Factors influencing the distribution of unionid mussels in the St. Croix River at Franconia, MN.

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Abstract

The factors influencing the distribution of mussels in the St. Croix River at Franconia, MN were examined. This stretch of the river contained a diverse assemblage of mussels, with 33 species found in the two years of this study. The dominant members of the community were *Truncilla truncata* and *Quadrula metanevra*. In addition, the federally endangered species, *Lampsilis higginsi* and *Quadrula fragosa* were found at this site. The density of mussels at the Franconia site was relatively high (mean density over all sampling sites was approximately 12/m^2). The sizes and density of mussels varied both along the length of the river and in relationship to the shore. Mussels size and density were found to be significantly correlated to sediment size, with larger and more numerous mussels found in coarser substrates. Generally mussel density and size was greater at inshore sites when compared to sites in the center of the river. The mussel density was lower in 1991 than in 1990 at comparable sites. The reason for this difference is not known but evidently was not related to sampling methodology. We also found that the total suspended solids varied over the bed. It appeared that resuspension of sediments over varying substrate type, rather than mussel filter-feeding, accounted for this variability. Mussels did, however, feed at relatively high rates (over 500 ml/hr for mean-sized *Quadrula metanevra*), and while they may not have significantly altered the total nutrient availability, it is possible that they influenced certain particle sizes. Despite the fact that the mussels may not have had a great influence on nutrient availability, the size and concentration of food particles significantly influenced mussel feeding rates. It was also apparent that, at least for the two species of mussels that we examined (*Truncilla truncata* and *Quadrula metanevra*), the functional feeding responses differed between mussels species. It is possible that these differences, in part, allowed for a multitude of species to co-exist in one area of a river and thus may help to explain why there are so many species of mussels found in the St. Croix. Clearly, substrate type, food availability (i.e. suspended solids), and water velocity all influenced the mussel assemblages in the river. There is a great interaction among these factors and it is not clear which of these are dominant in controlling mussel community structure.

INTRODUCTION

Freshwater mussels (Family Unionidae) are widely distributed throughout the United States. There are 44 species of freshwater mussels currently on the federally endangered species list (Fish and Wildlife Service, 1991). Despite this fact, there is little known concerning the factors which control the distribution of these organisms, especially in flowing water systems. Certainly, factors such as surface geology, stream size, water quality, substrate type, water flow, and food availability among others are important in determining the community structure and population dynamics of freshwater mussels (Strayer, 1983).

The recent introduction of the zebra mussel (*Dreissena polymorpha*) from Europe is likely to affect populations of native mussels. While currently not found in the St. Croix River, the presence of zebra mussels in the Illinois and Mississippi RIvers indicates that the potential exists for the introduction of this species into the present study area. There is the potential for both direct and indirect influence of *Dreissena* on the biodiversity of unionids. Direct effects include the attachment of *Dreissena* to unionids. Wiktor (1963) reported that in a lagoon in Poland *Dreissena* overgrows the unionids, *Unio* and *Anodonta* resulting in "suffocation" of the unionids. Hebert et al. (1989) indicated that *Dreissena* in Lake St. Clair were most often found in locations with a gravel substrate but could be found in sand and silt if they were attached to a hard substrate (e.g. a mussel shell). In gravel substrate, about two-thirds of the zebra mussels were attached to the gravel, the rest being attached to unionid mussels. From areas where *Dreissena* was abundant, up to 90% of the unionid mussels had attached *Dreissena*. Unionid mussels carried 0-38 *Dreissena*$\cdot$mussel^{-1}, with some sites averaging > 17$\cdot$mussel^{-1}. There was a positive correlation between unionid mussel shell length and number of *Dreissena* attached. Live mussels, rather than dead shells, were preferentially colonized. Most attached *Dreissena* were found attached to the posterior end of the unionid mussels near the siphons. Lewandowski (1976) reported in one lake in Poland that 85% of unionids had *Dreissena* attached. In 35% of the cases the zebra mussel biomass was greater from that of the underlying unionids. Laboratory experiments carried out by Lewandowski (1976) showed zebra mussels preferred live unionids to dead unionids or rocks as a substrate for settling. Unionids grown with zebra mussels on them did not differ in terms of tissue weight or length than those grown without *Dreissena*, although shell weight was slightly greater and small *Anodonta* grew in length slightly slower than controls. *Anodonta* (but not *Unio*) with zebra mussels attached showed deformations of the shell near the siphons. In one study in a river in Britain, Bishop and DeGaris (1976) indicated there was no correlation between the density of *Dreissena* and unionids. Presentations given by D.W. Schloesser, R.D. Hunter and R. Dermott given at the International Zebra Mussel Conference Dec. 5-7, 1990 at Ohio State supported idea that zebra mussels will have impact on the native molluscan community. Mackie (1991) has indicated that in Lake St. Clair, zebra mussels colonize all species of unionids. He also showed that there was an exponential increase in the number of zebra mussels on unionid shells in relation to the length and surface area of the host unionid and that often the weight of attached zebra mussels exceeds that of the host unionid.

