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Mussel (Bivalvia: Unionidae) Habitat Suitability Criteria

for the Otter Tail River, Minnesota

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Rick Alan Hart

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Title

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The Supervisory Committee certifies that this **disquisition** complies with North Dakota State University's regulations and meets the accepted standards for the degree of

MASTER OF SCIENCE

SUPERVISORY COMMITTEE:

Chair

Approved by Department Chair:

22 January 1996
Date

Signature

Abstract

Hart, Rick Alan, M.S., Department of Zoology, College of Science and Mathematics, North Dakota State University, May 1995. Mussel (Bivalvia: Unionidae) Habitat Suitability Criteria for the Otter Tail River, Minnesota. Major Professor: Dr. John J. Peterka.

Habitat suitability data for 4851 mussels, representing 13 species, were collected from sample sites on the Otter Tail River, MN. Habitat suitability criteria were developed for seven species of unionid mussels. *Amblema plicata, Fusconaia flava, Lasmigona costata,* and *Strophitus undulatus* all had similar preferences for velocity, depth, substrate, and cover. Velocities most preferred were about 80 cm/s with velocities < 25 cm/s having no suitability. Depths of 150 cm were the most preferred; depths < 60 cm had no suitability. These four mussel species were found most often in gravelly substrates with no instream cover. *Amblema plicata, Fusconaia flava, Lasmigona costata,* and Strophitus *undulatus* were found most often in the run habitats. Habitats most suitable for *Anodonta grandis* were slow moving (<10 cm/s), deep waters (135 cm) where aquatic vegetation was present. Headwater sites had lower mussel density and the least amount of species than did the downstream sites. Changes in density and species composition may be lack of suitable habitat, low stream flows in the upstream reaches, or downstream dams blocking the passage of glochidia-infected fish. The habitat suitability criteria developed in this study may aid in the establishment of protected stream flows, preserving the run habitats most suitable for the mussels residing in the Otter Tail River.

Acknowledgments

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I dedicate this thesis to my family, including my wife, Ranae, and son, Justin; my parents, Richard and Beverly Hart; and my in-laws, Kenneth and Virginia Wasnie. Without their emotional and financial support, this thesis would not have been possible. My wife, Ranae, and son, Justin, deserve great thanks for having patience and understanding while I was pursuing my educational goals. Words alone cannot express my love and appreciation for their support.

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Introduction

Freshwater mussels are one of the most imperiled faunal groups in North America, with 213 of the 297 known taxa listed as endangered, threatened, or of special concern (Fig. 1) (Williams et al. 1993). The primary reasons for the decline in mussel abundance and diversity are the construction of dams, stream channelization, pollution, siltation, and inadequate stream flows (Ortmann 1909, Cvancara 1970, Stansbery 1973, Williams et al. 1993). These environmental perturbations degrade suitable mussel habitats and disrupt the natural flow regime of rivers (Bates 1962, Haag and Thorp 1991).

Therefore, there is a need to develop habitat suitability criteria for freshwater mussels. These suitability criteria can be used in the Instream Flow Incremental Methodology (IFIM) to establish protected stream flows for mussels. The United States Fish and Wildlife Service developed the IFIM to evaluate and address changes in a stream's environment in relation to stream flow (Bovee 1986). One of the IFIM components is the Physical Habitat Simulation System (PHABSIM), which uses biological (habitat suitability criteria) and site-specific hydraulic data to predict how physicall habitat changes under various stream flow conditions (Milhous et al. 1989).

An important component of the PHABSIM is biological data in the form of habitat suitability criteria (Milhous et al. 1989). The collection and development of suitability criteria are some of the most labor intensive and expensive components of IFIM studies (Bovee 1986). To develop habitat suitability criteria

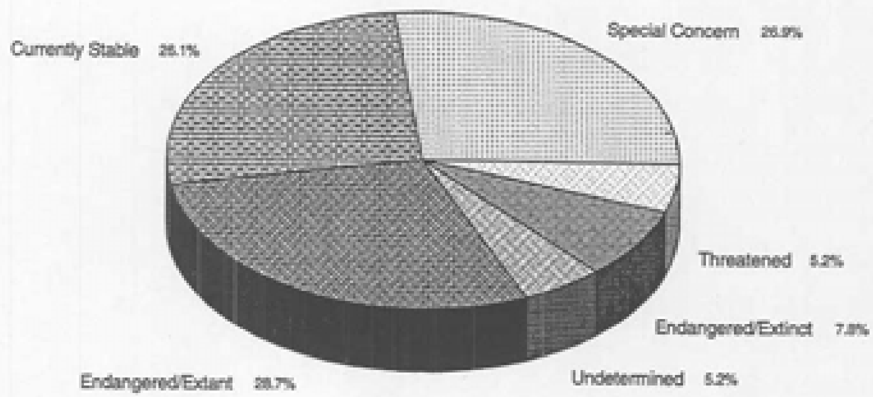

Figure 1. Current status of the 297 known taxa of North American freshwater mussels (Williams et al. 1993).

for an aquatic organism, quantitative habitat data have to be collected. Data consisting of mussel species occurrence and density, as well as microhabitat characteristics such as water depth, water velocity, substrate composition, and instream cover types, are measured in randomly selected sample sites (Bovee 1986).

Habitat suitability data can be expressed in the form of a habitat preference curve or histogram (Bovee 1986). The microhabitat suitability criteria (preference curves or histograms) are used as inputs into the PHABSIM models (Bovee 1986). PHABSIM uses the habitat suitability curves or histograms that best describe the instream suitability of the habitat variables most closely related to stream hydraulics and channel structure (depth, velocity, substrate, and cover) for each species under study (Milhous et al. 1989). The modeling results can be used to establish protected stream flows, thus ensuring adequate habitat for the species being studied.

Habitat suitability criteria have been developed for fish (Aadland et al. 1991) and aquatic insects (Gore and Judy, 1981, Orth and Maughan 1983). Gore and Judy (1981) investigated aquatic insects, which are important forage for fish and are sensitive to changes in stream flow. Orth (1987) and Aadland (1993) have recommended the selection of appropriate target species for IFIM studies. Target species should have a narrow range of habitat preferences, thus being most sensitive to changes in stream flow (Orth 1987). Because freshwater mussels have been reported to be sensitive to changes in stream flow (Ortmann

1909, Bates 1962, Cvancara 1970), it seems appropriate to include mussels in IFIM studies.

A method that is often used to evaluate differences in aquatic communities is measuring and comparing species densities and community composition at different sites along a river's length. Vannote et al. (1980) proposed the river continuum concept, which states that there should be a progressive shift from predominance of shredder and grazer invertebrates in the upstream reaches of a stream to more collector species (e.g., mussels) in the downstream reaches. Similar longitudinal shifts may also be evident for mussel communities where the upstream reaches are dominated by headwater species, while large river species dominate the downstream mussel assemblage (Dawley 1947, Strayer 1983).

Fish provide an important link for the glochidial stage of many species of mussels; therefore, fish distributions may be important in determining the distributions of mussels (Fuller 1974). Sheldon (1968) studied the fish community in Owego Creek, New York, and determined that the addition of fish species, rather than the replacement of species, was the primary form of longitudinal succession in this stream. Rahel and Hubert (1991) also found that fish species addition was occurring along the longitudinal gradient of Horse Creek, Wyoming, with the upstream fish assemblage being dominated by species of salmonids and the lower reaches by cyprinids and centrarchids.

Results of this mussel study may provide insight as to why certain species of mussels are found in areas where other mussel species are absent. The primary objectives of this study were to 1) develop habitat suitability criteria for mussels in the Otter Tail River and 42) describe mussel density and diversity along the longitudinal gradient of the Otter Tail River. The habitat suitability criteria developed in this study will have direct implications for the management of stream flows, protecting mussel species in warmwater streams.

Literature Review

Freshwater mussels (Molluscs: Bivalvia: Unionidae) are important components of aquatic food webs (McMahon 1991) by providing food directly to higher trophic levels (Neves and Odom 1989) and indirectly to lower trophic levels through the formation and discharge of pseudofeces (Libois and Hallet-Libois 1987). Mussels are often important forage for muskrats *(Ondatra zibethica)* (Neves and Odom 1989). Neves and Odom (1989) reported that 28% of the population of endangered shiny pigtoes *(Fusconaia edgariana)* in the North Fork Holston River, Virginia, were consumed by muskrats over eight years, placing some demes of shiny pigtoes in danger of extirpation. Raccoons *(Procyon lotor),* mink *(Mustela vison),* and otters *(Lutra canadensis)* also feed on mussels (McMahon 1991). Mammals are not the only animals that prey on mussels; several fish species also include juvenile mussels in their diet (McMahon 1991).

Mussels are important in the cycling of organic materials, and they are an integral part of the chemical processes that occur in aquatic ecosystems because they have the ability to filter large volumes of water (McMahon 1991). The organic matter in the water column that is siphoned in, but not eaten by the mussels, is expelled as pseudofeces providing an important food source for other benthic organisms (Libois and Hallet-Libois 1987). The filtering processes carried out by unionid mussels are important in the biological purification of water by removing and temporarily retaining deleterious chemicals and heavy metals from aquatic systems (Tudorancea 1972, Libois and Hallet-Libois 1987).

The demand for mussel shells for use as pearl nuclei for the Japanese cultured pearl industry has caused declines of some mussel populations in midwestern streams (Williams et al. 1993). The harvest of mussels from the Mississippi and Illinois Rivers in Illinois yielded 1.5 million kg of shells in 1991 (Donald Dufford, Illinois Department of Conservation, pers. communication) and 0.5 million kg of mussel shells valued at $0.8 million in 1992 (Walsh 1993). Harvest from the Otter Tail River, Minnesota, in 1991 totaled 73,636 kg of shells (Shawn Johnson, Minnesota Department of Natural Resources, pers. communication). Overexploitation of freshwater mussels is a concern in Illinois, Minnesota, and North Dakota. A position paper currently being drafted concerning the status of Illinois' mussels outlines the possible over-exploitation of the mussel population during the 1991 harvest season (Donald Dufford, Illinois Department of Conservation, pers. communication). Minnesota (Shawn Johnson, Minnesota Department of Natural Resources, pers. communication) and North Dakota (Kriel 1992) have both closed commercial harvesting of mussels in inland streams until more information can be compiled on the populations of native mussels.

While overexploitation is a threat to native mussel populations, the primary reason for the decline in mussels is habitat destruction. In a review of the literature, Williams et al. (1993) concluded that the construction of dams and impoundments frequently destroys habitats required by mussels These dams and impoundments result in the permanent loss of approximately 30% to 60% of the mussel fauna in the affected areas (Williams et al. 1993). Layzer et al. (1993) reported that the construction and operation of the Center Hill Dam in Tennessee devastated the resident mussel community; pristine riverine habitats were inundated upstream from the dam; and water discharges from the dam scoured the substrates downstream. In addition, reproduction of mussels was impeded by the discharge of cold water from the hypolimnion (Layzer et al. 1993).

Bates (1962) concluded that the impoundment of the Tennessee River by the Tennessee Valley Authority drastically altered the habitats within the stream. Bates (1962) also sampled mussels in the Kentucky Reservoir of the Tennessee River, finding the original inhabitants in the "old"' stream channel being present in low numbers, with only one of these "original" species being able to exploit the newly created lake-like environment. Several lentic species that had not been reported were collected in the newly formed shallow areas in high numbers, suggesting that the pre-impoundment mussel communities were being replaced (Bates 1962). Bates (1962) suggested that this change in species composition was partially due to the physical degradation of suitable habitats required by lotic mussels, as well as an unnatural flow regime caused by the reservoir.

