Hornbach et al 1996

Factors influencing the distribution and abundance of the endangered winged mapleleaf mussel, *Quadrula fragosa*

Daniel J. Hornbach, James March[1], Tony Deneka
Department of Biology
Macalester College
St. Paul, MN 55105

Nels Troelstrup[2] and James A. Perry
Department of Forest Resources
University of Minnesota
St. Paul, MN 55108

[1]Present Address: Institute of Ecology, University of Georgia, 711 Biological Sciences Bldg., Athens, GA 30602
[2]Present Address: Dept. of Biology & Microbiology, South Dakota State University, Box 2207B, Brookings, SD 57007-0595

ABSTRACT

In this study we examined physical and biological factors that may influence the distribution of the endangered winged mapleleaf mussel, *Quadrula fragosa* (Conrad, 1835). Quantitative sampling of the mussel community was undertaken at two sites in the St. Croix River known to harbor *Q. fragosa*. Additional species-specific searches were also conducted for *Quadrula fragosa*. For each quantitative sample, physical habitat characteristics including the substrate composition, flow and depth were assessed and mussels were identified and measured. *Q. fragosa* were located in shallower areas with lower bottom current velocity compared to the overall mussel community. There was no difference in the substrate composition in areas with and without *Q. fragosa*. Mussel community density and richness were higher in areas where *Q. fragosa* was found. The mussel community associated with *Q. fragosa* was not significantly different from the general mussel community in the area, however three species, *Truncilla truncata, Truncilla donaciformis* and *Quadrula metavevra*, had significant associations with *Q. fragosa*. It appears that *Q. fragosa* does not have habitat requirements different than the rest of the mussel community, and since it is associated with dense and diverse mussel communities, management for the entire mussel community should be effective in protecting this endangered species.

INTRODUCTION

North America possesses the largest number of species of fresh water mussels in the world. Unfortunately, of the 297 species and subspecies of freshwater mussels found in North America, 43% of the taxa are either extinct, endangered,threatened, or federal candidate species (Allan and Flecker, 1993). To reduce risk of extinction for these species, additional research needs to be conducted to better understand how physical habitat characteristics and mussel community composition affect the distribution and population characteristics of these species.

The most commonly cited factors which are hypothesized to influence mussel abundance and distribution are water velocity and depth, substrate type and fish host distribution. Water velocity has been shown to be significantly correlated with the distribution of mussels (Horne and Macintosh, 1979; Salmon and Green, 1983; Way *et al.*, 1989; Holland-Bartels, 1990). Studies on marine mussels have shown that current velocity can directly affect feeding and respiration (Fréchette *et al.*, 1989; Wildish and Miyares, 1990). Low current velocity can also affect reproduction by limiting gamete dispersion and the release of glochidia (Fuller, 1974).

Water depth is also known to influence the density of mussel communities (Brönmark and Malmquist, 1982; Stern, 1983;

Doolittle, 1988). Mussel populations have been known to perish from desiccation when water levels decrease dramatically, leaving the mussels exposed (Fuller, 1974; Strayer, 1983). Low water levels could also result in scouring of the substrate by ice during winter months and spring thaw, having serious direct effects on mussels (Johnson, 1995). Low water levels during the summer could also contribute to an increase in water temperatures unfavorable to mussels (Fuller, 1974).

Sediment characteristics are of considerable importance to mussel distribution (Brönmark and Malmquist, 1982). Harman's (1972) studies showed that mussel species diversity is positively correlated with substrate diversity. A study by Salmon and Green (1983) found an increase in frequency of mussel occurrence with coarse substrate. A few studies have theorized that the stability of the substrate rather than its particle size is most important in determining mussel distribution (Vannote and Minshall, 1982; Strayer and Ralley, 1991).

Some of the variables (water velocity and depth, substrate composition, and host fish distribution) which are hypothesized to influence mussel abundance and distribution ~~that~~ have been examined at both the macro- and microhabitat levels. At the macrohabitat level, Watters (1992, 1993) has shown that there is a high correlation between fish diversity and mussel diversity. ~~has~~ Stream size and tidal influence were the most effective predictors of mussel distribution in one study Strayer (1993). Di Maio and Corkum (1995) also have shown an association between various unionid communities and specific flow-related stream habitats.

Studies focused on microhabitat characteristics of unionids have not shown high predicative power. Holland-Bartels (1990), for example indicated that while mussel abundance varied significantly as a function of current and sediment, abundance could be accurately predicted from habitat variables in less than 50% of the sites examined. Likewise, Strayer and Ralley (1993) and Strayer *et al.* (1994) question the ability of microhabitat characteristics to be useful in predicting unionid distribution.

Certainly some mussel species have unique habitats (e.g., the salamander mussel and its unique host, the mud puppy *Necturus maculosus*, are found often under large flat rocks (Oesch, 1984); and there is a tendency for thin-shelled species or forms with obese shells to be found in fine-grained sediments (Fuller, 1974; Mackie and Topping, 1988). But as noted above, most studies have failed to demonstrate habitat characteristics having high predictive value for mussel community abundance or distribution. Unfortunately, little is known concerning the preference of individual species for specific habitat characteristics. Bailey (1989) has provided evidence that there may indeed be habitat selection in unionids and thus an examination of the relationships between habitat characteristics and species abundance and distribution is needed for endangered species management.

Quadrula fragosa is an endangered mussel about which we know little. Occurrences of *Q. fragosa* were frequently reported until the 1920's (Eldridge, 1991). *Quadrula fragosa* formerly occurred extensively in the Mississippi, Tennessee, Ohio and Cumberland River drainages in the states of Ohio, Indiana, Missouri, Tennessee, Nebraska, Iowa, Illinois, Wisconsin, Minnesota, Oklahoma, and Kentucky (Eldridge, 1991; Vaughan, *in press*).*Quadrula fragosa* was listed as an Endangered Species on July 22, 1991 (Eldridge, 1991). Presently, the only known population of *Q. fragosa* is found in the Saint Croix River, from Interstate Park to Osceola, Wisconsin (Fig. 1). The significant decrease in number and range of *Q. fragosa* is thought to be due to destruction and modification of its habitat (Eldridge, 1991). Recent reports of zebra mussels (*Dreissena polymorpha*) approximately 80 km downstream in the lower St. Croix River (Baker *et al.*, 1996), pose a further risk to these isolated populations of *Q. fragosa*.

The St. Croix River contains many diverse and dense mussel beds (Dawley, 1947; Fuller, 1980; Stern, 1983; Doolittle, 1988; Hornbach, 1992). Hornbach (unpubl. data) ~~has found~~ reported 38 species of mussels at densities ranging from 1 to 200 individuals/m^2. Although mussel community composition has been examined in the St. Croix River, there have been few studies conducted to specifically examine the distribution of endangered mussels. There have been only two recent studies of the last known population of *Q. fragosa*, 1990 (David Heath, pers. comm.) and 1992 (Glen Miller, pers. comm.). Through these population studies, 59 live individuals were found. Unfortunately the objective of these studies did not include the assessment of physical habitat characteristics. The objective of this paper is to characterize *Q. fragosa* habitat and community relationships in the St. Croix River. Data presented here will enable decisions about management plans targeted toward protecting this endangered species.