Not only are unionids important because of their diversity in flowing water systems, but based on the river continuum concept (Vannote et al. 1980) large filter-feeders (such as mussels) are extremely significant components of larger river systems. They are one of the few organisms that can process the fine particulate organic matter which makes up a significant portion of the energy basis for these reaches of river systems. Without filter-feeders such as mussels, the nutrients (small particles) would be swept downstream. However, with the mussels removing these particles from the water column, the residence time for nutrients in the stream increases. This allows for a more efficient use of the energy in these nutrients, since they become available to predators of the mussels (e.g. muskrats). Also, as the mussels die, they contribute biomass to the detritivores (decomposing organisms). It has also been suggested that the feces produced by mussels and deposited in the sediment helps to condition the sediment. The sediment then may be more readily inhabited by other benthic (bottom-dwelling) organisms that are also important in the aquatic food-chain as sources of energy for fish. No studies have been conducted to date which attempt to adequately quantify the role that mussels play in the nutrient processing in larger river systems, although a study by Cohen et al. (1984) has shown that the introduced asian clam *Corbicula* can influence phytoplankton concentrations in a river system. A significant amount of research has taken place in marine systems that have examined the role of mussels in removing nutrients in tidally influenced regions (similar to river systems). These studies indicate that mussels can have a tremendous impact on nutrient availability (Wildish and Kristmanson 1984, Fréchette et al. 1989) . There is evidence that mussels "upstream" of others may influence the nutrient available to those downstream. Despite the fact that little is known about the role of unionids in flowing water systems there is evidence that they are important in nutrient cycling in lake systems (Lewandowski and Stanczykowska, 1975; Kasprzak, 1986; Nalepa et al., 1991).

This study was conducted in the St. Croix River. There have been past studies on the unionids in the St. Croix River. Baker (1928) cited 15 species from the St. Croix River although he classified some additional species as statewide. Dawley (1947) reported 29 species of unionids from the St. Croix River (in addition to 4 species found in tributaries to the St. Croix but not in the river proper). Fuller (1978) recorded 23 species of unionids from the St. Croix River at Hudson, WI. Stern (1983) reported 14 species of unionids from a single site on the St. Croix. Doolittle (1988) has conducted the most extensive study to date on the distribution of unionids in the St. Croix River. Thirty-seven species of unionids (including 2 only represented by dead shells) were reported by Doolittle in the river proper.

In this study we attempted to examine some of the factors which may influence the distribution of unionids in flowing water systems (especially substrate type and food availability). In addition we conducted filter-feeding studies to ascertain whether mussels potentially compete for food and if they are likely to have a significant influence on the processing of nutrient in flowing water systems.

Material and Methods

Study Site

The study site was located on the St. Croix River at Franconia, MN (Fig. 1). We found a well developed bed of mussels that extends from the boat ramp, south to a point just below the opening to Close slough. This site is approximately 4 mi. downstream of an NSP hydroelectric dam. This is a peaking dam and thus greatly influences the daily flow regime at the sampling site. Figure 2 gives an example of the daily changes in flow that occur just below the hydroelectric dam (data from USGS gage 5-3405 at St. Croix Falls, WI.)

Mapping

The river bottom was mapped using a Lowrance Model X-19 recording sonar unit interfaced with a Maricom UMI-3X to a Magellan Model NAV1000 PLUS GPS unit. This allowed for determination of depth and latitude and longitude at a number of sites in this stretch of the river. In addition, the gray-scale value given by the sonar unit gives and indication of the substrate type - higher values indicate firmer substrate while lower values indicate softer substrate. Contour maps were derived from the data using the mapping program Surfer-Version 4 (Golden Software, Inc) on a Zeos 286 microcomputer.

Mussel sampling

Mussels were collected by divers using SCUBA equipment. In 1990, four sampling sites were established for quantitative sampling (outshore sites A, C, D, E - Fig. 1). At each of these sites a 2x5 m PVC grid was placed on the bottom of the river. Using this frame as a guide, 10 0.25 m^2 quadrat samples were taken. All of the substrate within the 0.25 m^2 quadrat was removed and placed in a bucket. The contents were then sieved and any mussels > 0.5 mm were collected. Mussels were identified and their shell length (anterior-posterior dimension) was measured to the nearest 0.05 mm with a dial caliper. In addition, during 1990 four qualitative transects were established at right angles to the flow of the river (Fig. 1). At 5 m intervals along the transects, two divers spent 2 minutes visually searching for mussels. Mussels were collected, identified and their shell length was measured. Mussels were then returned to the stream.