Dams alter the habitat required by mussels and may also impede the passage of the migratory fish required as hosts for the parasitic glochidial stage of freshwater mussels (Ortmann 1909). Wilson and Danglade (1912) realized the importance of fish for the successful survival of mussels. They recommended the installation of fishways which would allow for the passage of fish around the several dams located on the Otter Tail River near Fergus Falls, Minnesota (Wilson and Danglade 1912). Fuller (1974) stated that even if glochidia are successfully shed from the fish host, the environmental conditions produced by the dams may not be suitable for the survival of the immature mussels. The alteration of the physical environment within these newly created reservoirs occurs in part because the lowering of water velocities increases sedimentation rates (Layzer et al. 1993).

Current velocity is important in governing the distribution of mussels in streams. Cvancara et al. (1966) reported that the greatest concentration of mussels in the Turtle River, North Dakota, were found in areas of relatively high water velocities along the thalweg. They hypothesized that the high water velocities were ideal for uptake of food and dissolved oxygen by mussels. Strayer and Ralley (1993) reported a significant correlation between mussel density and intermediate current speeds in a New York stream. Way et al. (1989) sampled four sites within a large mussel bed in the Tennessee River, two sites 31 meters off shore from the stream bank (inshore sites) and two sites 61 meters off shore from the stream bank (offshore sites). The greatest densities of mussels occurred in the inshore sites where water velocities were 11 cm/s versus the offshore sites where velocities were 19 cm/s (Way et al. 1989). Way et al. (1989) concluded that current velocity was a dominant factor influencing the structure of the mussel community in their study sites.

Freshwater mussels require specific water depths to reach maximum densities in lotic environments (McMahon 1991). Stern (1983) collected mussels from the Wisconsin and St. Croix rivers at depths ranging from < 1 m to > 3.5 m, with the highest concentrations of mussels (60/m2) located in a depth range of 12 m. Tudorancea (1972) noted the mussels residing in the Crapina-Jijila complex of pools of the Danube River were found at specific depths, with the highest densities occurring at about 1 m. When the Crapina-Jijila pools experienced seasonal water withdrawals, the mussels migrated into the remaining deep-water areas (Tudorancea 1972). Haukioja and Hakala (1974) reported that several species of mussels had distinct depth preferences within the Suksela River, Finland, with most mussels being found in water slightly less than 1 m in depth. Haukioja and Hakala (1974) also reported that regardless of water depth, wherever clay substrates were present, no mussels were found, thus illustrating the importance of both depth and substrates in determining mussel occurrence and abundance.

Substrate composition is a habitat variable used to predict the occurrence and density of mussel species. To fully exploit lotic habitats, some freshwater mussel species require coarse, stable substrates, while others may inhabit soft, stable areas (McMahon 1991). Bailey (1989) found that in laboratory experiments, *Lampsilis radiata siliquoidea* placed in mud substrates remained there, while those placed in sandy substrates moved to the muddy substrates. 10

Bailey (1989) stated that although his experiments may not have simulated the actual substrate choices that the mussels are exposed to under natural conditions, they provided evidence for habitat selection in *L. r. siliquoidea.*

Salmon and Green (1983), Stern (1983), and Way et al. (1989) reported that the majority of the mussels they collected were in areas dominated by stable, sandy substrates. Haukioja and Hakala (1974) found that mussels needed a soft but firm substrate in both lentic and lotic environments. Haukioja and Hakala's (1974) findings were reinforced by Kat's (1982) study in Norwich Creek, Maryland. Kat (1982) found that high quality microhabitats were characterized by stable substrates, since mussels deposited in low quality microhabitats moved into areas more favorable for survival. Most of the mussels in the study conducted by Cvancara et al. (1966) in the Turtle River, North Dakota, were found in substrates varying from pebbly gravel to gravelly sand. While substrates are important in determining mussel distributions, the microhabitat variables of water velocity and water depth should also be considered when addressing habitat preferences of mussels.

Study Site Descriptions

The Otter Tail River watershed has an area of 3,284 km2 (Minnesota Conservation Department 1959) and joins with the Bois de Souix to form the Red River of the North, which is part of the Hudson Bay drainage system. The watershed is primarily agriculture, although forested lands, lakes, and wetlands account for a large percentage of the area. Grain farming is the main agricultural activity, with the headwaters area northeast of Detroit Lakes, Minnesota, consisting of commercially valuable timberland. Several wildlife refuges within the watershed provide habitat for migratory and resident animal populations.

Although the Otter Tail River begins at the outlet of Round Lake, the stream actually originates at Big Rock Lake in Clearwater County, Minnesota. From Big Rock Lake, Solid Bottom Creek (Fig. 2) flows through Big Elbow, Little Bemidji, Many Point, and Round Lakes. At Round Lake, Solid Bottom Creek is renamed the Otter Tail River. Major tributaries to the Otter Tail River are the Pelican, Dead, and Toad Rivers. The Otter Tail River is 290 km long and has an overall stream gradient of approximately 0.6 m/km (Fig. 3). This gradient contributes to the formation of diverse aquatic habitats ranging from shallow riffles to deep pools and runs.

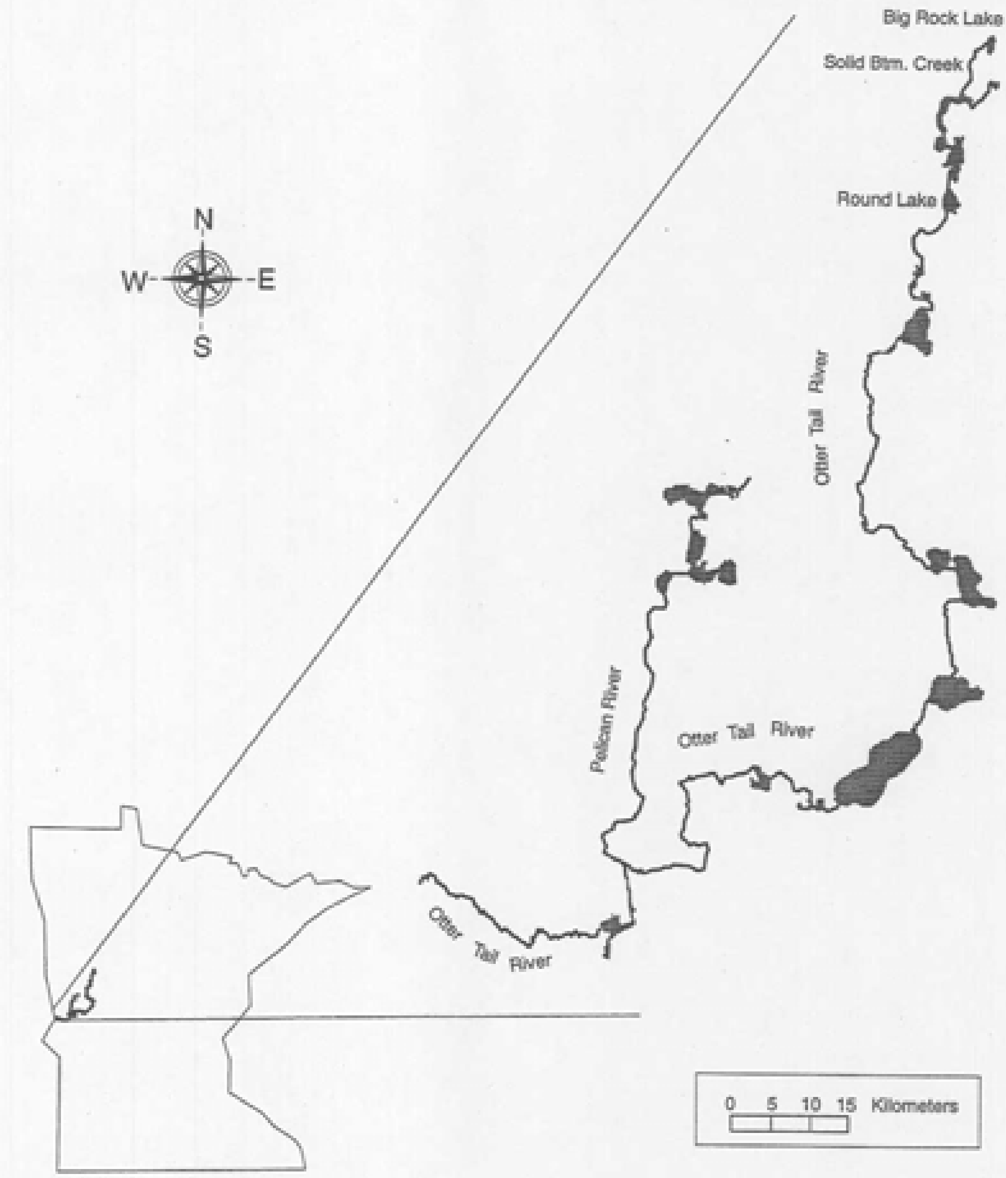

Figure 2. Otter Tail River system.

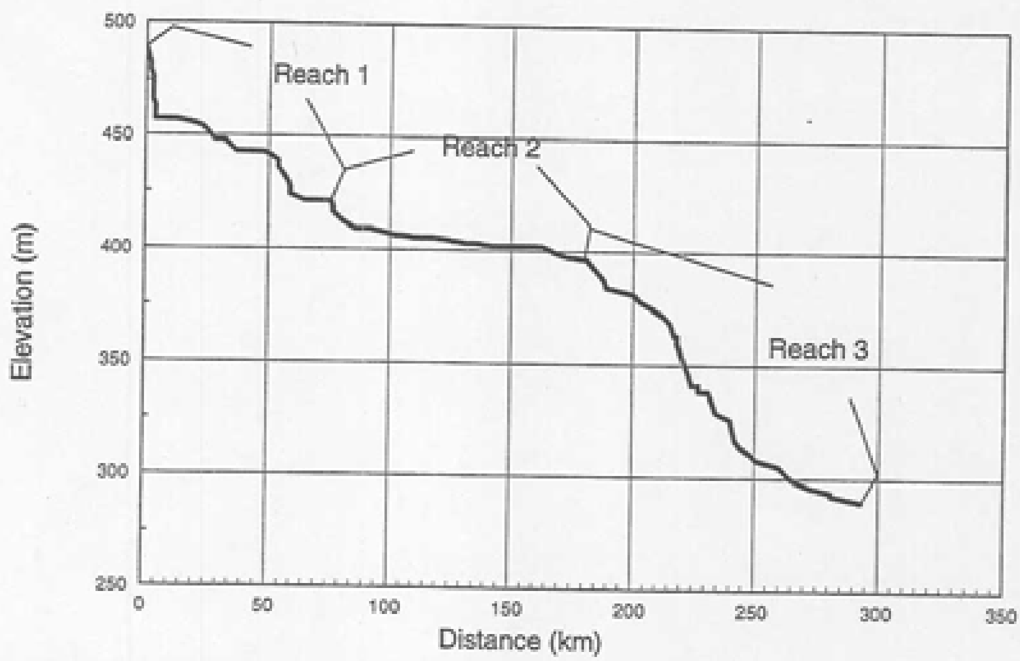

Figure 3. Otter Tail River longitudinal profile.

Methods

Habitat Measurements

Because mussel populations may exhibit clumped distribution patterns (Isom and Gooch 1986, Kovalak et al. 1986), a stratified random sampling design was used in this study. The Otter Tail River was measured on United States Geological Survey quadrangle maps, with distances and elevations recorded wherever topographic lines crossed the river.

