72	<0.001	-0.18	0.22	0.26	0.07
	240	-0.64	<0.001	0.71	<0.001	-0.13	0.36	0.28	0.05
	480	-0.65	<0.001	0.66	<0.001	-0.06	0.69	0.24	0.10
Wetland	30	0.47	0.001	0.22	0.12	0.83	<0.001	0.16	0.27
	60	0.47	0.001	0.22	0.12	0.83	<0.001	0.17	0.25
	120	0.47	0.001	0.22	0.13	0.83	<0.001	0.18	0.22
	240	0.48	0.001	0.19	0.20	0.83	<0.001	0.19	0.20
	480	0.47	0.001	0.15	0.32	0.82	<0.001	0.19	0.19
Agricultural	30	0.79	<0.001	-0.15	0.30	-0.49	<0.001	0.30	0.04
	60	0.80	<0.001	-0.15	0.30	-0.49	<0.001	0.30	0.04
	120	0.80	<0.001	-0.14	0.32	-0.49	<0.001	0.30	0.04
	240	0.81	<0.001	-0.11	0.44	-0.49	<0.001	0.30	0.04
	480	0.81	<0.001	-0.08	0.59	-0.45	0.001	0.31	0.03
Urban	30	-0.60	<0.001	-0.73	<0.001	0.17	0.25	0.25	0.09
	60	-0.60	<0.001	-0.74	<0.001	0.17	0.24	0.25	0.08
	120	-0.61	<0.001	-0.73	<0.001	0.17	0.23	0.26	0.07
	240	-0.60	<0.001	-0.73	<0.001	0.17	0.25	0.28	0.06
	480	-0.60	<0.001	-0.72	<0.001	0.13	0.38	0.27	0.06
%Variance Explained		40		27		24		7	

DISCUSSION

The Muskegon River lies near the division of southern and northern Lower Michigan, along which aquatic communities tend to stratify. Fish communities are generally dominated by warmwater species in the Grand and St. Joseph Rivers in southern Lower Michigan, and cool and coldwater species in the Manistee and Pere Marquette Rivers in northern Lower Michigan. Unionid mussels also tend to be more numerous in warmwater vs. cool/coldwater systems. For example, 32 unionid species have been reported from the Grand River (Goforth et al. 2000), and some of these species occurred in sufficient numbers to sustain a button factory in the early 1900's. In comparison, we have observed very few unionid mussel species and in very limited numbers in the typically cool/coldwater streams and rivers of northern Lower Michigan and the Upper Peninsula of Michigan. These patterns are generally consistent with the regional landscape ecosystem boundaries delineated by Albert (1995). This unique geographic context of the Muskegon River watershed therefore provides a unique opportunity to explore the nature of mussel communities and populations within the context of a transitional landscape.

The Grand River watershed lies just to the south of the Muskegon River wateshed and is characterized by higher MSR (32 species) compared to the historical MSR (18 species) reported by van der Schalie (1941) for the Muskegon River. This considerably lower MSR for the Muskegon River compared to the Grand River is not surprising and is suggestive of a transitional fauna between the more speciose southern rivers and the more faunally depauperate northern rivers in Michigan. However, the sharply lower MSR and abundances of unionids in the Muskegon River observed in 2002 were surprising when considered at both the watershed (14 species total) and site levels (0-8 sp/site). At the watershed scale, five unionid species have apparently been extripated from the Muskegon River over the past 65 years, including several species of global and regional concern. In addition, van der Schalie (1941) observed that unionids were consistently distributed throughout the watershed and were present in all areas of the river that he surveyed. Most mainstem sites surveyed in 2002 had no live unionids present, suggesting that native mussels have been nearly to completely extirpated in the mainstem reaches of the lower Muskegon River watershed. Based on our survey results, it appears that mussel populations have significantly declined and that mussel community structures have become dramatically altered from those reported historically by van der Schalie (1941).