After the sampling of 1990 it was apparent that there was a difference in the mussel community structure near the shore as compared to mid-stream. Consequently the number of quantitative samples was increased in 1991 to examine this difference. Five sampling sites were established in mid-stream and five near the shore. Again at each of these sampling sites, 10 0.25 m^2 quadrat samples were again taken as in 1990.

Substrate sampling

In 1990, substrate was sampled by taking a 7.62 cm diameter core next to each quantitative quadrat sample. The substrate was returned to the lab and dry sieved through a stack of 9 sieves (sieve mesh sizes - ASTM 6, 10, 18, 30, 40, 60, 100, 140 and 200). Based on the dry weights of the fractions the average particle size was determined (Lewis, 1984).

It was apparent that the size of the substrate sampler used in 1990 was too small to accommodate some of the larger cobbles found on the bottom of the river. Also it was evident that there was a great deal of local variability in substrate and thus taking a core next to each quantitative quadrat was inappropriate. Consequently in 1991 the substrate sampling was modified to account for these problems. When the quadrat samples were taken to ascertain the population density of mussels, the buckets containing the mussels and substrate were sieved and the wet weight of the substrate retained in each of four sieves (57, 12.7, 6.35 and 0.5 mm openings) was obtained. From the weights of the fractions the average particle size was determined (Lewis, 1984).

Water sampling

To determine the availability of nutrients to mussels, water samples were taken from the river. In 1990, samples were taken by divers near the bottom of the river and also near the surface. Samples simply taken with bottles. In 1991, the sampling technique was modified to take samples at the sediment water interface and at 0.5 m above the bottom. PVC standpipes (2.54 cm in diameter) were attached to a cement block so that the openings of the pipes could be oriented upstream. One pipe allowed samples to be taken at the sediment-water interface, while the other allowed sampling of the water column 0.5 m above the bottom. These pipes were connected by garden hoses to diaphragm pumps which permitted samples of water to be pumped to the surface. To adjust for day-to-day variation in the amount of suspended solids in the water column, all samples were taken within 1 hour at either the four (1990) or eight

(1991) sites where quantitative mussels samples were taken.

The amount of suspended solids in the water samples that were taken in 1990 and 1991 was determined by APHA (1980) methods using Whatman AH934 glass fiber filters. Both the total suspended solids as dry weight and the organic fraction of the total suspended solids (assessed by loss on ignition) was determined.

In 1991, the water samples were also subjected to an analysis which allowed for the determination of the number and size of particles suspended in the water column. This analysis involved taking a 15 ml subsample of the water, and placing the sample in a settling chamber (2.54 diameter tube) for 24 h. The chamber was them placed on an inverted microscope (Olympus Model CK2) connected to a Sony XC57 CCD video camera. The camera was interfaced with a Data Translation's QuickCapture DT2250 frame grabber card to a Macintosh II fx computer. The software package Image 1.37 (from Wayne Rasband, NIH) was used to count and measure the algae and detritus that had settled from the water column. Triplicate 15-ml subsamples were taken from each water sample collected from the river and triplicate sub-samples were counted from each settling chamber. The water taken from the sediment-water interface contained a significant amount of sand (see Results). However, since this sand fraction settled quickly after shaking the samples, the water analyzed for particle number and particle size distribution did not contain significant amounts of sand.

Filtration Rate Experiments

In 1990, experiments were conducted to examine the filtration rates of the two major species of mussels found at the Franconia site, *Truncilla truncata* and *Quadrula metanevra.* To conduct these experiments, mussels of various sizes (usually 6-8 individuals per experiment) were placed in solutions of plastic beads and maintained at 18 C. Six sizes of plastic beads were used (0.5, 1.1, 2.02, 5.6, 10.1 and 21.1 μm) with concentrations ranging from 10 to 60 mg/L. Thus for each species filtration rates for approximately 150 mussels were determined (6-8 mussels x 6 bead sizes x 4 concentrations). To measure the filtration rate, a fiber-optic spectrophotometer was used (Brinkman Model PC800).

As plastic beads were removed from the water column the water becomes more transparent to light. The rate of change in transparency is related to the filtration rate [see Hornbach et al., (1991) for a complete description of the method]. The filtration rates were determined by measuring the absorbance of the water at every 15 min. over a 2 h period. The tissue of specimens of both species was dried to constant weight at 100 C then ashed at 500 C to determine the ash-free dry weight of the mussels (AFDW). From this analysis it was found that $AFDW=0.011SL^{1.273}$ (SL=shell length; $r^2=0.97$, n=24) for *T. truncata* and $AFDW=0.003SL^{1.660}$ ($r^2=0.71$, n=20) for *Q. metanevra*. These equations were used to predict the tissue ash-free dry weight for mussels utilized in the feeding studies.