To aid in determination of study sites, a longitudinal profile of the Otter Tail River was constructed by plotting stream distance vs. stream elevation (Fig. 3) (Bovee 1982). This method facilitated the identification of stream gradient changes. The Otter Tail River was stratified into three reaches according to stream gradient: 1) an 81 km long, high-gradient reach (0.95 m/km) from the headwaters at Solid Bottom Creek to river km 81; 2) a 100 km long, low-gradient reach (0.15 m/km) from river km 81 to river km 180; and 3) a 109 km long, high-gradient reach (0.97 m/km) from river km 180 to the mouth of the river at Breckenridge, Minnesota (Fig. 3).

Stream gradients were calculated at approximately 8 km intervals by dividing each interval's length by the change in elevation recorded along the length. These 8 km segments were numbered; and by using a random numbers table, a high and a low gradient site were randomly chosen within reaches 1 and 3, and a low gradient site was selected in reach 2 (Fig. 4, Table 1). A high gradient site was not selected within reach 2 because there were none present.

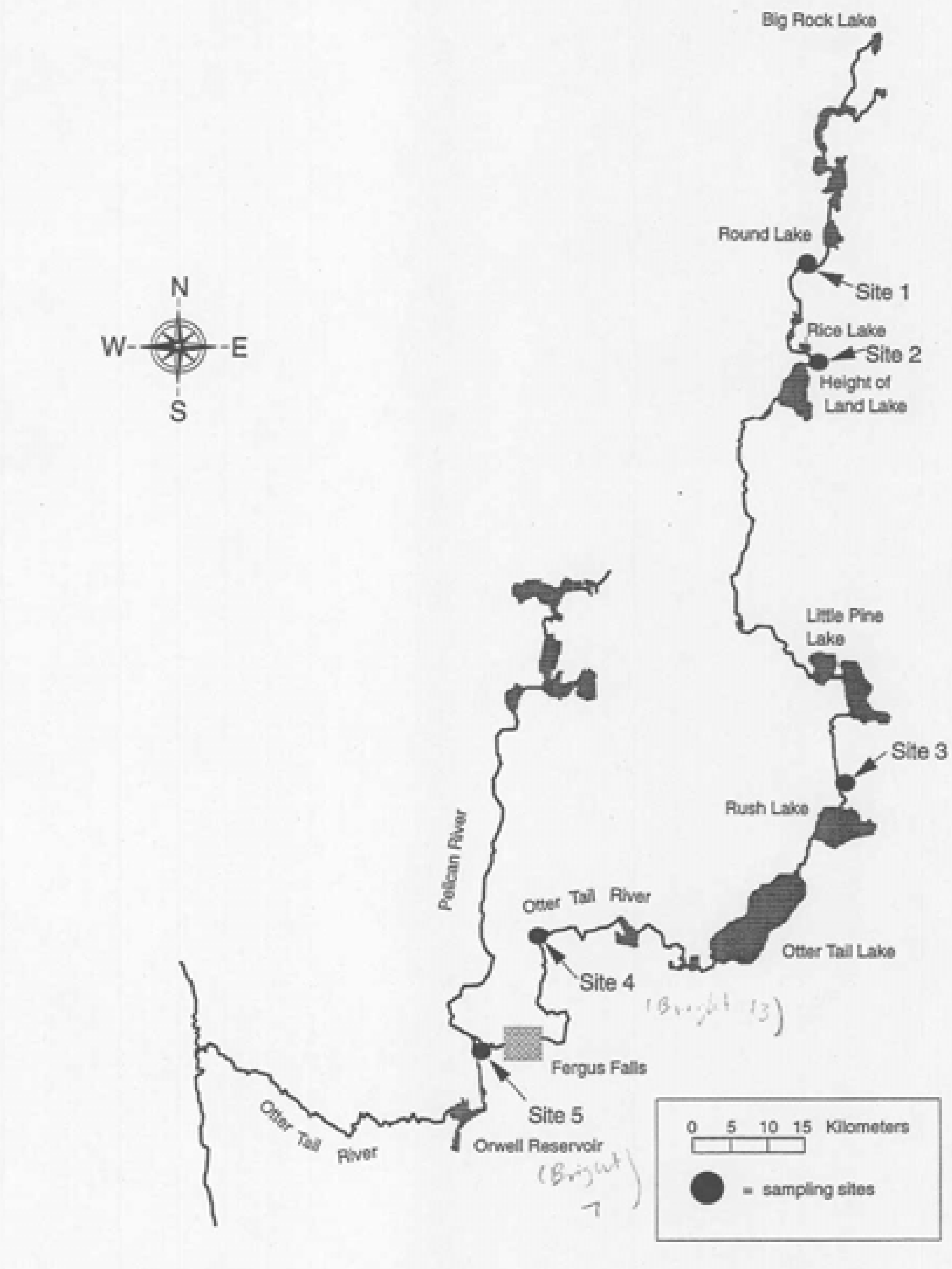

Figure 4. Otter Tail River sampling sites.

Table 1. Otter Tail River study site descriptions and sampling dates for mussels, 1994

	Sites				
	Site 1 - Tamarac Bridge	Site 2 - Outlet of Rice Lake	Site 3 - Perham	Site 4 - Co. Rd. 10 Crossing	Site 5 - Otter Tail / Pelican Confluence
County	Becker	Becker	Otter Tail	Otter Tail	Otter Tail
Township	141 N	140 N	135 N, 135 N	133 N, 134 N, 134 N	133 N
Range	39 W	39 W	39 W, 38 W	42 W, 42 W, 43W	43 W
Section	23 & 26	26	1, 6 & 7	6, 31, 36	32
Riparian Habitat	Mixed hardwoods in Tamarac National Wildlife Refuge	Mixed hardwoods in Tamarac National Wildlife Refuge	Mixed hardwoods and residential areas	Agricultural pastureland	Mixed hardwoods
Habitat Types	Riffles, runs, and pools	Runs and pools	Riffles, runs, and pools	Runs	Rapids, runs, and pools
Bank Condition	Stable	Stable	Stable	Minimum sloughing	Minimum sloughing
Stream Gradient	High 1.34m/km	Low 0.08m/km	Low 0.21m/km	Low 0.28m/km	High 1.31m/km
Sampling Dates	14 June 01 July	06 July 08 July 19 July 22 July 26 July	09 August 10 August 13 August	27 July 28 July 29 July 03 August 08 August	13 June 21 June 22 June

Lakes that the Otter Tail River flows through were not included in this study.

At each of the five study sites, three habitats were chosen for sampling, and three transects were selected within each habitat. Thirty sampling quadrats were sampled along each transect (Fig. 5). This procedure resulted in 270 quadrats being sampled at each of the five sites.

To facilitate study habitat selection and transect placement, the following procedures were used. Each of the five study sites was mapped by canoeing the site and identifying habitats as either riffles, runs, or pools. All of these habitats were numbered, and three study habitats were chosen at each of the five study sites by using a random numbers table. At all five sites, the length of each of the three selected study habitats' was measured to the nearest meter, and three distances were selected for transect placement by using a random numbers table.

At each of the selected transect locations, a fiberglass surveying tape was strung perpendicular to stream flow. To determine the placement of the 30, 0.37 m^2 sampling quadrats, the stream width at the site of the transect was measured, and quadrat placement was calculated as (stream width in meters + 0.61)/29. This procedure allowed for the center of the initial sampling quadrat to be placed 0.61 m from shore and subsequent quadrats to be equally spaced along the stream's width (Fig. 5).

Using scuba or snorkeling gear, samples were collected within each 0.37 m2 steel quadrat. This sampling design is the most effective method of quantitatively sampling mussels (Isom and Gooch 1986).

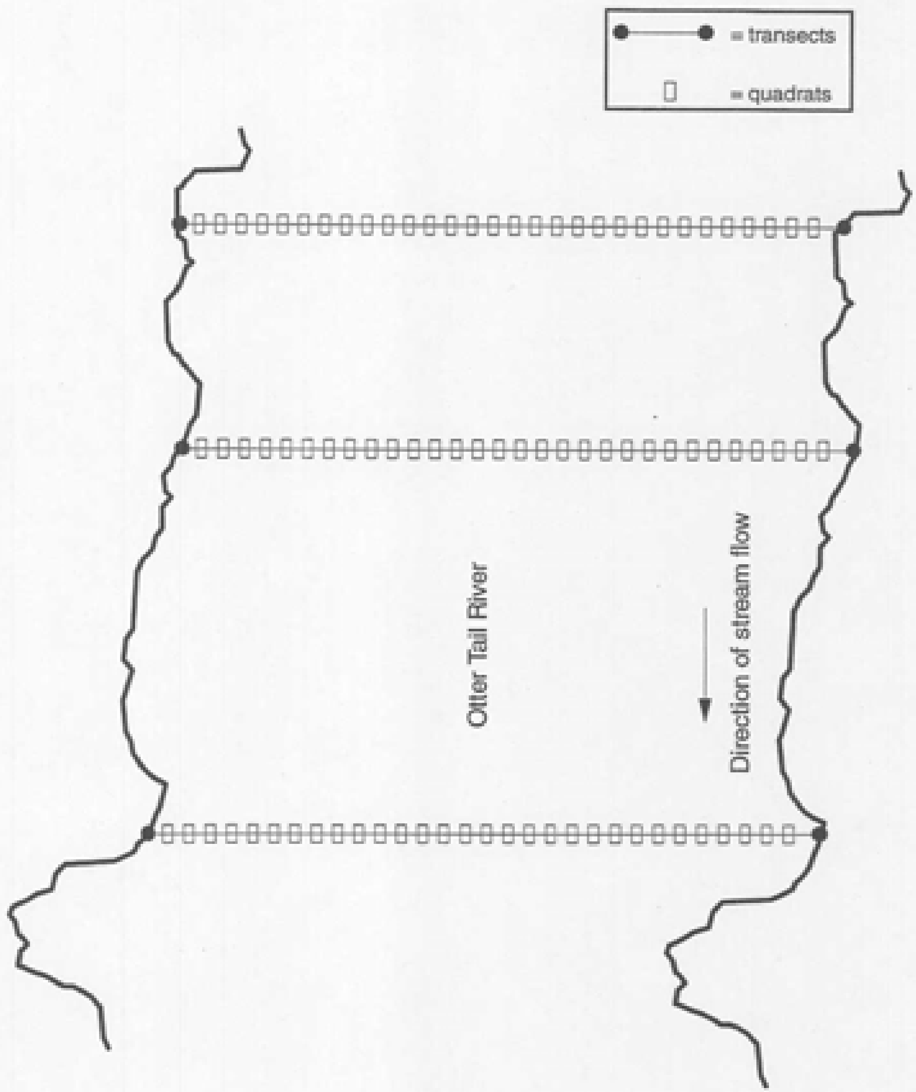

Figure 5. Hypothetical sampling habitat, showing transect and quadrat placement.

Microhabitat data were collected in each quadrat to obtain a habitat availability data set, whether or not mussels were present within the quadrat (Aadland et al. 1991). Microhabitat data collected included water velocity, water depth, percent of each substrate category, and instream cover present within each quadrat.