The observed declines in and losses of MSR in the Muskegon River watershed are cause for great concern, and there are multiple factors that have likely contributed to these changes in the mussel fauna. One major documented cause of mussel species declines is habitat loss related to increased siltation, pollution, stream channel modifications, and altered flow regimes (Pennak 1989, Bogan 1993, Williams & Neves 1995). While the Muskegon River has been influenced by many such anthropogenic stressors over the past 65 years, the factor for which we have the best comparative information is the alteration of the river's natural flow regime through the construction and operation of dams. Damming is known to drastically alter riverine environments and has been identified as the primary cause of several mussel species declines and extirpations (Ortmann 1909, Benke 1990, Bogan 1993, Yeager 1993, Vaughn & Taylor 1999).

When van der Schalie completed his survey in 1934, Rogers, Hardy, and Croton dams were already in place. In addition, there were also major dams at Newaygo and Big Rapids, which have since been removed. Yet, even with more operating dams in the 1930s than currently, there were more species in the river in 1934 than in 2002 (van der Schalie 1941). There are several possible explanations for this trend. Mussels are relatively long-lived creatures that are commonly characterized by life spans up to 50 years and delayed maturity (Bauer 1983, Bauer 1992, McMahon 1991, Badra et al. 1999). They are also characterized by reduced dispersal (Kat 1984), overall poor juvenile survival (Yeager et al. 1994, Sparks & Strayer 1998), and limited capacity to move in response to local habitat destruction (Sibly & Calow 1986, Townsend 1989, Badra & Goforth 2001). These traits contribute to a lag between habitat degradation and the demise of the species (Bogan 1993). While older, mature adults may be present at a site, unsuccessful recruitment of young mussels due to reduced reproductive potential of individual mussels will result in functional impairement of populations. Larger, older mussels are easier to detect using common mussel survey techniques, and the reproductive potential of the population may be overestimated based solely on these individuals. In the Muskegon River, where the majority of the dams were constructed in the early 1900's, the effects of altered hydrology may not have been detectable in 1934 based on the survey data collected by van der Schalie. Adult unionids that were persisting but no longer reproducing in 1934 would likely have been lost to natural mortality or environmental change in the time period between 1934 and 2002. Hence, detection of declining mussel populations in response to changes in hydrologic regime or other enviromental factors that were not apparent in 1934 would now be quite evident based on the absence of several species at both site and watershed scales in 2002.

Mussel species richness in a system has been shown to be significantly related to fish species richness, likely due to the reliance of mussels on fish to serve as hosts for larval stages of unionids (Strayer 1983, Bogan 1993, Goforth et al. 2001). This trend was apparent in the tributaries of the Muskegon River, where mussel species richness exhibited a positive relationship with fish species richness. However, this relationship was not observed for mainstem areas of the Muskegon River. There was no significant decline in fish species richness in these lower reaches, although there was a drastic decline in MSR. While the fish community of the mainstem has changed, due primarily to the stocking of sport fish, the magnitude of the loss in fish species is not equal to that of the loss of mussel species. The loss of mussel species in the mainstem of the Muskegon River without a corresponding loss of host fishes suggests that changes in the fish community are not likely to be the primary reason for the general decline observed in MSR for the watershed.

Another factor known to have devastating effects on native mussels is the presence of zebra mussels (Schloesser et al. 1998, Strayer 1999). Their presence in lower reaches of the watershed has likely contributed to the loss of native species. When the presence of zebra mussels was compared with the loss of native mussel species between 1934 to 2002, the results strongly suggested that zebra mussels have had a negative impact on the native mussels of the Muskegon River watershed. In fact, at sites where zebra mussels are present, no live native mussels were found. While at some sites zebra mussel densities were fairly low (i.e., limited to several individuals observed in the entire reach), a few sites were characterized by having all local substrates colonized heavily by *D. polymorpha*. While we cannot completely rule out other factors as conributing to the loss of unionids at these sites before colonization by *D. polymorpha*, there is little question that any remaining unionids at these sites were extipated by the presence of zebra mussels post-colonization. Further, the presence of *D. polymorpha* at these sites precludes any potential for recovery of native unionids at these sites.