MATERIALS AND METHODS

Study Sites

This study was conducted at two sites in the Saint Croix River: Interstate Park located near Taylor's Falls, Minnesota and St. Croix Falls, Wisconsin, and Franconia, MN (Fig. 1). The Interstate Park study site (River Mile 49.5-50.5) is located roughly 3.5 km downstream of a hydroelectric peaking dam and the Franconia site (River Mile 47.5-48.5) is approximately 3.2 km downstream of Interstate. These sites were chosen because of the known presence of *Q. fragosa* (David Heath, pers. comm.) and because of the dense and diverse mussel communities located at these sites (Doolittle, 1988). During the summers of 1991, 1992, 1993 and 1995, quantitative sampling of the mussel community took place. In 1991, 100 individual 0.25 m^2 quadrats were sampled at Franconia. Ten sites were oriented in pairs, parallel to the longitudinal axis of the river (Fig. 1). At each site, ten individual quadrats were sampled using a 5 m x 2 m PVC grid as a framework to prevent resampling of an area. The location of each site was noted with a Magellan Nav-5000 Geographical Positioning System. In 1995, these 10 sites were resampled, giving a total of 200 quantitative quadrats sampled at Franconia. At Interstate Park, 150 quadrats were sampled in the channel east of Folsum Island in 1992 (Fig. 1). In this effort, ten replicate quadrats were taken at each of 15 sites. In 1995, ten sites (the middle and eastern sites) were resampled. In 1993 three sites, near Blast Island (about 500 m downstream) were sampled, with eight replicates taken per site. Finally in 1995, two sites upstream of Blast Island were sampled, with ten replicates per site. This gave a total of 294 quadrats sampled at Interstate Park.

Sampling

The sampling methodology at each quadrat was consistent for all years. A 0.25 m^2 metal frame was placed on the sediment and roughly the top ten centimeters of substrate and all mussels found within were removed by researchers utilizing SCUBA. The substrate and mussels were placed into a 20 liter plastic bucket which was lifted to the surface. The contents of each bucket were passed through a series of four sieves with openings of 77, 12.7, 6.35 and 0.5 mm respectively. The substrate in each sieve was then weighed to the nearest 0.25 kg using a hanging spring balance. These weights were used to calculate the percent substrate size composition and an average sediment diameter (phi size (ϕ) = ($-\log_2$(sediment diameter)) (Lewis, 1984). Since a variety of sediment types can contribute to the calculation of a mean sediment size, an index of sediment diversity was also calculated for each quadrat using the Shannon index of diversity (Zar, 1984). All mussels were removed from the sieves and identified. Care was taken to collect juvenile mussels hanging from the sieves by their byssal threads. The mussels' length, width, and height were measured to the nearest 0.01 mm using dial calipers. At each quadrat the water depth and velocity were measured. The water velocity was measured using a Marsh-McBirney, model 201-D or Global Water 201 flow meter at the substrate water interface. The depth was measured to the nearest 0.02 m using a calibrated metal rod.

Sampling specifically for *Quadrula fragosa*

In the sampling regime noted above, only three *Q. fragosa* were found (one at Interstate Park and two at Franconia). Consequently, a specific search method for *Q. fragosa* was instituted. At Interstate Park, a total of 36 diving hours was spent searching specifically for *Q. fragosa* in 1992, 11.3 hours in 1993 and 7.25 hours in 1995. At Franconia, we spent 9.25 diver hours conducting species-specific searching in 1995. When a *Q. fragosa* individual was located, researchers marked the exact location with a buoy. The 0.25 m^2 quadrat was placed where each *Q. fragosa* was found and the substrate and mussels within were removed and analyzed in the same manner as mentioned above. The geographic position, depth and water velocity were also measured as described above. Each *Q.*

fragosa found was aged by counting its external growth rings, measured, and returned to the substrate by hand.

Statistical analyses were conducted using JMP 3.0 (SAS, 1994) on a Macintosh 8100. Non-parametric tests (e.g. Wilcoxon rank score test) were used because there were either no *a priori* reason to suspect that the distributions were normal (e.g. species richness, substrate size, etc.) or the distributions were not normal (Shapiro-Wilk W test).

RESULTS

A total of 2869 mussels representing 30 species, were examined in this study. Only 26 specimens of *Q. fragosa* were found and of the remaining 2843 mussels, 218 were found in the quadrats where the *Q. fragosa* were found. Twenty-three *Q. fragosa* were found at Interstate Park and only 3 were found at Franconia. All but three of the *Q. fragosa* specimens were found as a result of species-specific searching.

Water Velocity and Depth

The water velocity at the sediment-water interface varied considerably ranging from 0-0.6 m/s. Some of this variability is due to the presence of a hydroelectric peaking plant just upstream of the Interstate Park site. Johnson (1995) conducted an instream flow study of both of the sites examined in this study. He also analyzed the historical data on stream discharge at these locations. While there is a great deal of variability in discharge, the variation in water velocity at the sediment-water interface, where measurements were taken for this study, are damped. For example, on June 30, 1992 water depth and bottom velocity were measured at two discharge levels at a single location at Interstate Park. At a discharge of 46.35 m^3/s (1637 cfs) the water depth was 0.23 m and the bottom flow was 0.30 m/s. At 147.53 m^3/s (5210 cfs) the depth increased 196% to 0.68 m while the bottom flow only increased by 13% to 0.34 m/s. The range of 45.3 - 147.2 m^3/s (1600-5200 cfs) covered the large majority of the conditions under which we measured flow and depth and thus variability in bottom flow was relatively low and certainly less than that for water depth.

The water velocity at the sediment-water interface was lower for quadrats where *Q. fragosa* was found than in quadrats where *Q. fragosa* was not found (Wilcoxon Z=-1.97, p=0.049, Fig. 2B). The depth ranged from 0.17 m to 4.7 m, with 97.5% of the measurements less than 2.7 m. The water depth was significantly less at sites where *Q. fragosa* was found Wilcoxon Z=-3.09, p=0.002; Fig. 2A). Clearly part of the reason for these differences is greater presence of *Q. fragosa* at Interstate Park which has shallower water depths (1.1 m) than Franconia (1.9 m). Interstate Park also had greater water velocity (0.26 m/s) than Franconia (0.22 m/s).

Substrate Analysis

The percentage of sediment in each sieve was calculated for each quadrat and expressed as the mean phi for the whole quadrat. The mean phi for quadrats containing *Q. fragosa* ranged from 0.49 (sand) to -5.1 (large cobble). There were no significant differences found between quadrats with *Q. fragosa* and those without *Q. fragosa* (Wilcoxon Z=0.30, p=0.76; Fig. 2C). Not only can the average size of the sediment be an important factor for mussels but the presence of a variety of sediments may be important. Thus, a sediment diversity index was calculated. There was no significant difference in the sediment diversity index in quadrats with or without *Q. fragosa* (Wilcoxon Z=0.94, p=0.35; Fig. 2D).

Community Composition

Quantitative sampling resulted in the collection of 2869 individual mussels representing 30 species (Fig. 3). Overall, the average density was 22.08 mussels/m^2, with a maximum density of 148 mussels/m^2. The average richness was 2.71 species/ 0.25 m^2 quadrat, with as many as 12 species present in a single quadrat. Mussel density was significantly greater in quadrats where *Q. fragosa* was present (Wilcoxon Z=4.34, p<0.0001; Fig. 4a). Also, quadrats containing *Q. fragosa* had more mussel species than did quadrats without *Q. fragosa* (Wilcoxon Z=5.26, p<0.0001, Fig. 4b).

Mussel communities in quadrats with and without *Q. fragosa* were ~~found to be~~ significantly different (χ^2 = 31.16 10 df, p<0.0006; Fig 5).