Statistical analyses

All statistical analyses were conducted with JMP Version 2.0 (SAS Institute, 1989) using a Macintosh II ci microcomputer. Levels of statistical significance were assigned at the 0.05 level.

RESULTS AND DISCUSSION

Mapping of the Site

Figure 3 shows the depth map of the sampling area in the St. Croix River based on sonar soundings. The river is generally less than 3 m deep throughout this reach. Between sites A and B (Fig. 1) there is a wing dam from the west shore. The placement of this dam is probably responsible for the increased depth of the river between sites B and E. Figure 4 shows the grayscale values recorded from the sonar mapping of the river. Large grayscale values are indicative of coarse or hard substrate whereas small values indicate fine or soft substrates. Again it is apparent that the coarsest substrate is found below the wing dam and in the central portion of the river below site B.

Community and Population Structure

Based on the examination of over 627 mussels in 1990, we found 27 species of mussels, including 3 specimens of the endangered species, *Lampsilis higginsi* (Fig. 5). In 1991, 261 mussels were collected, representing 29 species (Fig. 5). Included in the 1991 were 2 specimens of the recently listed species *Quadrula fragosa*. Two species, *Truncilla truncata* and *Quadrula metanevra* dominated the community and from the two years a total of 33 species were found. These results compare to at least 15 species by Baker (1928), 29 species by Dawley (1947), 23 by Fuller (1987), 14 species by Stern (1983) and 37 by Doolittle (1988). The large number of species found in the relatively small sampling area of this study is somewhat surprising since most of the other studies cited (except for that by Stern and Fuller) included a number of sites in the St. Croix. In fact, Doolittle (1988) found 31 species of mussels at Taylor's Falls, MN, which is approximately 4 miles upstream from the Franconia site. Doolittle (1988) found that *Actinonaias ligamentina*, *Fusconia flava*, *Elliptio dilatata*, *Amblema plicata* and *Lampsilis radiata* were the most common and abundant species found in the river as a whole. Also, these species were often found associated with one another. He also noted, however, that less common species, such as *Truncilla truncata*, *Quadrula metanevra* and *Tritigonia verrucosa* are also found associated with one another. This association of apparently less common species was that which dominated the Franconia site.

From qualitative samples taken in 1990, it was noted that the mussels community composition changed both along the length of the bed (Fig. 6 - X^2=38.9, 15 df, p=0.0007) and perpendicular to flow (Fig. 7 - X^2=181.8, 117 df, p=0.0001). It became obvious that the community richness decreased from the area near the shore towards the center of the river (Fig. 7 - r^2=0.40, F=7.95, 1,13df, p=0.02). This led us to change our quantitative sampling regime in 1991 to include both inshore and outshore areas (Fig. 1). Figure 8 indicates that based on our quantitative samples, the species composition in the river varied both along the length of the river and in relationship to the shore. In both 1990 and 1991 the quantitative samples taken indicated that there were changes in the density of mussels at various sites throughout the river (Fig. 9). An analysis of variance indicated that both site and relationship to the shore and their interaction significantly influence density (F=26.1, df=4,99, F=6.2, df=1,99 and F=6.0, df=4,99 for site, relationship to the shore and their interaction, respectively). Again it was apparent that there was a greater number of species near the shore as compared to the center of the river and there were significantly more mussels per square meter at inshore sites.

Overall the mussel density at all sites averaged 12.31 mussels/m^2 (std. dev.= 11.6). An analysis was conducted to test whether there was a difference in mussel density between 1990 and 1991. The average density at outshore sites (A, C, D, E) in 1990 was 17 mussels/m^2 (std. dev. = 10.84) while at outshore sites in 1991 (A-E) the density was 10.56 mussels/m^2 (std. dev. = 10.92). A t-test indicated these means were significantly different (t=3.66, 88 df). Even if site B was eliminated from the data set from 1991 the mean density was different. Since the standard deviations were not different, it appears that there was little difference in the sampling error from year-to-year. The underlying reason for the difference in density between years is unknown. Water levels were quite low in 1990 as compared to 1991 and it is possible that the higher flows in 1991 destabilized the substrate and dislodged the mussels. However, this possibility may be remote since the water levels in 1991 were not unusually high.

From the quantitative samples, we measured the shell lengths of the mussels collected. Figure 10 shows that there were changes in the sizes of mussels collected at various sites in the river. An analysis of variance indicted that the relationship to shore significantly affected mussel size, while neither site nor the interaction of site and relationship to the shore significantly influenced mussel size (F=0.9, df=4,260, F=22.9, df=1,260 and F=1.3, df=4,260 for site, relationship to the shore and their interaction, respectively). Larger mussels tended to be found in sites B-E when compared to site A although this relationship was not statistically significant. Mussels were significantly larger at inshore sites compared to outshore sites (Fig. 10).