One of the more notable mussel species that has apparently become extirpated from the Muskegon River watershed is *E. triquetra*, the snuffbox. This globally threatened species was apparently not common in the Muskegon River historically; the site reported by van der Schalie (1941) is the only known occurrence in the watershed. However, this historical rarity should not be interpreted as indicating an insignificant or insecure population of *E. triquetra.* Recent surveys of the Grand River conducted by Goforth et al. (2000) have documented several species that were rare in both the 1940s and in 1999 (e.g., *L. recta* and *Cyclonaias tuberculata*). Despite these low numbers, multiple age classes were observed in 1999, suggesting recent successful reproduction and recruitment events (Goforth et al. 2000). This suggests that some mussel species may naturally occur in low, but sustainable densities. In fact, occurrences of *E. triquetra* in the Grand River suggest that this species also exhibits this low density strategy (Goforth et al. 2000). However, the implications of existing in low numbers also makes populations of these species more susceptible to stochastic catastrophic events that can lead to extipation. Low densities of individuals would also make these species more susceptible to chronic environmental stresses due to the decreased likelihood of sparsely distributed individuals to be reproductively successful under these conditions.

While MNFI did find a spent *E. triquetra* valve at the historical site described by van der Schalie (1941), no live specimens were observed in 2002. This site, which was classified as always having a dam, is in the lower reaches of the watershed and is downstream of all the major impoundments. In 2002, only live zebra mussels were found at this site, although van der Schalie (1941) reported ten unionid species. Chronic environmental degradation of the lower portion of the river related to altered hydrology and the presence of introduced species (i.e., *D. polymorpha*) have likely caused *E. triquetra* to be extirpated from this site and the basin overall. In addition, the only known fish host for this species in Michigan is the logperch (*Percina caprodes*) (Sherman 1994). Logperch were rare in the lower portion of the river historically, and the University of Michigan research team did not collect logperch at the *E. triquetra* site. The rarity of logperch may be affecting the reproductive success of the snuffbox. However, it must be noted that although *P. caprodes* was identified as the only successful host in one study, a truly comprehensive evaluation of fish hosts species for *E. triquetra* has not been performed, and there may be other successful fish hosts in the lower reaches of the Muskegon River watershed that have not yet been discovered. Hence, while the absence of *E. triquetra* in our surveys and concomitant disappearance of *P. caprodes* suggests that fish host loss is a major factor for the decline of *E. triquetra* in the Muskegon River watershed, we can not completely rule out other factors that may have contibuted to or caused the apparent extirpation of this species.

Other unionid species not observed in 2002 include *P. alatus, P. sintoxia*, *L. recta,* and *L. compressa*. *P. alatus*, like *E. triquetra*, was only reported at one lower watershed site in 1934 (van der Schalie 1941). The only known host for this species is the freshwater drum (*Aplodinotus grunniens*) (Watters 1994), which was found in the mainstem of the river in 2002 (Riseng and Wiley, unpub. data). *P. sintoxia* and *L. recta* were found at several Muskegon River mainstem sites in 1934 (van der Schalie 1941). While MNFI did find spent shells of these species, most of the areas that these mussels once inhabited were devoid of live mussels in 2002. Both species have a variety of known hosts, including bluegill (*Lepomis macrochirus*) (Watters 1994), which occur commonly throughout the Muskegon River watershed. Thus, the apparent extirpations of these species in the lower watershed does not appear to be attributable to lack of a host species. Both species appear to naturally occur in small numbers in Michigan rivers, and their absence from sites in 2002 surveys was likley the result of the inabilities of these species to remain reproductively successful in response to chronic environmental degradation (e.g., hydrologic alterations), habitat loss, and invasions of *D. polymorpha* in the Muskegon River.

L. compressa was also found in 1934, but not in 2002. Unlike the other absent species, this species was found more commonly in tributary streams. The hosts of this mussel are not currently known, and little information exists regarding its specific habitat requirements. In general, it typically occurs in small rivers and streams with variable substrates (Clarke 1981). While it is considered to be widespread, occurring throughout most of the Midwest and eastern Canada, it is locally uncommon throughout much of its range (Cummings & Meyer 1992). It is considered threatened, endangered, or of special concern throughout much of its range, although it is not currently listed in Michigan (NatureServe 2003). Its absence from a watershed where it was once common, occurring at over half of the tributary sites surveyed in 1934, is cause for concern and may indicate a need for a heightened conservation status for this species.