This analysis entailed grouping a large number of species (compare Fig. 3 and Fig. 5) into an "other" group to reduce the number of cells that had expected frequencies of 5 or less (Zar 1984). It is apparent from Fig. 5 that the major factor contributing to differences in the community structure between quadrats with and without *Q. fragosa* is a large percentage of "other" individuals associated with *Q. fragosa*. In fact, based on the χ^2 analysis, only 31 "other" individuals were expected to be found in the quadrats with *Q. fragosa*, however 55 individuals were actually found. This supports the data which showed a greater number of species associated with *Q. fragosa* (Fig. 4b). We attempted to determine spatial associations among *Q. fragosa* and other mussel species using a $\chi 2$ test of association (Ludwig and Reynolds, 1988). Three species were significantly positively correlated with the presence of *Q. fragosa*: *Quadrula metanevra* ($\chi 2$=4.39, 1 df, p=0.036), *Truncilla donaciformis* ($\chi 2$=13.20, 1 df, p=0.0003), and *Truncilla truncata* ($\chi 2$=6.06, 1 df, p=0.014).

In general, mussels found in quadrats with *Q. fragosa* were larger than those found in quadrats without *Q. fragosa* (Wilcoxon Z=3.91, p=0.001; Fig 4c). Of the three species found to be significantly associated with *Q. fragosa*, only *T. truncata* had significantly larger individuals associated with the presence of *Q. fragosa* (Wilcoxon Z=2.53, p=0.011; Fig. 4D).

?

Overall, *Q. fragosa* preferred habitat differs greatly from the average riverine condition but is quite similar to conditions under which other mussel species excel (Table 1).

Discussion

Quadrula fragosa is limited in its current distribution to a small area just below Taylor's Falls, MN on the St. Croix River. The exact reasons for this limited distribution are unknown. This study indicates that *Q. fragosa* is found in areas of slightly lower velocity and shallower depth than other areas which we sampled (Fig. 2A, B). The size and diversity of substrate in which *Q. fragosa* was found was not different than that noted for other areas sampled. Because *Q. fragosa* was found in areas of greater mussel density and richness (Fig. 2 A, B), we conclude that this rare species is found only in areas of high mussel species diversity. Doolittle (1988) found that the Interstate Park area exhibited the highest species density and richness of the entire St. Croix River basin. This site is downstream of a hydroelectric peaking dam; a former low waterfall. Some studies have shown a higher density of mussels below dams (Fuller, 1974). This increased density has been attributed to the maintenance of a stable substrate, increased food availability due to phytoplankton growth in reservoirs behind dams and highly oxygenated water. Other studies have shown that regulation of streamflow can adversely influence mussel populations (Tudorancea, 1972; Fuller, 1974; Miller *et al.*, 1984; Williams *et al.*, 1993). It appears that the area below the dam provides an outstanding resource for mussels in the St. Croix River.

Depth appears to have an important impact on the mussel community. Doolittle (1988) found most mussels in the St. Croix River at a depth near two meters. In a study on the Wisconsin and St. Croix Rivers, Stern (1983) found the maximum density of mussels at a depth of approximately 1.7 meters. In this study, we also found that species richness and density peaked at depths near 2.0 meters. In fact, while the average depth where *Q. fragosa* was found was less than that for other quadrats, no *Q. fragosa* were found in depths less than 0.42 m. A number of studies have shown that desiccation can lead to high mortality of mussels (Fuller, 1974; Strayer, 1983; Miller *et al.*, 1984).

Q. fragosa in the St. Croix River had similar substrate preferences to other mussels (Fig. 2C, D). Strayer and Ralley (1993) hypothesized that the correlations between mussel communities and substrate may be related to substrate stability and the habitat it provides rather than its particle size. A recent study by Strayer (1993) supports this theory. Vannote and Minshall (1982) also found substrate stability to be an important factor affecting mussel distribution. In the St. Croix River, Doolittle (1988) indicated that the majority of mussels are found in stable substrates. Since we chose to sample only in areas of known high mussel abundance, it is not surprising that there was little difference in the substrate where *Q. fragosa* was or was not found.

Three species of mussel, *Q. metanevra, T. truncata* and *T. donaciformis*, were associated with *Q. fragosa*. The nature of that association is unknown. Doolittle (1988) has found associations between *Truncilla truncata*, and *Quadrula metanevra* in the St. Croix River. *T. truncata* is the dominant species at Interstate Park, so one might expect a correlation between it and *Q. fragosa*. However, *Q. metanevra* and *T. donaciformis* are comparatively few in number. A common fish host(s)or similar environmental requirements may explain the correlation between *Q. fragosa* and these other species. *Truncilla truncata, T. donaciformis* and *Q. metanevra* all share the sauger (*Stizostedion canadense*) as a fish host (Watters, 1994) which is found in the St. Croix River (Fago, 1986). Currently, the fish host for *Q. fragosa* is unknown.

It is interesting to note that *Q. fragosa* seems to exist only in areas of high mussel density and high species richness (Fig 4A, B). This supports the hypothesis that while *Q. fragosa* may have a set of preferred depths and water velocities, its hydrodynamic niche is one which favors mussels in general and is not unique for this species (Table 1). It is also possible that the specific microhabitat favored by *Q. fragosa* has high substrate stability because larger individuals, which are presumably older are found associated with *Q. fragosa* (Fig. 4C, D).

A similar set of findings has been reported for other endangered species. The endangered Higgins' Eye Pearly mussel (*Lampsilis higginsi*) is usually found in local habitats which appear to be optimal for the majority of sympatric unionacean species (Holland-Bartels, 1990; Wilcox *et al.*, 1993; Hornbach, *et al.*, 1995; Miller and Payne, 1995). Vaughn and Pyron (1995) have found that mussel species richness at a given site is the best individual predictor of the occurrence of the endangered Ouachita rock-pocketbook mussel (*Arkansia wheeleri*). Also, Miller *et al.* (1986) found that the habitat characteristics for the endangered mussel *Plethobasus cooperianus* were similar to other mussels, and that this species primarily was found in very diverse and densely populated mussel beds.

The simplest explanation for the highly localized distribution of an endangered species is that many species, including rare species, do well in "optimal" habitat. Unlike abundant species, however, densities of rare species such as *Q. fragosa* remain below threshold densities for successful spawning except in these optimal habitats. Water currents are known to be extremely important for reproduction in unionids. Evermann and Clark (1918) and Wilson and Clarke (1912) attribute low glochidial infection rates of fish and small mussel population sizes in lakes and ponds to lack of flow and the scattering of adults. While sparsely distributed organisms may have two individuals of the opposite sex close enough for reproduction, stochastic events can easily overcome the advantages that proximity may provide. Added to the variance associated with successful fertilization, are the probabilities of glochidial larval attachment to, and dispersal by, the proper host fish, metamorphosis and location of suitable substrate for settling (Fuller, 1974). To survive a unionid mussel must have a highly clustered distribution, and produce very large numbers of glochidia larvae.

The corollary to the above argument is that thinly distributed unionacean bivalves will fail to reproduce, at least on a dependable basis. Even in a healthy species, scattered individuals at the fringes of reproducing populations will not contribute significantly to the maintenance of the population due to the spatial distribution of these fringe populations. Thus, scattered individuals of a long-lived species like *Quadrula fragosa* may persist well after all reasonable chance of reproduction has ceased.

The future for *Q. fragosa* seems uncertain. After 494 quantitative samples and 63.8 diver-hours of specific searching, only 26 specimens of *Q. fragosa* were found. The population of *Q. fragosa* appears to be very small and localized, making it prone to stochastic disturbances. Reproductive probabilities may have already st the species on the path to extinction. The impending invasion of the zebra mussel to the St. Croix River (Baker *et al.,* submitted), and its detrimental effects on unionids (Mackie, 1991; Hunter and Bailey, 1992) seems to further decrease *Q. fragosa*'s chances of survival.