Water velocity and water depth were measured in the center of each sampling quadrat with a Price AA current meter mounted on a calibrated wading rod. Following standard hydrological procedures (Leopold et at. 1964), water velocity was measured at 0.6 of total depth where water depths were < 76 cm. At water depths > 76 cm, velocities were measured at 0.2 and 0.8 of total depth (Leopold et al. 1964). Mean column velocities were used to develop preference curves in this study, even though these velocities may not be encountered by the benthic organisms (Gore 1985). Mean column velocities have been shown to be highly correlated to the shear conditions and boundary layers that benthic invertebrates experience (Statzner 1981). Water velocities measured at the substrate-water interface are often near zero whether measured in riffle or backwater habitats; therefore, substrate-water interface velocities may not be an accurate, predictive variable (Aadland et al. 1991).

Substrates within each quadrat were excavated to about 15 cm and measured according to the grain size classes modified from Bovee (1986) (Aadland et al. 1991) (Table 2). The percentage of the area within each quadrat

Table 2. Substrate size classifications (Aadland et al. 1991)

Substrate type	Diameter (mm)
Clay	
Silt	0 - ≤ 0.062
Sand	>0.062 - ≤ 3.2
(gravel	>3.2 - ≤ 64
Gobble	>64 - ≤ 128
Rubble	>128 - ≤ 256
Small boulder	>256 - ≤ 508
Large boulder	>508 - ≤ 1016
Bedrock	>1016

that was covered by each substrate type was recorded to the nearest 10% (Aadland et al. 1991).

Instream cover types were assigned to the following categories: none = no cover present, aquatic vegetation, branches, logs, or boulders; and recorded as either present or absent.

All of the mussels present within each quadrat were removed, identified, counted, and returned to the substrate. Mussels were identified with the use of dichotomous keys provided in McMahon (1991) and Cummings and Mayer (1992). Voucher specimens for each species collected from each of the five sites were reposited at the Bell Museum of Natural History, St. Paul, Minnesota.

Data Analysis

Habitat suitability criteria

Mussel habitat suitability criteria were frequency distributions along depth and velocity gradients and substrate and cover types. These were calculated by determining density within 10 cm intervals for depth and velocity and within each substrate and cover type. All of the data analysis was performed on weighted data (habitat-use weighted by the numbers of individuals of each species present within the sample). A normalized preference value ranges from 0 to 1. Zero siignifies the unused, or the least preferred habitat, and a value of 1 signifies the most often used, or the most preferred habitat (Bovee 1986).

Habitat availability. Frequency distributions of the microhabitat data were calculated to represent the available habitat for sampled areas within the 22 sites. Availability was calculated separately for each site, for each habitat variable, where a mussel species was collected. This procedure allowed for the calculation of availability only at sites where the species under study resided. Sites where a species were not collected were not considered available for use. The frequency distributions of available habitat were used in combination with mussel habitat-use data to create habitat preference histograms and curves. A generalized habitat availability frequency distribution using hypothetical data for depth is presented in Figure 6.

Habitat use and preference or density relationships. Habitat use and preference or density values were calculated for each species for velocity, depth, dominant substrate, and instream cover. A generalized habitat use frequency distribution using hypothetical data for depth is presented in Figure 7. To calculate these, each habitat variable was divided into intervals; for example, a depth interval would be set up as 0 cm, >0-10 cm, >10-20 cm, >20-30 cm, etc. For each depth interval, the total number of samples taken, the number of samples which contained the species of interest, and the number of individuals of the species were calculated. The proportion of samples that were taken in each available depth interval was calculated as the number of samples taken within the depth interval divided by the total number of samples collected. Habitat use was calculated as the number of individuals collected within the habitat interval diivided by the total number of individuals collected.

Preference or density was calculated as habitat use within the interval

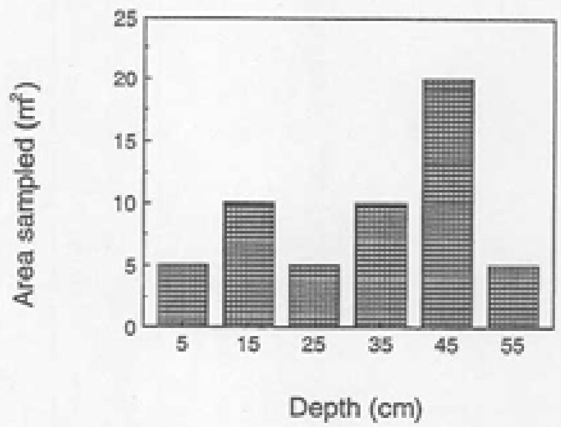

Figure 6. Generalized habitat availability frequency distribution.

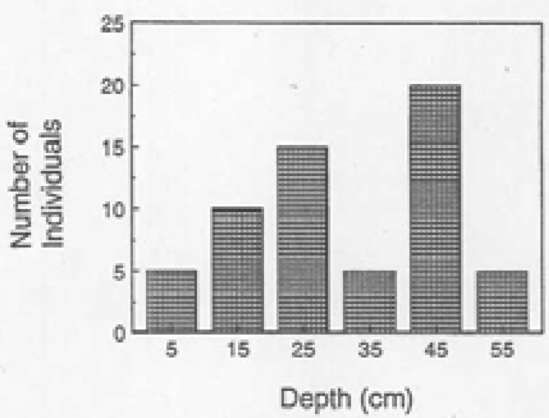

Figure 7. Generalized habitat use frequency distribution.

(Fig. 7) divided by habitat available within the interval (Fig. 6). A typical preference or density distribution using hypothetical data is depicted showing both preference or density and normalized preference or density (Fig. 8). Preference data from the five sites were composited by weighting by sample size.

Development of habitat preference curves. Preference curves were constructed for each species and represent the optimum range for the microhabitat variables of depth and velocity. Histogram analysis and nonlinear regression techniques were used to construct the habitat preference curves from the preference values (Bovee 1986). Preference curves were developed for depth and velocity. Histograms were used to depict preferences for cover and substrate types.

Nonlinear regression. Nonlinear regressions were calculated to fit curves to preference values for depth and velocity. The NONLIN module of SYSTAT (Wilkinson 1988) was used in this study. Nonlinear regression requires input of an appropriate equation to describe the preference function and derives "best fit" coefficients. Preference values for depth or velocity are fed into the program with the equation used to describe the relationship. Coefficients in the equation are manipulated by the computer until the sum of the squared deviations of the preference values from the curve is minimized (least squares). The generalized Poisson density function yields a low least squares value and is robust, accurately fitting skewed distributions typical of habitat preference data

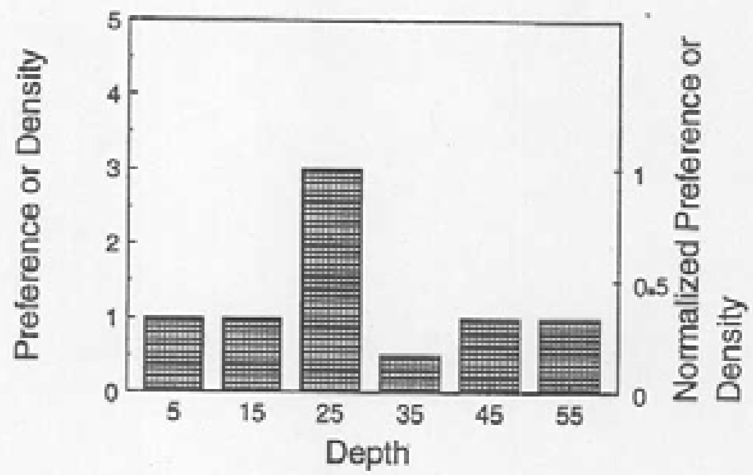

Figure 8. Generalized habitat preference or density frequency distribution.

(Aadland et al. 1991). The Poisson equation describes a bell-shaped curve (it may be severely skewed) and is most appropriate where preference approaches zero at the upper end of the variable range (Bovee 1986). Depth and velocity preference curves were fit using the following generalized Poisson equation:

$$\text{Preference} = \left[\frac{B-X}{B-A}\right]^{C} * e^{\frac{C}{D}\left(1-\left(\frac{B-X}{B-A}\right)^{D}\right)}$$

where A = value of "X" where f(X) = 1.0,

B = value of "X" where f(X) = 0.0 (X<B),

C = shape parameter for part of the curve to the right of X=A,

D = shape parameter for part of the curve to the left of X=A,

e = base of the natural logarithm, and

X = habitat variable (Bovee 1986).

The Quasi-Newton NONLIN minimization method was used to fit the Poisson equation to the preference data. By using first and second derivatives of the least squares function, the Quasi-Newton minimization method calculates the degree to which it should change the coefficients from one iteration to the next. Once satisfactory coefficients were attained, the equation was transferred to a spread sheet, and the estimates for any value of the habitat variable were calculated.

Mussel density and diversity

Mussel densities were calculated within each study site by treating the transects, instead of the quadrats, as samples to reduce the probability of pseudoreplication (Hurlbert 1984). Densities were calculated for each transect as follows:

$$\text{Density} = \frac{X}{Y * Z}$$

where X = the total number of mussels collected within the quadrats sampled along the transect,

Y = the number of quadrats sampled along the transect, and

Z = the area of the sampling quadrat.

Mean densities for each site were calculated by summing the densities of the nine transects sampled at each site and dividing this value by nine. Densities were compared between sites using a Kruskal-Wallis nonparametric analysis of variance test and Dunn's multiple comparison procedure incorporating an experimentwise error rate of P = 0.15 (Daniel 1978).

Results

Habitat Suitability Criteria

Microhabitat suitability data for 4851 mussels, representing 13 species, were collected. Habitat preference curves and histograms were developed for seven mussel species that were collected in sufficient numbers (>30 total observations) (Table 3).

Amblema plicata (Threeridge)

A total of 2432 threeridge mussels were collected from sites 3, 4, and 5, with densities being the greatest at site 4 (Table 3). Threeridges showed a marked preference for fast (80 cm/s), deep waters (175 cm) and were rarely found in slow, shallow areas (Figs. 9 and 10). Threeridges were found in all substrate types, with the most suitable areas dominated by gravel substrates (Fig. 11). Habitats with or without instream cover in the form of aquatic vegetation were equally suitable (Fig. 12).