Substrate Analysis

We believed that much of the variability in mussel density and size was due to differences in substrate type. Though different methods of substrate analysis was utilized in 1990 and 1991 (see materials and methods), it was apparent that the substrate was significantly more course at stations downstream from site A (Fig. 11). One reason for this difference is the presence of a wing-dam between site A and the downstream sites. This wing-dam serves to increase the velocity of the water, thus reducing sedimentation of small particles. Also, the inshore sites generally had courser substrate than outshore sites. This difference is likely due to the scouring effects of the water at the inshore sites. Daily changes in water level (e.g. Fig. 2), due to varying releases of water from the hydroelectric power plant at St. Croix Falls, are probably responsible for the scouring effects.

Figure 12A shows the relationship between the mussels density and the average sediment particle size from each of the samples taken in 1991. It is evident that mussel density was greatest in areas of course substrate (r^2 for relationship = 0.45, F=79.1, 1,99 df, $p<0.0001$) . A similar relationship between sediment size and mussel density was noted by Stern (1983) for sites in the St. Croix and Wisconsin rivers. Doolittle (1988) also found that the greatest percentage of mussels in the St. Croix River were found in sand/gravel and sand/rock or gravel/rock substrates. Other studies have suggested similar trends for thick shelled species of unionids. Thin shelled species are often found in greater density in fine substrates (e.g. silt) [Ortmann's (1920) "Law of Stream Distribution" - see discussion in Mackie and Topping (1988)]. Sediment size was also significantly related to the size of the mussels collected. Figure 12B shows that larger mussels tended to be found in regions where the sediment is more course (r^2=0.31, F=44.83, 1,99 df, $p<0.0001$). One hypothesis for the significant relationship between sediment size, mussel size and density states that course substrates are indicative of stable habitats. These stable habitats are thus inhabited by greater numbers of mussels. These mussels are also able to grow to larger sizes or live longer in the more stable habitats.

Water Analysis

In addition to position in the river and sediment size, the other major factor that we examined that may influence the mussel distribution in the St. Croix River was food availability. Also based on the River Continuum concept, it was hypothesized that the mussels may have a significant influence on the level of suspended solids in the water column. In 1990, water samples were taken above the sediment water interface and at the surface of the river to examine whether there were changes in food availability among various sites in the river. The first sampling for suspended solids occurred on July 31, 1990. An analysis of variance indicated neither site nor position in the water column (top or bottom) nor their interaction significantly influenced the amount of total suspended solids as dry weight ($F=1.51$, $df=3,40$, $F=2.30$, $df=1,40$ and $F=2.09$, $df=3, 40$ for site, position in the water column and their interaction, respectively). Figure 13A shows that the amount of suspended materials (as dry weight) along the bottom of the riverbed appeared lowest at site A where there are few small mussels and greatest at site D where there were more and larger mussels (Fig. 9 - 1990). This was in keeping with the hypothesis that the mussels may have an effect on the nutrient availability in the river. Figure 13A also shows that there was little difference in the amount of suspended solids at the surface of the river along the length of the bed, again supporting the hypothesis that the mussels may influence nutrient availability, especially at the bottom of the water column where they are found. Unfortunately, as mentioned above, none of these relationships were statistically significant.

Figure 13A also shows that the difference between the surface concentration of suspended materials and the bottom concentration was not very great, and, in fact, the concentration of suspended solids at site A was actually greater at the bottom when compared to the top. This may tend to indicate that factors other than the mussels are significantly influencing the suspended solids concentrations in the water column. For example, at site A, the substrate is mainly sand (Figure 11 - 1990) and thus the high amount of suspended material at the bottom of the water column may be due to resuspension of sediments. At the other sites (particularly site D), the average sediment particle size is greater (Figure 11- 1990) and thus resuspension of sediments may be much lower. Again, the analysis of variance showed that these trends were not statistically significant.

Figure 13B, shows the amount of suspended materials in the water as ash-free dry weight, a measure of the organic content of this material. Again, an analysis of variance showed that neither site, nor position in the water column, nor their interaction significantly influenced the amount of total suspended solids as ash-free dry weight ($F=0.74$, $df=3,40$, $F=0.12$, $df=1,40$

and F=0.59, df=3,40 for site, position in the water column and their interaction, respectively). The amount of total suspended solids as ash-free dry weight was greatest at site C, where mussel size and density was greatest in 1990. This is opposite of what would be expected if the mussels had an impact on the level of suspended nutrients, and supports the idea that resuspension effects were greatly influencing the amount of suspended solids in the water column. At site A, where sand predominates and the total suspended solids are high, the organic content is low, suggesting that resuspension of inorganic material (sand) contributes greatly to the total amount of suspended material in the water. The increased amount of organic material over the area where mussels are abundant may be due to the growth of algae on the larger rocks found in this area or due to fecal production by the algae. An analysis of variance indicated that site (but not position in the water column or the interaction between site and position in the water) significantly influenced the percent organic matter of the suspended solids (F=3.48, df=3,40, F=0.95, 1,40, F=0.76, df= 3,40 for site, position in the water column and their interaction, respectively), which supports the idea that substrate type may be influencing the overlying water column.