If managers wish to increase the probability of *Quadrula fragosa* survival, the most viable strategy appears to be maintenance of localized patches of preferred mussel habitats which encourage highest density and diversity of unionid species (Table 1).

ACKNOWLEDGMENTS

This work was in part funded by the Environmental Protection Agency Cooperative Agreement # CR820083, the United States Department of the Interior, Fish and Wildlife Service , National Park Service, the Wisconsin Department of Natural Resources Endangered Species Program and the Minnesota Department of Natural Resources Nongame Wildlife Program. The authors wish to acknowledge the assistance of John Foley, Kate Howe, Aleria Jensen, Emily Mugnolo, Lindsay Powers, Amy Ramquist, Mark Ruebel, Megan Tyrrell, and Scott Villinski.

Literature Cited

ALLAN, J. D., AND A. S. FLECKER. 1993. Biodiversity Conservation in Running Waters. *Bioscience* **43**:32-43.

BAILEY, R. C. 1989. Habitat selection by a freshwater mussel: an experimental test. *Malacologia* **31**: 205-210.

BAKER, P., S. JENNINGS AND D.J. HORNBACH. 1996. Can zebra mussels force a species to extinction? Submitted to *Dreissena*!

BRÖNMARK, C. AND B. MALMQUIST. 1982. Resource partitioning between unionid mussels in a Swedish lake outlet. *Holarctic Ecol.* **5**:389-395.

DAWLEY, C. 1947. Distribution of Aquatic mollusks in Minnesota. *Am. Midl. Nat.* **38**: 671-697.

DI MAIO, J. AND L. D. CORKUM. 1995. Relationship between the spatial distribution of freshwater mussels (Bivalvia: Unionidae) and the hydrological variability of rivers. *Can. J. Zool.* **73**: 663-671.

DOOLITTLE, T. C. J. 1988. Distribution and relative abundance of freshwater mussels in the Saint Croix National Scenic Riverway. Report to the Wisconsin Division of Natural Resources, Bureau of Endangered Resources.

ELDRIDGE, J. L. 1991. Determination of endangered status for the winged mapleleaf freshwater mussel. *Federal Register* **56**(119): 28345-28349. June 20, 1991.

EVERMANN, B. W. AND H. W. CLARK. 1918. The Unionidae of Lake Maxinkuckee. *Proc. Indiana Acad. Sci.* **1917**:251-285.

FAGO, D. 1986. Distribution and relative abundance of fishes in Wisconsin #7. *Wisc. DNR Tech. Bull.* #159.

FRÉCHETTE, M., C. A. BUTMAN, AND W. R. GEYER. 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis* L.. *Limnol. Oceanogr.* **34**:19-36.

FULLER, S. L. H. 1974. Clams and mussels (Mollusca: Bivalvia), p. 215-260. *In* : C. W. Hart and S. L. H. Fuller (eds.). Pollution Ecology of Freshwater Invertebrates. Academic Press, New York.

FULLER, S. L. H. 1980. Freshwater mussels (Mollusca: Bivalvia: Unionidae) of the Upper Mississippi River: observations at selected sites within the 9-foot navigation channel project for the St. Paul District, United States Army Corps of Engineers, 1977-1979. Vol. I and II. Acad. Nat. Sci., Philadelphia.

HARMAN, W. N. 1972. Benthic substrates: their effect on fresh-water mollusca. *Ecology* **53**: 271-277.

HOLLAND-BARTELS, L. E. 1990. Physical factors and their influence on the mussel fauna of a main channel border habitat of the upper Mississippi River. *J. N. Am. Benthol. Soc.* **9**:327-335.

HORNBACH, D. J. 1992. Factors influencing the distribution of unionids in the St. Croix River, Minnesota, USA. pp. 25-28. *In* F. Giusti and G. Manganelli (eds.). Abstracts of the 11th International Malacological Congress, Siena, Italy. University of Siena, Siena, Italy.

———————, P. Baker AND T. Deneka. 1995. Abundance and distribution of the endangered mussel, *Lampsilis higginsi* in the lower St. Croix River, Minnesota and Wisconsin. Final Report to the US Fish and Wildlife Service, Contract # 14-48-000394-1009.

HORNE, F. R. AND S. McINTOSH. 1979. Factors Influencing distribution of mussels in the Blanco River of central Texas. *Nautilus* 94:119-133.

HUNTER, R. D. AND J. F. BAILEY. 1992. *Dreissena polymorpha* (zebra mussel): Colonization of Soft Substrata and Some Effects on Unionid Bivalves. *Nautilus* **106**:60-67.

JOHNSON, S. L. 1995. Instream flow requirements of *Quadrula fragosa* and the aquatic community in the lower St. Croix River downstream of the Northern States Power hydroelectric dam at St. Croix Falls, Wisconsin. Report to the Bureau of Endangered Resources, Wisconsin Department of Natural Resources, Madison, WI.

LEWIS, D. W. 1984. Practical sedimentology. Hutchinson Ross Publishing Co., Stroudsburg, PA. 229 p.

LUDWIG, J. A. AND J. F. REYNOLDS. 1988. Statistical ecology: a primer on methods and computing. John Wiley and Sons, New York. 338 pp.

MACKIE, G. L. 1991. Biology of the exotic zebra mussel, *Dreissena polymorpha*, relative to the native bivalves and its potential impact in Lake St. Clair. *Hydrobiologia* **219**:251-268.

———— AND J. M TOPPING. 1988. Historical changes in the unionid fauna of the Sydenham River watershed and downstream changes in shell morphometrics of three common species. *Can. Field-Nat.* **102**: 617-626.

MILLER, A. C., B. S. PAYNE AND R. TIPIT. 1984. Changes in the naiad fauna of the Cumberland River below Lake Cumberland in central Kentucky. *Nautilus* **98**:107-110.

————, ———— AND T. SIEMSEN. 1986. Description of the habitat of the endangered mussel *Plethobasus cooperianus*. *Nautilus* **100**:14-18.

———— AND ————. 1995. The importance of a mussel bed near McMillian Island, Pool 10 of the Upper Mississippi River for *Lampsilis higginsi*. Report for the Fish and Wildlife Service from the Army Corps of Engineers, Waterways Experiment Station, Vicksburg, Mississippi.

OESCH, R. D. 1984. Missouri Naides. A Guide to the Mussels of Missouri. Missouri Department of Conservation, Jefferson City, MO. 270 pp.

SALMON, A., AND R. H. GREEN. 1983. Environmental determinants of unionid clam distribution in the middle Thames River, Ontario. *Can. J. Zool.* **61**: 832-838.

SAS. 1994. JMP Statistics and graphics guide. SAS Institute Inc., Cary, NC. 580p.

STERN, E. M. 1983. Depth distribution and density of freshwater mussels (Unionidae) collected with SCUBA from the lower Wisconsin and St. Croix rivers. *Nautilus* **97**:36-42.

STRAYER, D. L. 1983. The effects of surface geology and stream size on freshwater mussel (Bivalvia: Unionidae distribution in southeastern Michigan, USA. *Freshwat. Biol.* **13**:253-264.

————. 1993. Macrohabitats of freshwater mussels (Bivalvia: Unionacea) in streams of the northern Atlantic slope. *J. N. Am. Benthol. Soc.* **12**:236-246.