Fusconaia flava (Wabash pigtoe)

The habitat preferences of the 1289 pigtoes collected in this study closely resembled those exhibited by the threeridge. Pigtoes were only found at sites 3, 4, and 5, with the highest densities at site 4 (Table 3). Similar to threeridges, fast (75 cm/s), deep water (170 cm) had the highest suitability for pigtoes. Few pig toes were found in areas of current velocity < 20 cm/s or depths <60 cm (Figs. 1 13 and 14). Pigtoes were found in all of the substrates available except detritus, preferring areas dominated by coarse, gravel substrates (Fig. 15). Figure 16

Table 3. Otter Tail River mussel densities in mussels/m^2 (totals in parentheses) at the five sampling sites, 1994

Mussel species	Site 1	Site 2	Site 3	Site 4	Site 5	Total
Subfamily Ambleminae						
Amblema plicata (Say, 1819)	0.0 (0)	0.0 (0)	0.01 (1)	23.48 (2363)	0.68 (68)	4.87 (2432)
Fusconaia flava (Rafinesque, 1820)	0.0 (0)	0.0 (0)	0.30 (30)	11.71 (1178)	0.81 (81)	2.58 (1289)
Quadrula quadrula (Rafinesque, 1820)	0.0 (0)	0.0 (0)	0.0 (0)	0.04 (4)	0.01 (1)	0.01 (5)
Subfamily Anodontinae						
Anodonta grandis (Say, 1829)	0.01 (1)	0.88 (88)	0.04 (4)	0.38 (38)	0.0 (0)	0.26 (131)
Anodontoides ferussacianus (Lea, 1834)	0.01 (1)	0.12 (12)	0.02 (2)	0.07 (7)	0.0 (0)	0.04 (22)
Lasmigona complanata (Barnes, 1823)	0.0 (0)	0.01 (1)	0.12 (12)	0.0 (0)	0.03 (3)	0.03 (16)
Lasmigona compressa (Lea, 1829)	#81 0.06 (6)	0.0 (0)	0.0 (0)	0.15 #62 (15)	0.0 (0)	0.04 (21)
Lasmigona costata (Rafinesque, 1820)	0.0 (0)	0.0 (0)	0.01 #105 (1)	1.74 #79 (175)	0.03 #107 (3)	0.36 (179)
Strophitus undulatus (Say, 1817)	0.01 (1)	0.02 (2)	0.12 (12)	2.11 (212)	0.05 (5)	0.46 (232)
Subfamily Lampsilinae						
Actinonaias ligamentina (Lamarck, 1819)	0.0 (0)	0.0 (0)	0.01 #167 (1)	0.0 (0)	0.0 (0)	0.002 (1)
Lampsilis siliquoidea (Barnes, 1823)	0.21 (21)	1.49 (148)	0.26 (26)	2.16 (217)	0.03 (3)	0.83 (415)
Lampsilis cardium Rafinesque, 1820	0.0 (0)	0.18 (18)	0.40 (40)	0.27 (27)	0.21 (21)	0.21 (106)
Ligumia recta (Lamarck, 1819)	0.0 (0)	0.0 (0)	0.0 (0)	0.01 #114 (1)	0.01 #201 (1)	0.004 (2)
Site averages	0.30	2.70	1.29	42.12	1.86	9.70
Number of mussels collected	(30)	(269)	(129)	(4237)	(186)	(4851)
Standard error	(0.06)	(0.75)	(0.30)	(4.00)	(0.31)	(2.57)

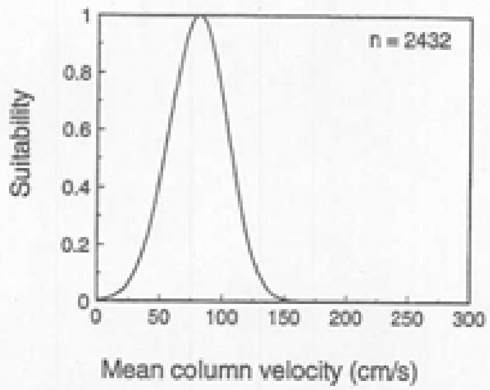

Figure 9. *Amblema plicata* velocity preference.

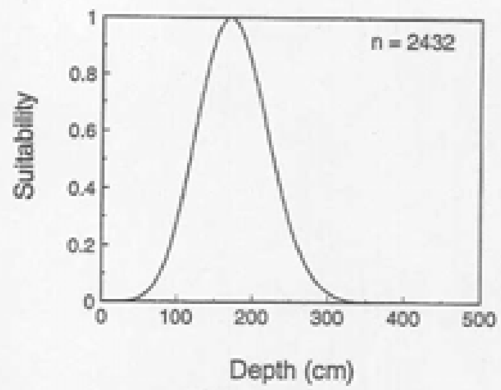

Figure 10. *Amblema plicata* depth preference.

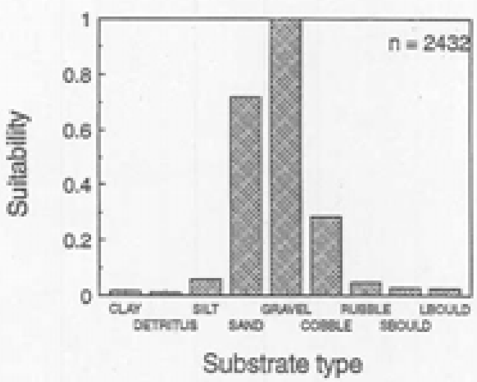

Figure 11. *Amblema plicata* substrate preference.

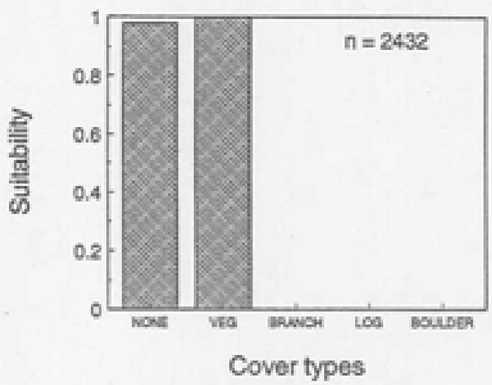

Figure 12. *Amblema plicata* cover preference.

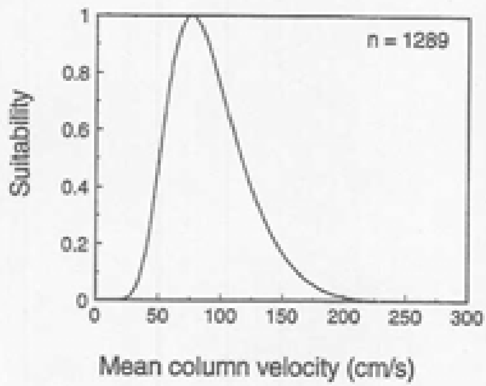

Figure 13. *Fusconaia flava* velocity preference.

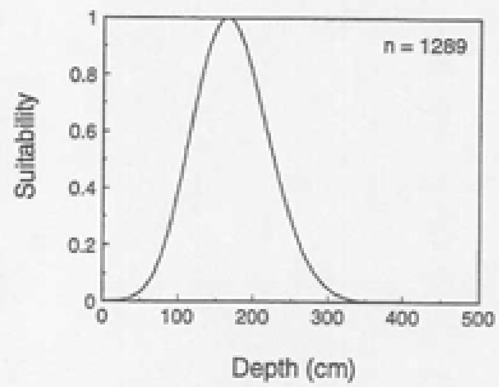

Figure 14. *Fusconaia flava* depth preference.

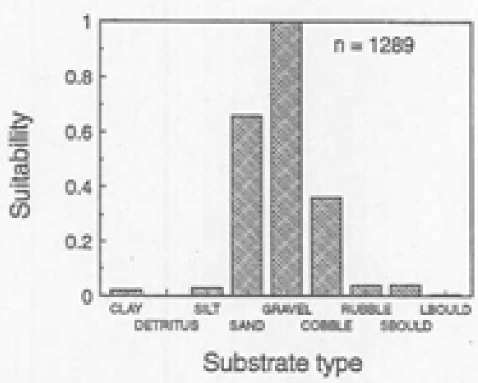

Figure 15. *Fusconaia flava* substrate preference.

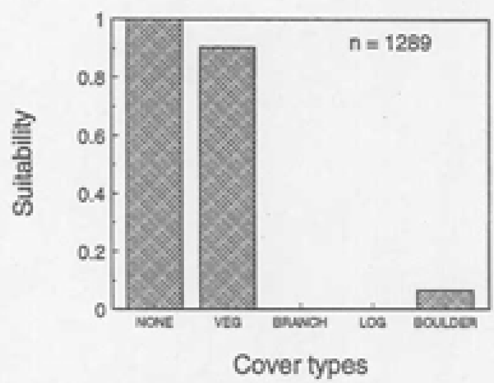

Figure 16. *Fusconaia flava* cover preference.

reveals that areas with aquatic vegetation and areas without instream cover were almost equally suitable for pigtoes.

***Anodonta grandis* (Giant floater)**

A total of 131 giant floaters were collected from sites 1-4, with the highest densities occurring in site 2 (Table 3). Giant floaters showed a high preference for slow moving (10 cm/sec), deep water (135 cm), dominated by fine substrates (Figs. 17, 18, and 19), with instream cover in the form of aquatic vegetation (Fig. 20). In one area of site 2, large numbers of giant floaters were collected within dense beds of *Potamogeton sp.* in clay substrates. This area was unique, with no similar habitats found in the other sampling sites.

***Lasmigona costata* (Fluted shell)**

Fluted shells were collected in sites 3-5 (Table 3), with the greatest density in site 4. The 179 individuals collected in this study exhibited a peak velocity preference of 60 cm/s, with slower current areas not being used (Fig. 21). Depths < 50 cm were not used very often and had low suitability values. Depths most suitable for fluted shells were about 145 cm (Fig. 22). Fluted shells were found in most of the available substrates, except detritus and boulders, with the highest preference being for gravel-dominated areas (Fig. 23). Instream cover suitability was similar to that of threeridges and pigtoes, as areas with or without aquatic vegetation were preferred almost equally (Fig. 24).

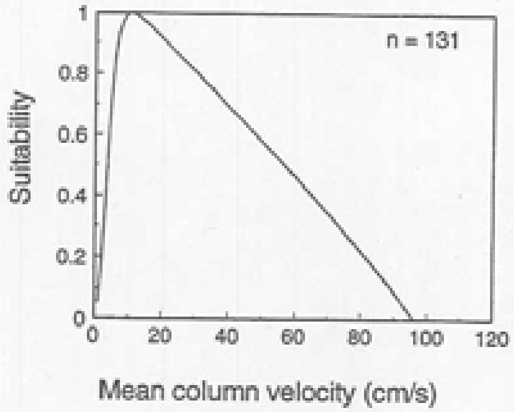

Figure 17. *Anodonta grandis* velocity preference.

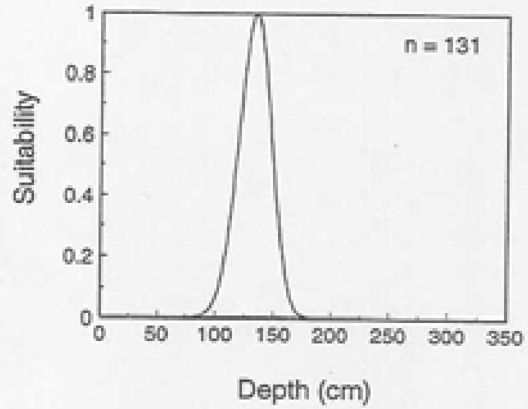

Figure 18. *Anodonta grandis* depth preference.

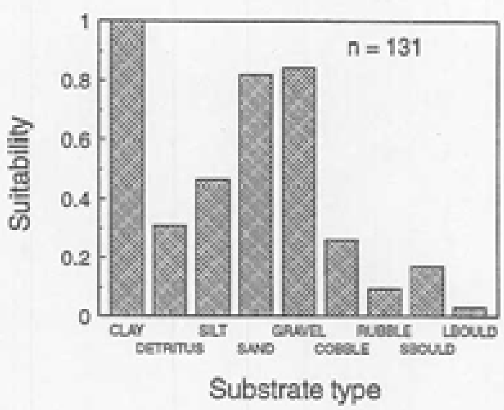

Figure 19. *Anodonta grandis* substrate preference.

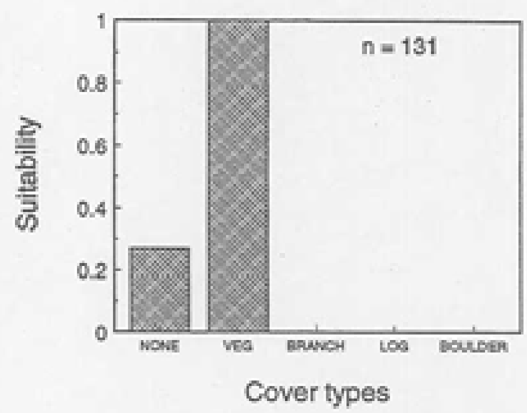

Figure 20. *Anodonta grandis* cover preference.