On two additional dates in 1990, water samples were taken to examine whether the pattern noted on July 31, 1990 was repeatable. Figure 14 shows that for the total suspended solids as dry weight in the water column just above the bottom, the trend along the bed remained similar. This was true even though flow rates were higher on these two succeeding dates.

In 1991 the sampling regime for suspended solids was altered. A sampling device was constructed to insure that samples taken near the bottom were not influenced by the divers and that a "reference" sample was always taken 0.5 m above the bottom. This reference allowed for a standardized examination as compared to the sampling in 1990 where the sample from the top of the river could be from 1 to 3 m above the bottom. Figure 15 shows the results of the water sampling. It is apparent that the pattern of change in the total suspended solids was different from that noted in 1990. First, the amount of total suspended solids as dry weight was always greatest on the bottom when compared to the middle of the water column (compare Figs. 13A and 15A). Second, the total suspended solids at site A where not always greater than at other sites (Fig. 13A and 14 vs. 15A). Similar statements could be made comparing the total suspended solids as ash-free dry weight (Figs. 13B and 15B). What is especially interesting are the differences in the percent organic matter in the suspended solids between the bottom of the river and the middle of the river (FIg. 15C). The low percent organic matter in the bottom samples was mainly due to the large amount of sand found in these samples. This sand transport along the sediment-water interface could be important to mussels for it is from the water at this interface that they are removing their nourishment. Differences noted among sites, especially near the bottom, are probably due to varying amounts of sediment resuspension and transport. The reasons for the differences in the results between 1990 and 1991 are most likely due to differences in sampling technique. However, water level and flow rates were much higher in 1991 when compared to 1990, and this may also account for greater sediment transport rates.

Not only were there differences in the weight of particles suspended in the water column above the mussel bed in 1991, but there were differences in the number of particles and the size distribution of particles above the bed. Figure 16 shows that, in general, the number of particles suspended in the water column was greatest at the sediment water interface (bottom) when compared to the overlaying water at the same site. Table 1 shows the F-values from an analysis of variance with the number of particles as the dependant variable and site, relationship to shore, height in the water column and their interactions as independent variable. The F-values indicated that site, height in the water column, site and its interaction with height in the water column, relationship to the shore and its interaction with site all significantly influenced the number of particle in the water column. These counts of particles do not include sand particles and thus may be more indicative of actual food availability to the mussels.

Figure 17 shows that the particle size distributions also varied with site and depth from which the water samples were taken [LogLikelihood tests indicated that site, relationship to the shore (I/O), height in the water column (B/M) and their interactions had significant influences on the distribution of particle sizes - (Wald χ^2 , df)= 476.6, 36; 51.4, 9; 757.6, 36; 107.7, 9; 1810.9, 36; 309.0, 9; 395.5, 36; for site, I/O, site•I/O, B/M, site•B/M, I/O•B/M and site•I/O•B/M, respectively]. No general patterns of particle size variation could be detected with either water depth or along the length of the river. Each site seemed to differ from the others in a unique way. Further statistical analysis is needed to examine whether there is any relationship between substrate type, mussels density, the number of particles suspended in the water column and the size of the particles suspended.

The complex nature with which the amount, size and type (organic vs. inorganic) varies with site, relation to the shore and depth, has made it difficult to examine whether these factors directly influence the distribution of mussels in the St. Croix River.

Filtration Rates

Analyses of covariance indicated that particle size (an independent variable - PS), particle concentration (a covariable - PC) and mussel size (shell length, another covariable - SL) significantly influenced filtration rates (FR) for *Truncilla truncata* and *Quadrula metanevra*. From these analyses of covariance, regression equations were derived to predict filtration rate from PS, PC and SL. For *Q. metanevra* FR=f(PS, PC, PC•PS, SL) and for *T. truncata* FR=f(PS, PC, PC•PS, SL, SL•PS, PC•SL) with r^2-values for these two relationships of 0.43 and 0.41, respectively. This indicates that there is indeed a great deal of variability in filtration rates in these species. The response curves in Figs. 18 and 19 are based on these regression equations. For both species filtration rates determined for 0.497 μ beads were extremely low indicating that mussels did not efficiently remove particles of this size. For particle sizes > 0.497 μ, filtration rate tended to increase with increasing particle size. Paterson (1984, 1986) reported that for the unionid *Elliptio complanata*, filtration rate increased with increasing particle size from 1.26 to 3.16 μ, then decreased with particle sizes greater than 3.16 μ. For many (but not all) sizes of mussels in our study there tended to be a decrease in filtration rate with increasing particle concentration (Figs. 18 and 19). This is a well known response in filter-feeding bivalves (Jørgensen, 1975; Winter, 1978) and has also been reported for *E. complanata* by Paterson (1984). Also, within a given concentration, smaller mussels often (but not always) had higher weight-specific filtration rates than larger mussels. Again, this is a pattern followed by many filter-feeding organisms. The implications of those cases where trends did not follow those expected are not clear. For example, for *T. truncata* at 1.05 μ and 60 mg/L larger mussels had higher weight-specific filtration rates that smaller mussels. This could be due to a greater extraction efficiency or a real increased pumping rate by larger mussels. These experiments did not allow for the determination of the underlying causes of these anomalies.