———— AND J. RALLEY. 1991. The freshwater mussels (Bivalvia: Unionidae) of the upper Delaware River drainage. *Am. Malacol. Bull.* **9**:21-25.

———— AND ———— .1993. Microhabitat use by an assemblage of stream-dwelling unionaceans (Bivalvia), including two rare species of *Alasmidonta*. *J. N. Am. Benthol. Soc.* **12**:247-258.

———————, D. C. HUNTER, L. C. SMITH AND C. K. BORG. 1994. Distribution, abundance, and roles of freshwater clams (Bivalvia, Unionidae) in the freshwater tidal Hudson River. *Freshwat. Biol.* **31**:239-248.

TUDORANCEA, C. 1972. Studies on Unionidae populations from the Crapina-Jijila complex of pools (Danube zone liable to inundation). *Hydrobiologia* **39**:527-561.

VANNOTE, R. L. AND G. W. MINSHALL. 1982. Fluvial processes and local lithology controlling abundance, structure, and composition of mussel beds. *Proc. Natl Acad. Sci.* **79**:4103-4107.

VAUGHAN, P. *in press*. Winged mapleleaf mussel (*Quadrula fragosa*) recovery plan. U.S. Fish and Wildlife Service. Twin Cities, MN.

VAUGHN, C. C. AND M. PYRON. 1995. Population ecology of the endangered Ouachita rock-pocketbook mussel, *Arkansia* (Bivalvia: Unionidae), in the Kiamichi River, Oklahoma. *Amer. Malacol. Bull.* 11:145-152.

WATTERS, G. T. 1992. Unionids, fishes, and the species-area curve. *J. Biography* **19**:481-490.

———————. 1993. Mussel diversity as a function of drainage area and fish diversity: management implications, p. 111-116. *In* : K. S. Cummings, A. C. Buchanan and L. M. Koch (eds.). Conservation and Management of Freshwater Mussels. Proceedings of an UMRCC Symposium, 12-14 October 1992, St. Louis, MO. Upper Mississippi River Conservation Committee, Rock Island, IL.

———————. 1994. An annotated bibliography of the reproduction and propagation of the Unionoidea (primarily of North America). *Ohio Biol. Surv. Misc. Cont.* No. 1. 158p.

WAY, C. M., A. C. MILLER, AND B. S. PAYNE. 1989. The influence of physical factors on the distribution and abundance of freshwater mussels (Bivalvia: Unionidae) in the lower Tennessee River. *Nautilus* **103**:96-98.

WILCOX, D. B., D. D. ANDERSON AND A. C. MILLER. 1993. Survey procedures and decision criteria for estimating the Likelihood that *Lampsilis higginsi* is present in areas within the upper Mississippi River system, p. 163-167. *In* : K. S. Cummings, A. C. Buchanan and L. M. Koch (eds.). Conservation and Management of Freshwater Mussels. Proceedings of an UMRCC Symposium, 12-14 October 1992, St. Louis, MO. Upper Mississippi River Conservation Committee, Rock Island, IL.

WILDISH, D. J., AND M. P. MIYARES. 1990. Filtration rate of blue mussels as a function of flow velocity: preliminary experiments. *J. Exper. Mar. Biol. Ecol.*.**142**:2133-2190.

WILLIAMS, J. D., M. L. WARREN Jr., K .S. CUMMINGS, J. L. HARRIS and R. J. NEVES. 1993. Conservation Status of Freshwater Mussels of the United States and Canada. *Fisheries* **18**:6-22.

WILSON, C. B. AND H.W. Clarke. 1912. The mussel fauna of the Kankakee basin. *Bur. Fish Document*. **781**, 52 p.

ZAR, J.H. 1984. Biostatistical Analysis. Second Edition. Prentice-Hall. New Jersey. 718 p.

Table 1. Summary of preferred habitat for the *Quadrula fragosa* community and for the "average unionid site" as sampled in the St. Croix River. Variables asterisked are significantly different at $p<0.05$. All variables are expressed as mean ± one standard deviation.

Variable	*Q. fragosa* community	Overall unionid community
Water Depth (m)*	0.98 ± 0.46	1.42 ± 0.79
Velocity at sediment-water interface (m/s)*	0.19 ± 0.10	0.25 ± 0.13
Velocity at 0.6 depth * (m/s)	0.28 ± 0.20	0.47 ± 0.19
Conductivity µmho/cm	175 ± 22	161 ± 25
Dissolved oxygen (% saturation)	94 ± 7.4	88.9 ± 7.0
pH	7.5 ± 0.3	7.3 ± 0.7
Substrate size (ϕ)	-1.9 ± 1.1	-1.9 ± 1.4
Substrate diversity	1.0 ± 0.3	0.9 ± 0.4
Unionid density * (mussels/m^2)	37.5 ± 18.2	21.3 ± 22.6
Unionid richness * (species/0.25 m^2)	4.9 ± 1.8	2.6 ± 2.0
Unionid shell length * (all species - mm)	44.6 ± 22.3	40.0 ± 23.5
Truncilla truncata * shell length (mm)	36.8 ± 12.8	33.9 ± 12.7

Figure Captions

Figure 1. Map of study area. Dots indicate areas where multiple 0.25 m^2 quadrats were taken.

Figure 2. Relationship between various physical habitat parameters and the presence or absence of *Quadrula fragosa*. Bars give means and vertical lines are 1 standard deviation. P-values are for the null-hypothesis of equal ranks (Wilcoxon Rank-sum test).

Figure 3. Mussel community composition in the St. Croix River from Franconia, MN to Interstate Park, MN and WI. Numbers at the end of the bars are percent of the community that each species comprises.

Figure 4. Relationship between various mussel community and population parameters and the presence or absence of *Quadrula fragosa*. Bars are means and vertical lines are 1 standard deviation for the mean. P-values are for the null-hypothesis of equal ranks (Wilcoxon Rank-sum test).

Figure 5. Relationship between mussel community composition and the presence or absence of *Quadrula fragosa*.

FIG 1.