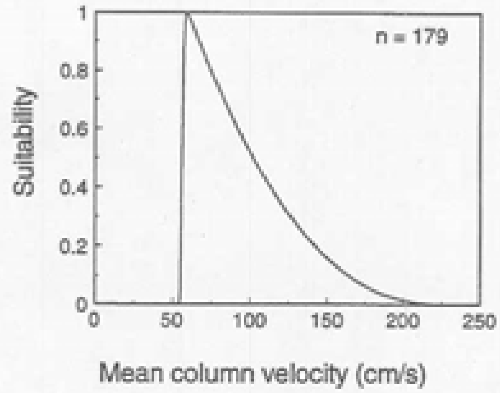

Figure 21. *Lasmigona costata* velocity preference.

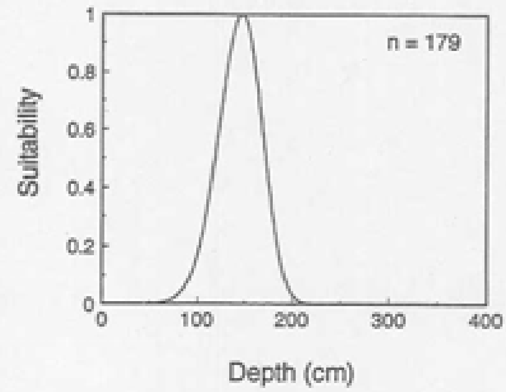

Figure 22. *Lasmigona costata* depth preference.

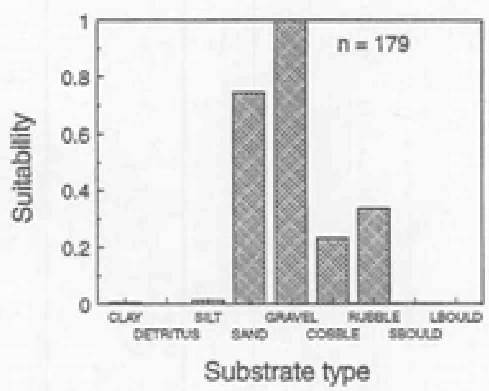

Figure 23. *Lasmigona costata* substrate preference.

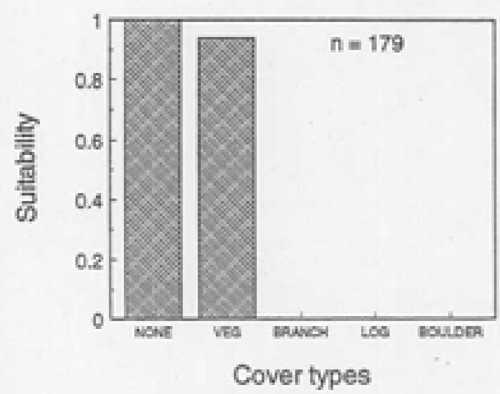

Figure 24. *Lasmigona costata* cover preference.

***Strophitus undulatus* (Squawfoot)**

A total of 232 squawfoot mussels were collected in all of the five study sites, with the highest density occurring at site 4 (Table 3). The majority of the squawfoots collected in this study were in moderately fast current areas, with the greatest number of mussels being in areas of about 88 cm/s (Fig. 25). Squawfoots most often selected water depths of approximately 150 cm (Fig. 26). Squawfoots were collected in all the substrates available except detritus, silt, and boulders. Gravel- and sanddominated substrates were the most preferred benthic habitats (Fig. 27). Areas with, or without, aquatic vegetation had similar suitability for squawfoots (Fig. 28).

***Lampsilis siliquoidea* (Fat mucket)**

Fat muckets were found in all of the five sampling sites, with the greatest densities being found in sites 2 and 4 (Table 3). The most preferred habitats were characterized by current velocities equal to 91 cm/s, with habitats < 20 cm/s being avoided entirely (Fig. 29). Fat muckets were found in several depth ranges, with the most preferred areas being about 175 cm deep (Fig. 30). Fat muckets were found in all of the substrate categories measured, with areas dominated by boulder substrates being the most suitable (Fig 31). The majority of the fat muckets found were nestled in crevices created wherever large boulders were positioned extremely close together. Fat muckets had a preference for several instream cover types. The most preferred stream habitats had a combination of aquatic plants and large boulder-strewn areas (Fig. 32).

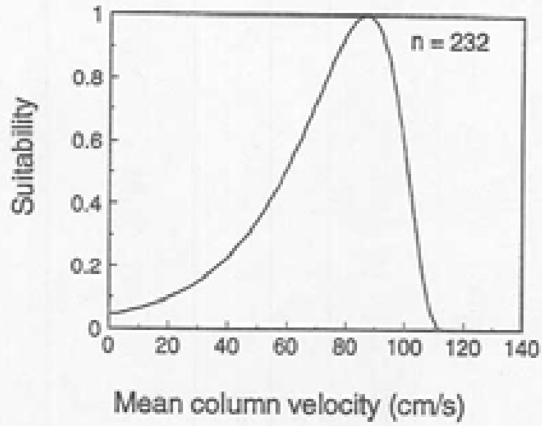

Figure 25. *Strophitus undulatus* velocity preference.

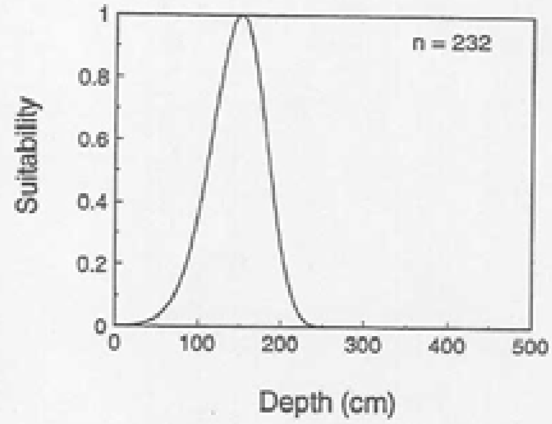

Figure 26. *Strophitus undulatus* depth preference.

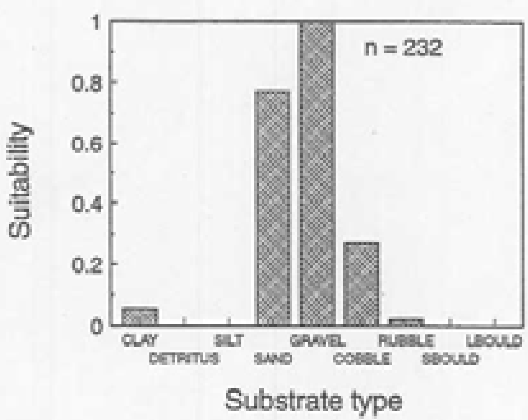

Figure 27. *Strophitus undulatus* substrate preference.

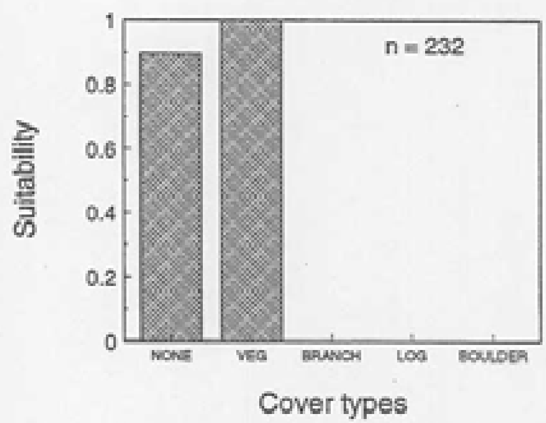

Figure 28. *Strophitus undulatus* cover preference.

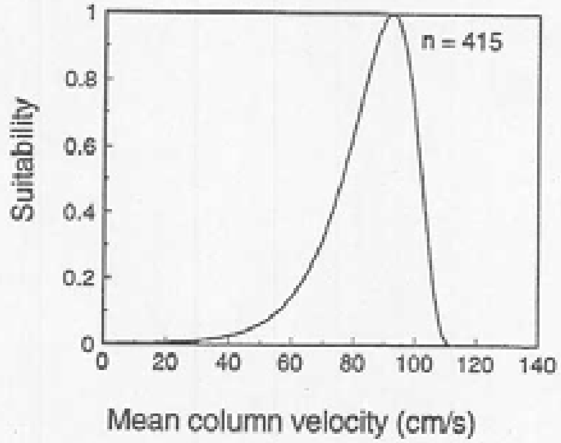

Figure 29. *Lampsilis siliquoidea* velocity preference.

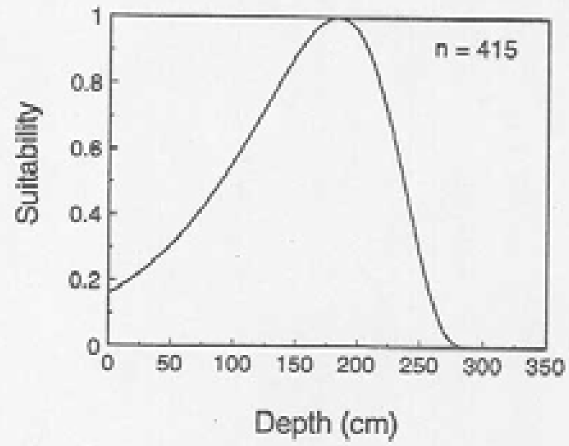

Figure 30. *Lampsilis siliquoidea* depth preference.

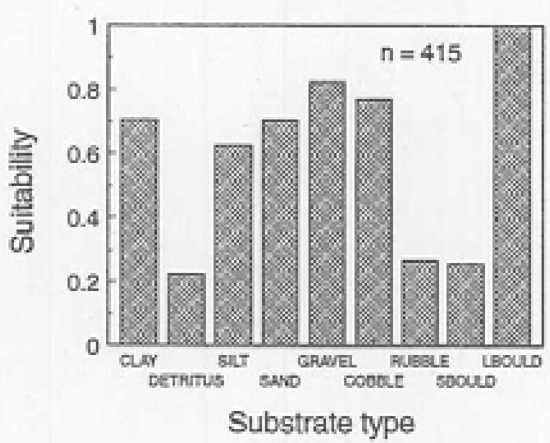

Figure 31. *Lampsilis siliquoidea* substrate preference.

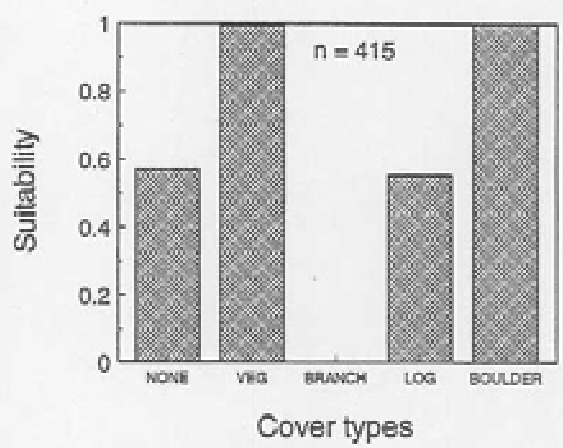

Figure 32. *Lampsilis siliquoidea* cover preference.