It is apparent from the examination of Figures 18 and 19 that the feeding response of the two species of mussels that we examined differed from one another. Figure 20A shows that for most particle sizes, *Quadrula metanevra* had higher weight-specific filtration rates than *Truncilla truncata*. This was somewhat surprising since smaller animals tend to have higher weight-specific physiological rates than larger animals. Since *Q. metanevra* is a larger species than *T. truncata*, the higher weight-specific rates along with the greater weight means *Q. metanevra* had much higher filtration rates. For example a mean-sized (shell length 99.2 mm; AFDW 6.24 g) *Q. metanevra* filtered 51-568 ml/hr while a mean-sized *T. truncata* (43.12 mm shell length, AFDW 1.33 g) only filtered 7.5-92 ml/hr depending on particle size (Fig. 20B). Paterson (1984, 1986) reported rates in the range of 40-300 ml/hr for *Elliptio complanata* of approximately 65 mm whereas Leff et al. (1990) reported filtration rates of less than 30 ml/hr. Kryger and Riisgård (1988) reported filtration rates 2.1-4.6 L/hr for 3 species of *Unio* and 1 species of *Anodonta*. They claim that their rates are at least 4 times higher than other studies since they measured filtration rates in undisturbed mussels (i.e. buried in substrate).

It is possible that the differences in the functional feeding responses of the two species examined in this study reduces competition for food between them. Levinton (1972) claims that based on theoretical considerations it is unlikely that there is competition for food among filter-feeding organisms. However a number of studies in marine systems (e.g. Wildish and Kristmanson 1984, Fréchette et al. 1989) indicate that food may be limiting to bivalves and competition for food may be an important factor controlling bivalve growth. It is not clear from this study, however, if food levels in the river are likely to be limiting. Additional studies are needed to quantify not only the weight of particles suspended in the water column but their food value as well. Also, additional information is needed to ascertain the nutritional requirement of unionid mussels.

Conclusions

In conclusion, we found that the St. Croix River at Franconia, MN houses a diverse and relatively dense bed of mussels. The sizes and density of mussels inhabiting this bed vary, and this variation is probably related to sediment variability. We also found that the total suspended solids vary over the bed, but that resuspension of sediments over varying substrate type rather than mussel filter-feeding most probably account for this variability. Mussels did, however, feed at relatively high rates, and while they may not significantly alter the total nutrient availability, it is possible that they influence certain particle sizes. Despite the fact that the mussels may not have had a great influence on nutrient availability, the size and concentration of food particles did significantly influence mussel feeding rates. It was also apparent that, at least for the two species of mussels that we examined, the functional feeding responses differed between mussels species. It is possible that these differences, in part, allowed for a multitude of species to co-exist in one area of a river, and thus may help to explain why there are so many species of mussels found in the St. Croix. Clearly, substrate type, food availability (i.e. suspended solids), and water velocity all influence the mussel assemblages in the river. There is a great interaction among these factors, and it is not clear which of these are dominant in controlling mussel community structure. Also, this study was not designed to examine the role that fish host distribution potentially has on the distribution and abundance of mussels. It is clear that the presence of fish is required for most species of mussels to complete their life cycle. It is possible that the habits of the host fish may influence where metamorphosing juvenile mussels are deposited in the river and this could affect the distribution of mussels in the river.

Acknowledgements

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Literature Cited

APHA (American Public Health Association). 1980. Standard methods for the examination of water and wastewater. 15th Edition. American Public Health Association: Washington, D.C. 1134 pp.

Baker, F.C. 1928. The fresh water Mollusca of Wisconsin. Part II. Pelecypoda. Bulletin of the Wisconsin Geological and Natural History Survey, No. 70. 495 pp.

Bishop M.J. and H. DeGaris. 1976. A note on population densities of mollusca in the River Great Ouse at Ely, Cambridgeshire. Hydrobiologia 48: 195-197.