One mussel species was found in the Muskegon River in 2002 that had previously not been reported, *L. nasuta*. *L. nasuta* typically occurs in lakes and back-water areas of rivers, in mud or sand (Clarke 1981). This species was generally found higher in the watershed, near the Dead Stream Flooding, and it is assumed that the flooded, still-water habitat created by the construction of Reedsburg Dam in 1940 led to the creation of habitat for this species. While there are no records of this species in any areas of the watershed, thorough surveys have not been completed for most of the lakes. This species was probably historically found in Houghton and Higgins Lakes and has since spread into the slack-water areas of the river created by the construction of dams.

Understanding the influences that landscape-driven processes have on mussel populations is key for effective conservation of these taxa (Arbuckle & Downing 2002). In general, land uses that result in the removal of vegetative land cover alter hydrology, increase erosion rates, and contibute greater nutrient loads to adjacent streams and rivers, influencing physical habitat and water quality over multiple spatial scales (Richards & Host 1994, Roth et al. 1996, Arbuckle & Downing 2002). Therefore, population persistence of aquatic organisms in general, and unionid mussels in particular, can be influenced by landscape features such as land use, surface geology, and soil (Strayer 1983, Morris & Corkum 1996, Brim Box & Mossa 1999, Kopplin 2002).

Principal components ordinations of sites based on land cover properties of buffers delineated over multiple landscape contexts yielded no apparent aggregations of sites based on four land cover types (i.e., agricultural, urban/residential, forest, and wetland). However, MSR data were significantly related to several synthetic variables derived from the PCAs. The strongest relationship observed was between MSR and the local land cover component described by Local-1. This principal component explained variation along an agriculture-forest continuum, with MSR increasing as the spatial extent of land covers transitioned from largely forest to largely agriculture. While this outwardly appears to suggest that MSR benefits from an association with agricultural land covers, it is more likely that both agricultural land uses and mussels are related to underlying surface geology features of the buffer areas used for analysis (Strayer 1983, Badra et al. 1999, Kopplin 2002). Highly permeable, generally coarser surface geology types and associated soils are more desirable for agricultural production, but they also provide desirable substrates and higher groundwater influx to streams that are favorable to mussel populations (e.g., Badra et al. 1999). Other areas of the watershed are dominated by poorly drained, finer surface geology and soil types. Stream reaches associated with these areas tend to be characterized by deeper channels with large amounts of fine sediments and relatively high turbidity, properties that are generally not tolerated by most mussel species. Adjacent land covers in these areas of the river are generally broad floodplain forests that are seasonally inundated and unusable for agriculture, hence their persistence in a landscape where agriculture would otherwise dominate. While this explanation for the relationship of MSR with Local-1 seems likely, targeted analysis of covariance for the MSR and land cover data relative to surface geology characteristics of local buffers is needed to evaluate this hypothesis. Regardless, the apparent coincidence of preferred mussel habitat with nearstream areas that are desirable for agricultural land uses suggests that careful management of these agricultural lands is necessary to help to insure the long-term viability of local mussel populations.

Mussel faunas are known to change along the course of a river, with some species dominating headwaters, while others thrive in the large mainstem areas of rivers, (Ortmann 1919, van der Schalie 1938, Strayer 1983, Goforth et al. 2000). However, the drastic pattern of decline seen along the course of the Muskegon River should be regarded with great concern. When comparing the pattern reported here with that seen in other large Lake Michigan tributary rivers, including the nearby Grand and St. Joseph Rivers, the loss in mussel species richness in the mainstem of the Muskegon River is extreme. In both of these rivers, unlike the Muskegon River, there are sustainable populations (i.e., smaller individuals present indicate recent reproduction) of several mussel species in the lower mainstem areas of these rivers. However, when the Muskegon River is compared with another heavily impacted river system in Michigan, the River Raisin, a tributary to Lake Erie, a similar trend of decreasing species richness and density lower in the watershed has been reported (Kopplin 2002). The Muskegon River, like the River Raisin, appears to be suffering from the cumulative impacts, both down river and through time, of human settlement and sustained development in the watershed, that has led to a drastic decrease in its mussel population, most notably in the lower portions. As other large rivers, like the Grand and St. Joseph River, accumulate more human impacts, this trend may become more pronounced and lead to a loss of mussel diversity in the mainstem portion of these rivers as well.

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