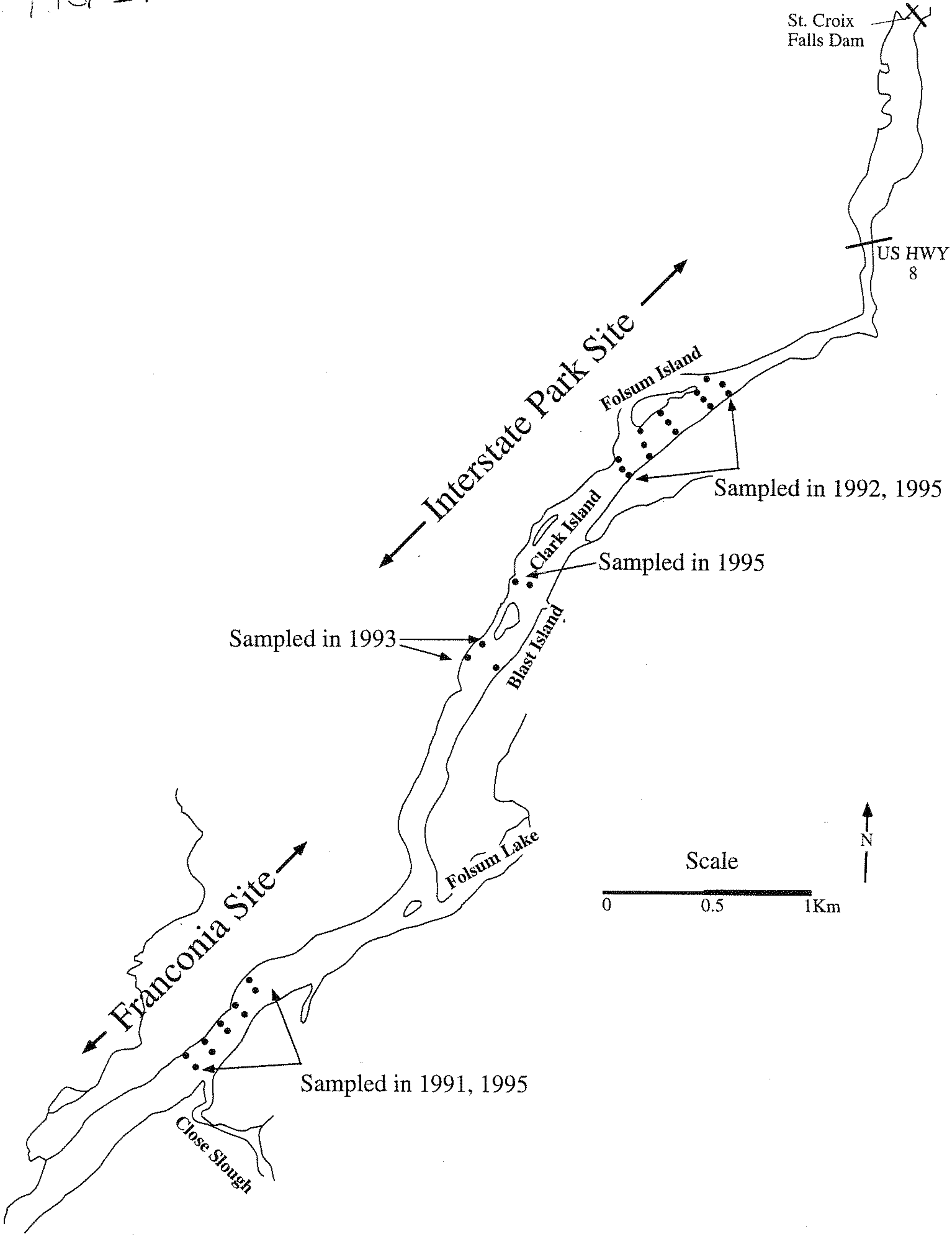

St. Croix
Falls Dam
US HWY
8
Interstate Park Site
Folsum Island
Sampled in 1992, 1995
Clark Island
Sampled in 1995
Sampled in 1993
Blast Island
Folsum Lake
Scale
0
0.5
1Km
N
Franconia Site
Sampled in 1991, 1995
Close Slough

FIG. 2

or questionable credibility

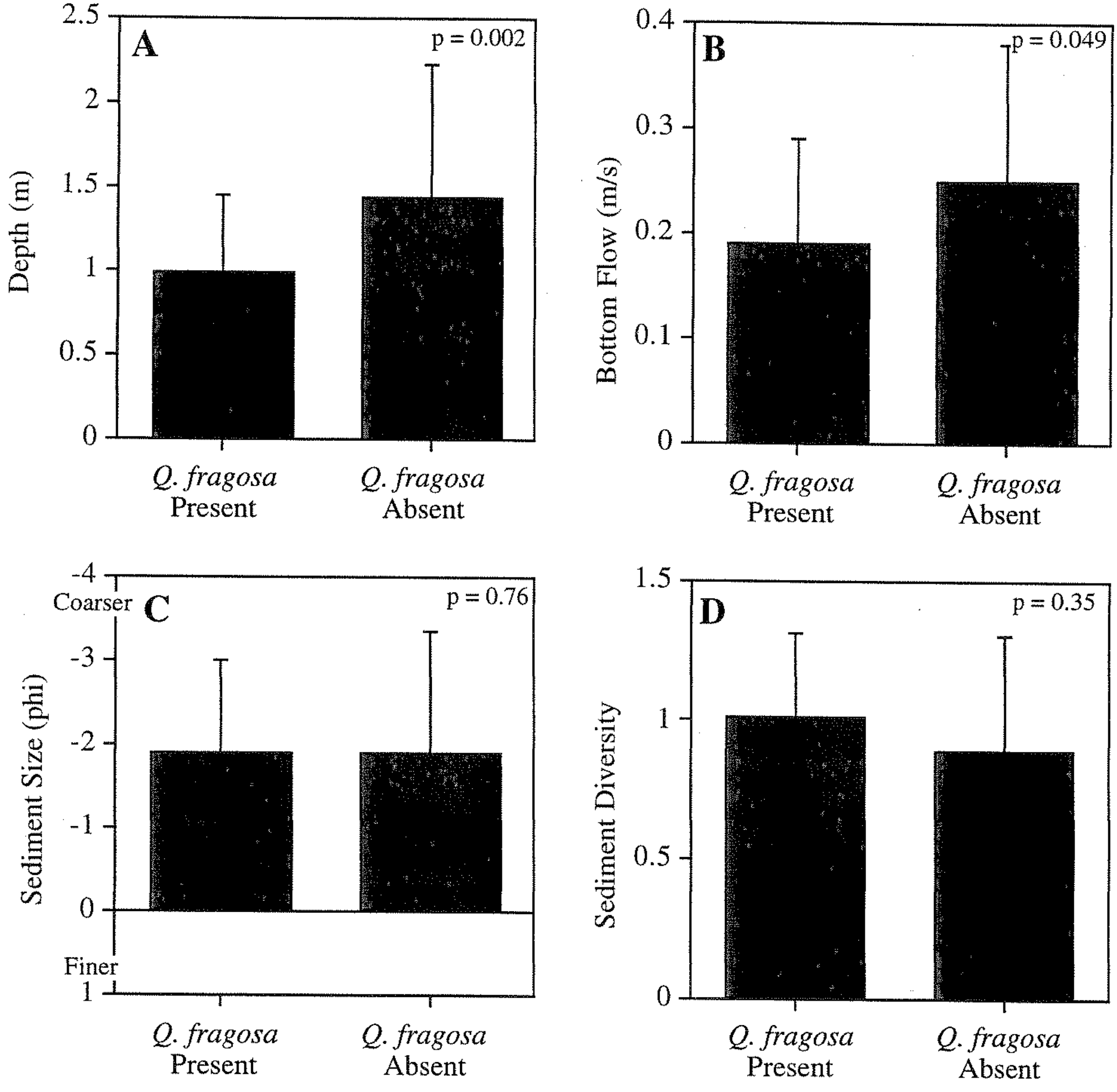
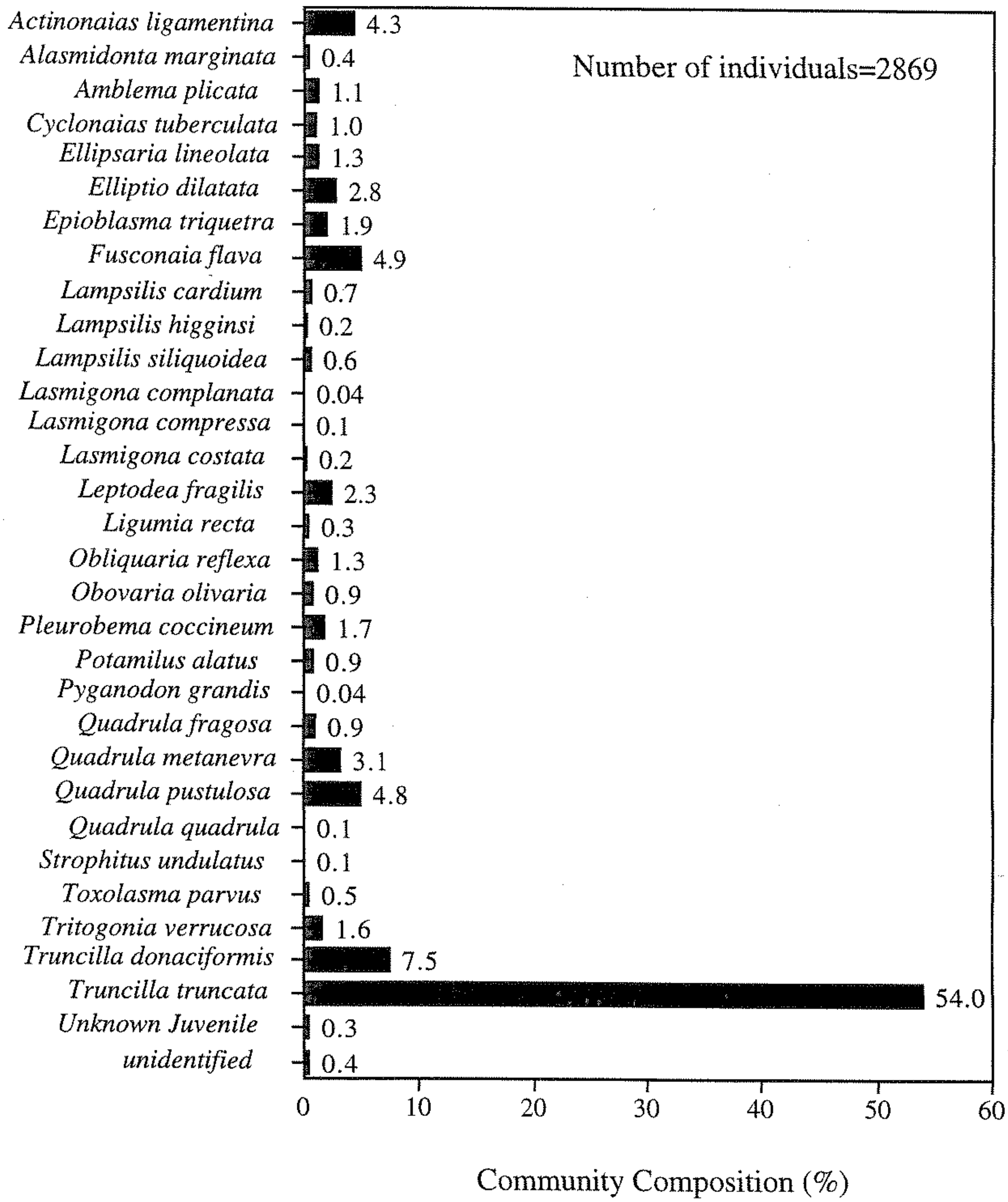