***Lampsilis cardium* (Plain Pocketbook)**

The plain pocketbook, a species closely related to the fat mucket, was collected at sites 2-5, with the highest densities occurring at site 3 (Table 3). The 106 pocketbooks found in this study showed a preference for water velocities equal to 115 cm/s (Fig. 33). Pocketbooks were often found in shallow, as well as deep, sections of the river, with the highest suitability being areas about 175 cm in depth (Fig. 34). Pocketbooks were collected from most of the substrate types, except detritus and boulder areas, showing the highest preference for areas dominated by rubble and cobble substrates with no instream cover present (Figs. 35 and 36).

Mussel Density and Diversity

Mussel densities were lowest at the most upstream high gradient study site 1 and were significantly greater in low gradient site 4 ($p<0.0001$, Kruskal-Wallis ANOVA) (Fig. 37). Species richness generally increased with distance downstream. Sites 1 and 2 had the lowest number of mussel species present, with only five species collected at site 1 and six species of mussels collected at site 2 (Table 4).

A total of 10 mussel species were collected at site 3. One of the species collected at site 3, *Actinonaias ligamentina,* has been reported from the Hudson Bay Drainage (Dawley 1947, Clarke 1973), although the species identifications have been questioned (Clarke 1973, Cvancara 1983). The *Actinonaias ligamentina* collected in this study was verified and reposited at the Bell Museum

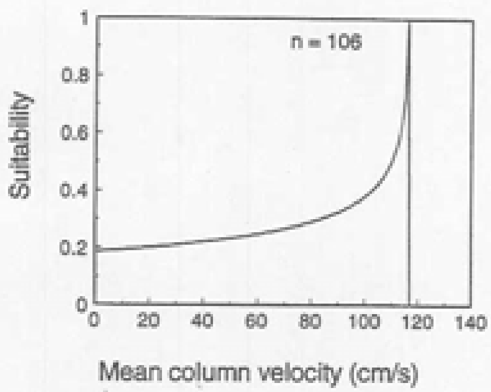

Figure 33. *Lampsilis cardium* velocity preference.

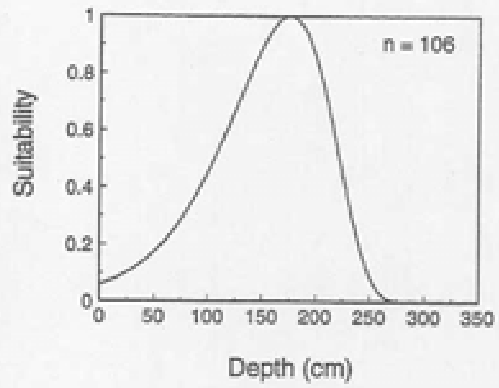

Figure 34. *Lampsilis cardium* depth preference.

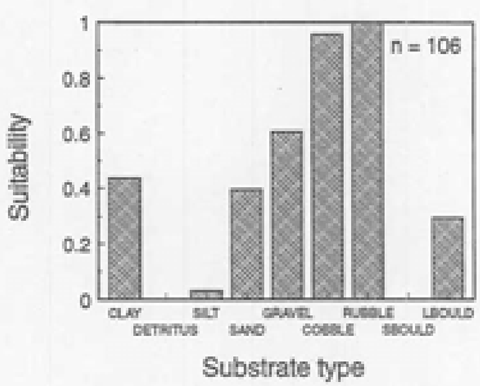

Figure 35. *Lampsilis cardium* substrate preference.

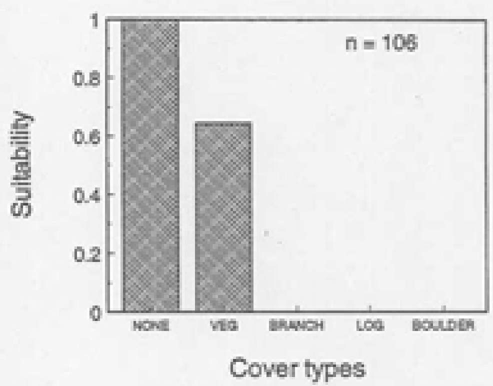

Figure 36. *Lampsilis cardium* cover preference.

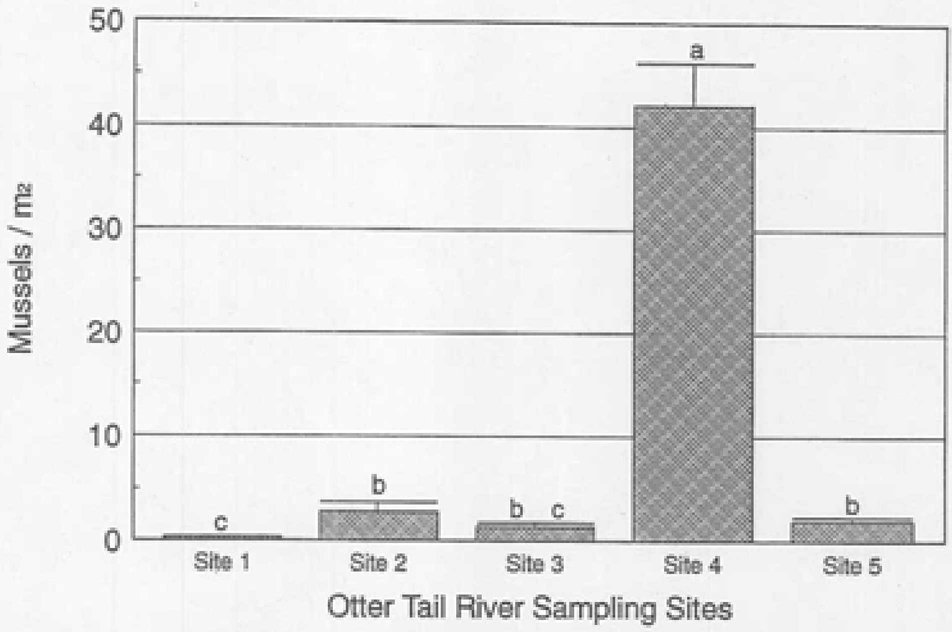

Figure 37. Otter Tail River sampling sites densities + 1 standard error. Means with a common letter are not significantly different (P>0.15) using a Kruskal-Wallis ANOVA and Dunn's multiple comparison test incorporating an experiment-wise error rate.

Table 4. Species of mussels collected at five different sites on the Otter Tail River

Mussel species	Sampling sites				
	Site 1	Site 2	Site 3	Site 4	Site 5
Actinonaias ligamentina (Lamarck, 1819)			X		
Amblema plicata (Say, 1817)			X	X	X
**Anodonta grandis* (Say, 1829)	X	X	X	X	
**Anodontoides ferussacianus* (Lea, 1834)	X	X	X	X	
**Fusconaia flava* (Rafinesque,1820)			X	X	X
**Lampsilis siliquoidea* (Barnes, 1823)	X	X	X	X	X
**Lampsilis cardium* Rafinesque, 1820		X	X	X	X
**Lasmigona complanata* (Barnes, 1823)		X	X		X
**Lasmigona compressa* (Lea, 1829)	X			X	
Lasmigona costata (Rafinesque, 1820)			X	X	X
**Ligumia recta* (Lamarck, 1819)				X	X
Quadrula quadrula (Rafinesque, 1820)				X	X
**Strophitus undulatus* (Say, 1817)	X	X	X	X	X

* Signifies headwaters or small river species (Dawley 1947).

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Site *4* had the greatest species richness, with 11 of the *13* mussel species found in the Otter Tail River collected there (Table 4). Nine mussel species were collected at site 5 (Table 4). The reduction in the number of species at site 5, when compared to site *4,* was attributed to the absence of *Anodontoides ferussacianus, Anodonta grandis,* and *Lasmigona compressa* and the addition of *Lasmigona complanata.*

Discussion

Habitat Suitability Criteria

In this study, *Amblema plicata, Fusconaia flava, Lasmigona costata,* and *Strophitus undulatus* all had similar habitat suitability criteria values in the Otter Tail River. Cvancara (1983) reported that *Amblema plicata, Fusconaia flava,* and *Strophitus undulatus* collected in the Red River of the North and some of its tributaries had similar habitat preferences. *Lasmigona costata* was not found in North Dakota rivers (Cvancara 1983). Previous mussel surveys within the basin of the Red River of the North have shown that different mussel species were often found in various habitats, yet some species had specific requirements (Wilson and Danglade 1912; Dawley 1947; Cvancara 1970, 1983; Clarke 1973).

In my study of the Otter Tail River, *Amblema plicata, Fusconaia flava, Lasmigona costata,* and *Strophitus undulatus* were usually found occurring together, with the highest densities in the stream's thalweg. Cvancara et al. ('1966) reported that most of the mussels they found in the Turtle River, North Dakota, were also located in the stream's thalweg. The thalweg areas in the Otter Tail River were most obvious in run habitats. These runs were characterized by shallow shoreline areas with deep, fast waters and gravel substrates in the midstream sections. The runs in the Otter Tail River are critical for the continued survival of mussels and should be protected with stream flow regulations that will provide these suitable habitats.

Water velocity is one of the physical factors regulating the distribution of mussels in the Otter Tail River. Velocity preferences for *Amblema plicata, Fusconaia flava, Lasmigona costata,* and Strophitus *undulatus* peaked at about 80 cm/s, with velocities much less than 25 cm/s having low or zero suitability. This velocity preference may occur for several reasons. These relatively fast velocities may allow for the optimum uptake of food and oxygen (Cvancara et al. 1966), as well as creating the required conditions for the successful fertilization of female mussels (Fuller 1974).

Anodonta grandis was the only mussel collected in large numbers in slow moving water. A possible explanation may be that most individuals of *Anodonta grandis* cannot physically tolerate high current velocities because they lack the pseudocardinal and lateral hinge teeth that aid in the alignment of the mussel's shell (Coen 1985). Mussel shells lacking large hinge teeth sheared apart at significantly lower forces when compared to shells having teeth. The absence of hinge teeth may force *Anodonta grandis* to expend significant amounts of energy to prevent their shells from shearing apart in areas of high water velocity (Coen 1985).

Shallow regions of the Otter Tail River did not support high densities of mussels, indicating ,that a minimum water depth is a factor in governing the distribution of mussels. Depths of about 150 cm had the highest suitability overall for all the mussel species collected in the Otter Tail River. Areas of the Otter Tail that were shallower than about 60 cm had either extremely low or zero suitability. These depth preferences were also noted by Isley (1914) for mussels 45 in Shoofly Creek and the Chikaskia River, Oklahoma. When *Amblema pficata* were transplanted into waters < 60 cm, the mussels would move to areas of water > 90 cm (Isley 1914). Negus (1966) also noted that mussel densities vary with water depth, with the maximum densities of four species found at depths ranging from 2-3 m.

Possible reasons for low mussel densities in shallow areas may be that periods of low flow, as well as high predation rates, prevent mussels from successfully exploiting the shallows (Fuller 1974). Most of the mussels collected in shallow areas in this study were juveniles, with adults being almost completely absent. Mussels that occupy the shallow areas near shore probably do not survive in these habitats very long (Fuller 1974). Since shallow areas of streams are more sensitive to reductions in stream flows (Aadland 1993), the mussels in these shallow areas would be subjected to increased periods of low or no flow, freezing and scouring during winter months, and desiccation during drought years (Cvancara 1970). Mussels in the shallow areas of the stream (< 60 cm) may also experience a higher risk of mammalian predation (McMahon 1991). Because raccoons forage near the shallow shoreline areas, mussels in the deeper habitats of the stream would probably not be collected often by these predators (McMahon 1991).