FIG. 3



Number of individuals=2869
Actinonaias ligamentina 4.3
Alasmidonta marginata 0.4
Amblema plicata 1.1
Cyclonaias tuberculata 1.0
Ellipsaria lineolata 1.3
Elliptio dilatata 2.8
Epioblasma triquetra 1.9
Fusconaia flava 4.9
Lampsilis cardium 0.7
Lampsilis higginsi 0.2
Lampsilis siliquoidea 0.6
Lasmigona complanata 0.04
Lasmigona compressa 0.1
Lasmigona costata 0.2
Leptodea fragilis 2.3
Ligumia recta 0.3
Obliquaria reflexa 1.3
Obovaria olivaria 0.9
Pleurobema coccineum 1.7
Potamilus alatus 0.9
Pyganodon grandis 0.04
Quadrula fragosa 0.9
Quadrula metanevra 3.1
Quadrula pustulosa 4.8
Quadrula quadrula 0.1
Strophitus undulatus 0.1
Toxolasma parvus 0.5
Tritogonia verrucosa 1.6
Truncilla donaciformis 7.5
Truncilla truncata 54.0
Unknown Juvenile 0.3
unidentified 0.4
0
10
20
30
40
50
60
Community Composition (%)

FIG. 4

delete if N=26 vs N=~500

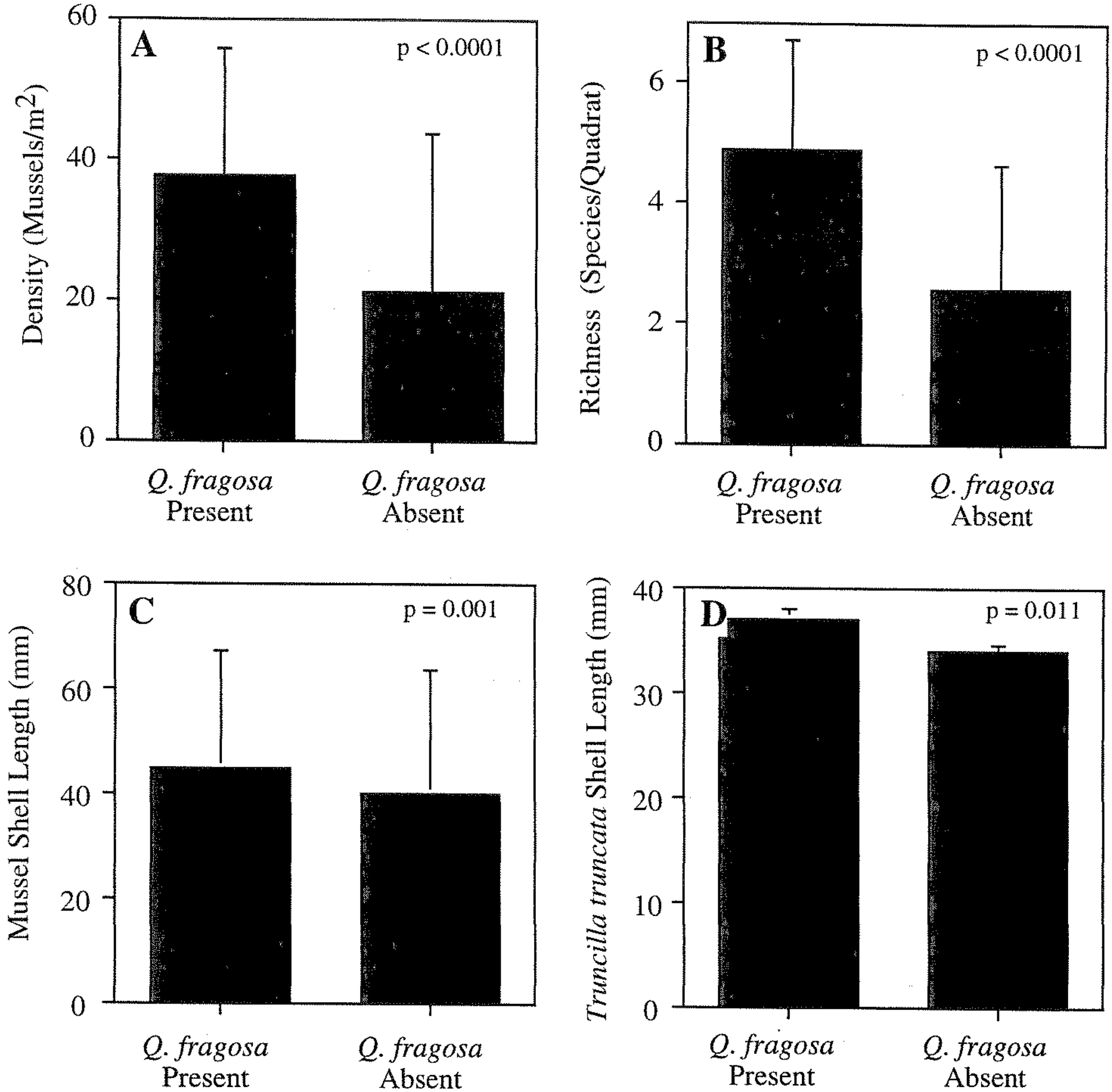
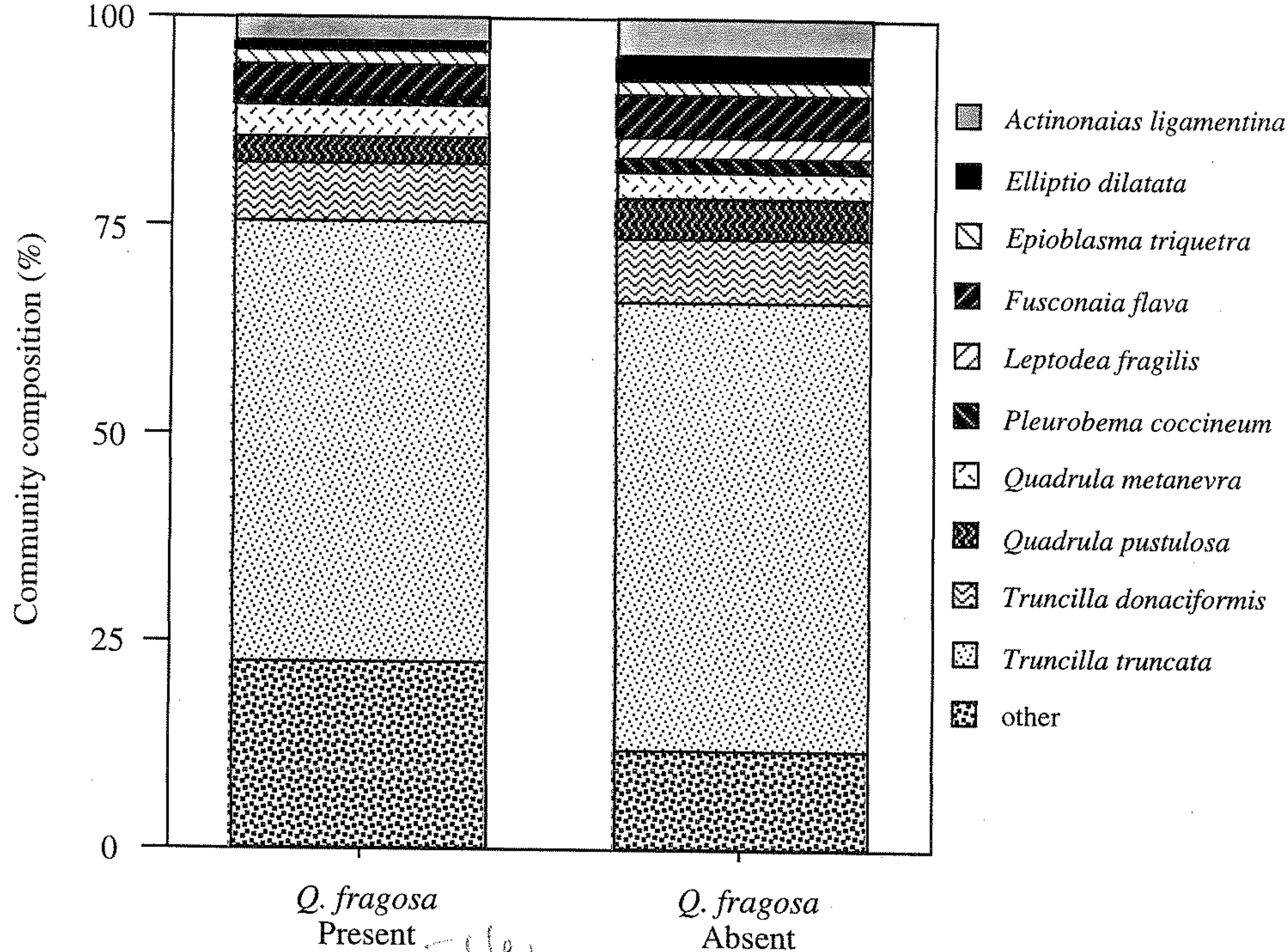


FIG. 5



questionable value

delete

Comment Page
Hornbach et al. Manuscript

Title

Add 'in the St. Croix River, Wisconsin' because this is a specific site analysis of 1 population.

Introduction

This is much too long for this article (4 of 17 pages). The authors need to eliminate generic statements and reduce speculations on physical factors that affect mussel occurrences. Stick with those variables addressed in their work.

Materials and Methods

There are several questions that need to be answered in this section. What was the rationale for sampling in a 5x2 m grid? Statistically, this does not allow independence of samples which would affect analyses. Even non-parametric statistics abide by the assumption of independence of samples. Were the 10 quadrats/site randomized within the grid, and were resamples taken in the quadrants not sampled initially? There needs to be further description of the sampling design.

What is the rationale for calculating sediment diversity and what real value could it have?

Why were length, width and height measurements taken if only lengths were analyzed?

Describe how Q. fragosa was searched for specifically? Did divers pick up all mussels until they found one?

The statistical testing paragraph makes no mention of what was being tested or any hypotheses being tested in the study. What was planned for analysis?

Results