The greatest numbers of mussels in the Otter Tail River, in terms of both total density and species richness, occurred in areas dominated by coarse substrates. Gravel substrates had the highest suitability for *Amblema plicata,* *Fusconaia flava, Strophitus undulatus,* and *Lasmigona costata.* Reasons for this preference may be that gravelly substrates provide optimum microhabitats for mussels (Fuller 1974), because they do not hinder the mussels' ability to burrow (Lewis and Riebel 1984). These firm, gravel substrates may also aid the mussels in anchoring themselves (Harman 1972), thus maintaining the correct orientation required for filtering and respiration (Cvancara et al. 1966). Substrate suitability values for *Lampsilis siliquoidea* were the highest for coarse substrates in the Otter Tail River, although they were often found in all of the substrates available. *Lampsilis siliquoidea* has been characterized as a substrate generalist by Clarke (1981), and my study suggests this as well.

Silt and detritus laden substrates had very low, or zero, suitability for all of the mussel species collected in this study with the exception of *Lampsilis siliquoidea* and *Anodonta grandis.* The absence of mussels in otherwise suitable habitats has been found to be correlated with the accumulation of large amounts of silt (Stansbery 1970, Salmon and Green 1983). Fine, unstable substrates may not provide sufficient physical support for most mussel species (Salmon and Green 1983). For mussels to maintain their filtering positions in silty substrates, an increase in energy expenditure and burrowing efforts is required (Lewis and Riebel 1984). Silt also has the potential for clogging the gills of mussels, thus hindering respiration, feeding, and reproduction (Fuller 1974, Aldridge et al. 1987). Hynes (1970) stated that current velocities > 20 cm/s are required to remove silt from the substrates. Hynes' (1970) results illustrated the interrelationship between substrate composition and water velocity. This relationship is also reflected in the substrate and velocity suitability values presented in this study.

The majority of the mussel species collected in this study did not show any significant preference for instream cover. *Anodonta grandis* was the only species found in high densities in areas with large growths of aquatic vegetation. Clarke (1973) reported that *Anodonta grandis* was found 89% of the time in areas of moderate to dense growths of vegetation. *Anodonta grandis* may have been present in these vegetated areas because the plants lowered water velocities.

Mussel Density and Diversity

Mussel community changes that occurred along the longitudinal gradient of the Otter Tail River were primarily due to the addition of new species in the downstream reaches. The greatest addition of species occurred between sites in reaches 1 and 2, over an approximate drop in elevation of 75 m (Fig. 3). Most of the mussels that were collected in the headwater areas were also found in the downstream reaches, suggesting that species addition, not replacement, was occurring (Table 4). The addition of mussel species with increasing stream size was also found by Strayer (1983) in southeastern Michigan streams.

Some of the possible reasons for differences in densities and species richness found between sites may be due to different flow regimes (Strayer 1983), habitat availability, stream size (Vannote et al. 1980, Strayer 1983), or fish host availability (Dawley 1947, Fuller 1974). The lowest mussel densities were found at site 1, a headwaters site, which was located within the Tamarac National Wildlife Refuge (Fig. 37). A possible reason for low densities and low species richness at site 1 may be that headwater reaches of streams are more likely to experience a higher degree of instream flow variability than are downstream reaches (Strayer 1983, Rahel and Hubert 1991). Upstream reaches may also have low food availability for filter feeding invertebrates (Vannote et al. 1980). The unstable conditions of upstream reaches may provide too harsh of an environment for some mussel species (Strayer 1983).

The majority of the mussels collected at site 1 were. found in the deepest water available. Riffles and shallow run habitats dominated site 1. I observed that the shallow areas in this site were almost completely devoid of mussels, perhaps due to increased predation, spring floods that scour the stream bottom, or the prolonged low flow conditions that occur during the late summer months. These adverse conditions have been shown to limit suitable mussel habitats in other streams (Cvancara 1970, Strayer 1983). Aadland (1993) documented that the shallow riffle and run areas of streams are sensitive to alterations of instream flows.

Mussel density and species richness were higher at site 2 than at site 1. Site 2 was located approximately 50 m downstream of the Rice Lake Dam. This dam has the effect of stabilizing the stream flow within the site. The increase in stream flow stabilization may make this area more suitable for mussels (Cvancara 1970, Strayer 1983) by acting as a reset mechanism for the river continuum concept (by giving this headwater area more downstream attributes) (Vannote et al. 1980). All of the mussels collected at sites 1 and 2 are considered to be small-stream or small-river species (Dawley 1947) (Table 4).

Mussel densities were not significantly different when comparing sites 1 and 3 (Fig. 37). Although there were no significant differences in mussel density, there was an increase in species richness from 5 species at site 1 to 10 species at site 3. Since site 3 has more large-stream characteristics, the increase in species richness may be due to an increase in food availability such as fine organic particulate matter in the water column (as predicted by Vannote et al. 1980). The four species that ,joined the assemblage at site 3 are considered to be more typical occupants of medium-sized rivers (Dawley 1947) (Table 4).

Three subfamilies of mussels were collected in the Otter Tail River, with Anodontinae and Lampsilinae being found mostly in the upstream reaches and Ambleminae dominating the downstream sites (Fig. 38). These results follow the findings of Dawley (1947), who stated that Minnesota headwater streams would be dominated by members of the subfamily Anodontinae.

The farthest downstream sites, sites 4 and 5, also had greater mussel densities and species richness than did site 1. The downstream reach where sites 4 and 5 are located has a wider channel width and greater stream discharge than the upstream reaches. These stream characteristics give sites 4 and 5 more large river attributes, so an increase in mussel density and species richness is expected (Vannote et al.1980, Strayer 1983). Most of the mussel 50

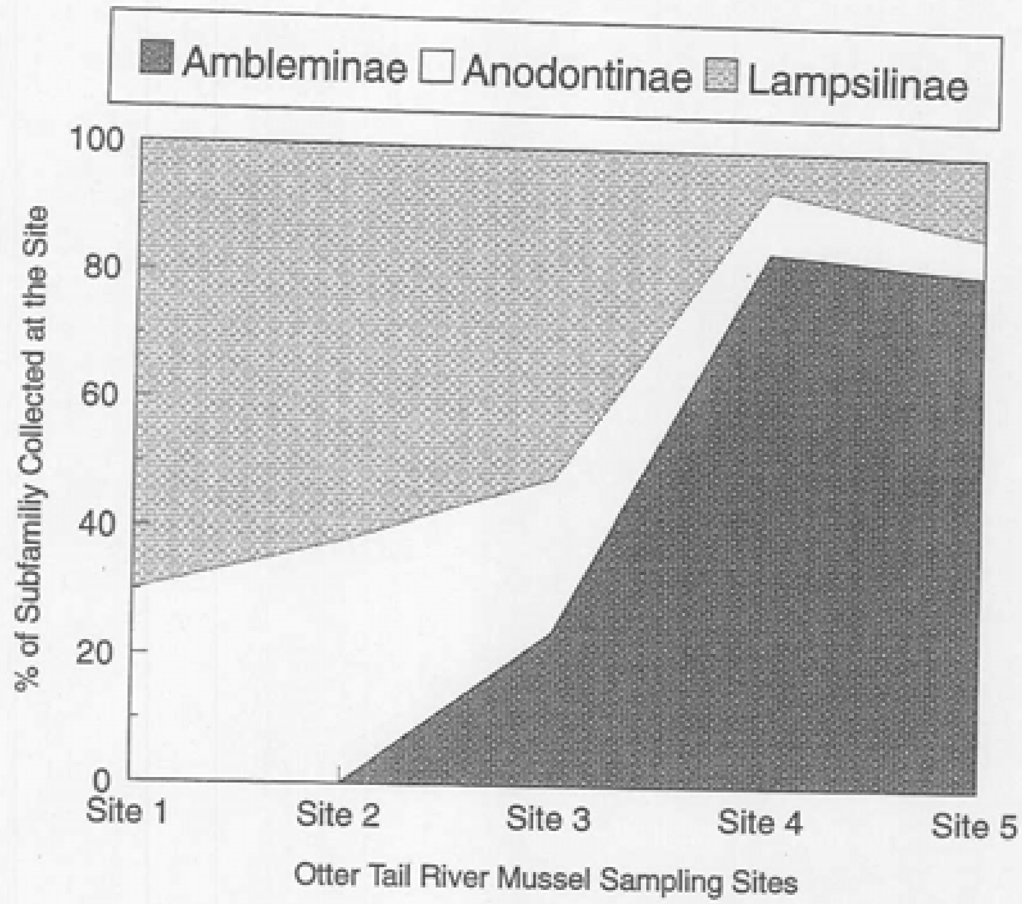

Figure 38. Percent composition of mussel subfamilies within the Otter Tail River.

species that were added to the Otter Tail River mussel assemblage at sites 4 and 5 have been classified by Dawley (1947) as large-river species (Table 4). Their domination can also be seen in Figure 38.

The occurrence or absence of suitable fish hosts for mussel glochidia is known to affect mussel distributions (Fuller 1974). Several species of mussels were not collected at sites 1 and 2, although their implicated fish hosts were present (Fuller 1974, Schmidt 1993). The occurrence of these fish does not necessarily mean that the fish are infected with glochidia. The reason for the lack of mussel species in these upstream sites could be that the numerous dams on the Otter Tail River prevent the exchange of glochidia-infected fishes between stream reaches (Ortmann 1909, Wilson and Danglade 1912). Although some fish may be able to migrate over lowhead dams during high water periods, low flows would impede their passage, preventing the colonization of some mussel species (Fuller 1974). Dams on the Otter Tail River include both low head (seasonally impassable) and high head dams which are impassable year round (Luther Aadland, Minnesota Department of Natural Resources, pers. communication).

Conclusions

Results from this study indicated that mussel species have specific habitat preferences. Although there was a lot of similarity among species, especially since shallow, low velocity habitats did not support mussel communities and deep, moderately fast current areas did. These areas are characteristic of run habitats. These runs provided the optimum water and substrate conditions required for these mussels to thrive. Measures should be taken within the Otter Tail River and other similar midwestern streams to ensure the protection of these run habitats. Considering the current status of North American mussels, the habitat suitability criteria developed in this study will become an important tool for stream ecologists in the future. Mussel populations are continuing to decline due to anthropogenic disturbances, and these criteria can be used to protect and identify suitable habitats for mussels.

Mussel density and species composition changed significantly when comparing upstream sites to downstream sites. The farthest upstream site located in the Tamarac National Wildlife Refuge had the lowest density of mussels, as well as the fewest number of species present. Low densities and low species richness may be due to inadequate stream flows during certain periods of the year. Water appropriations should be carefully monitored during periods of low flows in these and similar areas.

Low mussel density and species richness may also be caused by the lack of glochidia-infected fish at the upstream sites. Several downstream dams on the Otter Tail River block the passage and exchange of fish within the stream

(Wilson and Danglade 1912). The presence of dams are an obstacle to the continued survival of mussels in streams (Ortmann 1909). The removal of the Otter Tail River dams or the fitting of fish passage structures through the dams, first suggested in 1912 by Wilson and Danglade (1912), has not occurred and should be considered as a way to restore the connectivity of the Otter Tail River system with the Red River of the North.

The use of mussel species habitat data in instream flow assessments represents a community-orientated approach to establishing protected stream flows for aquatic communities residing in warm water streams (Aadland et al. 1991) and should be considered in other areas of the United States where mussel conservation is a concern.

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