Both sites were downstream of a hydroelectric dam that manipulates discharge. In my opinion, analyses of preferred water velocities and depths of Q. fragosa are not relevant because conditions vary among days and within days. In effect, all mussels are exposed to anthropogenic whim. A snap-shot of measurements (N=26) within 4 different years only constitutes what the species was exposed to at those particular times (p. 10). There probably were some days where no Q. fragosa were collected, but habitat data was collected for the quadrats taken. Inferences on habitat preference for lower water velocity and lower depths may be artifacts of sample size and time of samples.

The authors do not address sample size in their analyses.. Ostensibly, because 26 specimens of Q. fragosa were found, N=26 for habitat measurements. Conversely, nearly 500 quadrat samples, without the winged mapleleaf, contained habitat data. Did the authors assume that the accuracy and precision of N=26 was equal to N= ~500? It is very likely that these data sets are not of equal accuracy and therefore can lead to spurious results. Statistical tests with unequal N are valid, but such a discrepancy in N is questionable. Conclusions about water depths and velocities have very low credibility.

The section on community composition can be dramatically reduced in length. In essence Q. fragosa occurred where the greatest richness and abundance of unionids occurred; i.e., the best habitat (whatever that is) for unionids. This is the case for most endangered mussels in rivers. Again N=26 in these analyses, and this species tended to co-occur with the more abundant unionids at these sites. There are no data presented which can be presumed to indicate 'preferred habitat' (p. 12) for this species. Preference cannot be assumed from purely descriptive presence/absence data.

Discussion

Five pages of discussion are too long for the amount of new and definitive data presented in this MS. The conclusion that "this rare species is found only in areas of high mussel species richness" is about all that can be concluded from what is presented in results. All else is speculative and filler in the Discussion. Statements about "preferred" depths, water velocities, etc. are unacceptable. As stated on p. 14, the authors "chose to sample only in areas of known high mussel abundance". Is the conclusion stated above of any surprise then? The last statement of the Discussion could have been concluded without any of the data collected. Therefore, what new information does this study provide resource agencies responsible for the conservation of this species? The Introduction claims that "data presented here will enable decisions about management plans targeted toward protecting this endangered species". Where are the management applications to this species?