Cohen, R.R.H., P.V. Dresler, W.J.P. Phillips and R.L. Cory. 1984. The effect of the asiatic clam *Corbicula fluminea*, on phytoplankton of the Potomac River Maryland. Limnology and Oceanography 29: 170-180.

Dawley, C. 1947. Distribution of aquatic mollusks in Minnesota. American Midland Naturalist 38: 671-697.

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.

Fish and Wildlife Service, 1991. Endangered and threatened wildlife and plants. 50 CFR 17.11 & 17.12. July 15, 1991.

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. Limnology and Oceanography 34: 19-36.

Fuller, S.L.H. 1978. Fresh-water mussels (Mollusca: Bivalvia: Unionidae) of the upper Mississippi River: Observations ar selected sites within the 9-foot channel navigation project on behalf of the United States Army Corps of Engineers. Final Report No. 78-33, Academy of Natural Sciences of Philadelphia, Division of Limnology and Ecology, Philadelphia, PA. 401 pp.

Hebert, P.D.N., B.W. Muncaster and G.L. Mackie. 1989 Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 46: 1587-1591.

Hornbach, D.J., T. Wilcox, L. Powers, J. Layne and T. Davis. 1991. A method for assessing clearance rates in suspension-feeding organisms using a fiber-optic colorimeter. Canadian Journal of Zoology (in press).

Jørgensen, C.B. 1975. Comparative physiology of suspension feeding. Annual Review of Physiology 37: 57-79.

Kasprzak, K. 1986. Role of Unionidae and Sphaeriidae (Mollusca, Bivalvia) in the eutrophic Lake Zbechy and its outflow. Int. Rev. Ges. Hydrobiol. 71: 315-334.

Kryger, J. and U. Riisgård. 1988. Filtration rate capacities in 6 species of European freshwater bivalves. Oecologia 77: 34-38.

Leff, L.G., J.L. Burch and J. V. McArthur. 1990. Spatial distribution, seston removal, and potential competitive interactions of the bivalves *Corbicula fluminea* and *Elliptio complanata*, in a coastal plain stream. Freshwater Biology 24: 409-416.

Levinton, J. 1972. Stability and trophic structure in deposit-feeding and suspension-feeding communities. American Naturalist 106: 472-486.

Lewandowski, K. 1976. Unionidae as a substratum for *Dreissena polymorpha* Pall. Polish. Archiv für Hydrobiologia 23: 409-420.

Lewandowski, K. and A. Stanczykowska. 1975. The occurrence and role of bivalves of the family Unionidae in Miklajskie Lake. Ekologia Polska 23: 317-334.

Lewis, D.W. 1984. Practical sedimentology. Hutchinson Ross Publishing Co., Stroudsburg, PA. 229 pp.

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

Mackie, G.L. 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. Canadian Field-Naturalist 102: 617-626.

Nalepa, T.F., W.S. Gardner and J.M. Malczyk. 1991. Phosphorus cycling by mussels (Unionidae: Bivalvia) in Lake St. Clair. Hydrobiologia 219: 239-250.

Ortmann, A.E. 1920. Correlation of shape and station in freshwater mussels. Proceedings of the American Philosophical Society 59: 269-312.

Paterson, C. 1984. Particle-size selectivity in the freshwater bivalve *Elliptio complanata* (Lightfoot). Veliger 29: 235-237.

Paterson, C. 1986. A technique for determining apparent selective filtration in the fresh-water bivalve *Elliptio complanata* (Lightfoot). Veliger 27: 238-241.

SAS Institute, 1989. JMP User's Guide. Version 2 of JMP. SAS Institute: Cary, NC. 584 pp.

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. 1983. The effects of surface geology and stream size on freshwater mussels (Bivalvia, Unionidae) distribution in southeastern Michigan, U.S.A. Freshwater Biology 13: 253-264.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell and C.E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130-137

Wildish, D.J. and D.D. Kristmanson. 1984. Importance to mussels of the benthic boundary layer. Canadian Journal of Fisheries and Aquatic Sciences 41: 1618-1625.

Wiktor, J. 1963. Research on the ecology of *Dreissena polymorpha* Pall. in the Szczecin Lagoon (Zalew Szczecunski). Ekologia Polska. 11(9): 275-280.

Winter, T.E. 1978. A review on the knowledge of suspension-feeding in Lamellibranchiate bivalves, with special reference to artificial aquaculture systems. Aquaculture 13: 1-33.

Table 1. F-values for analysis of variance with number of particles suspended in the water column as the dependant variable.

Independent variable	F-value	degrees of freedom
Site	14.65	4,175
Relationship to the shore (I/O)	13.98	1,175
Height in the water column where the sample was taken (B/M)	24.51	1,175
Site•I/O	2.71	4,175
Site•B/M	5.08	4,175
I/O•B/M	1.03*	1,175
Site•I/O•B/M	0.11*	4,175

*not significant at the 0.05 level

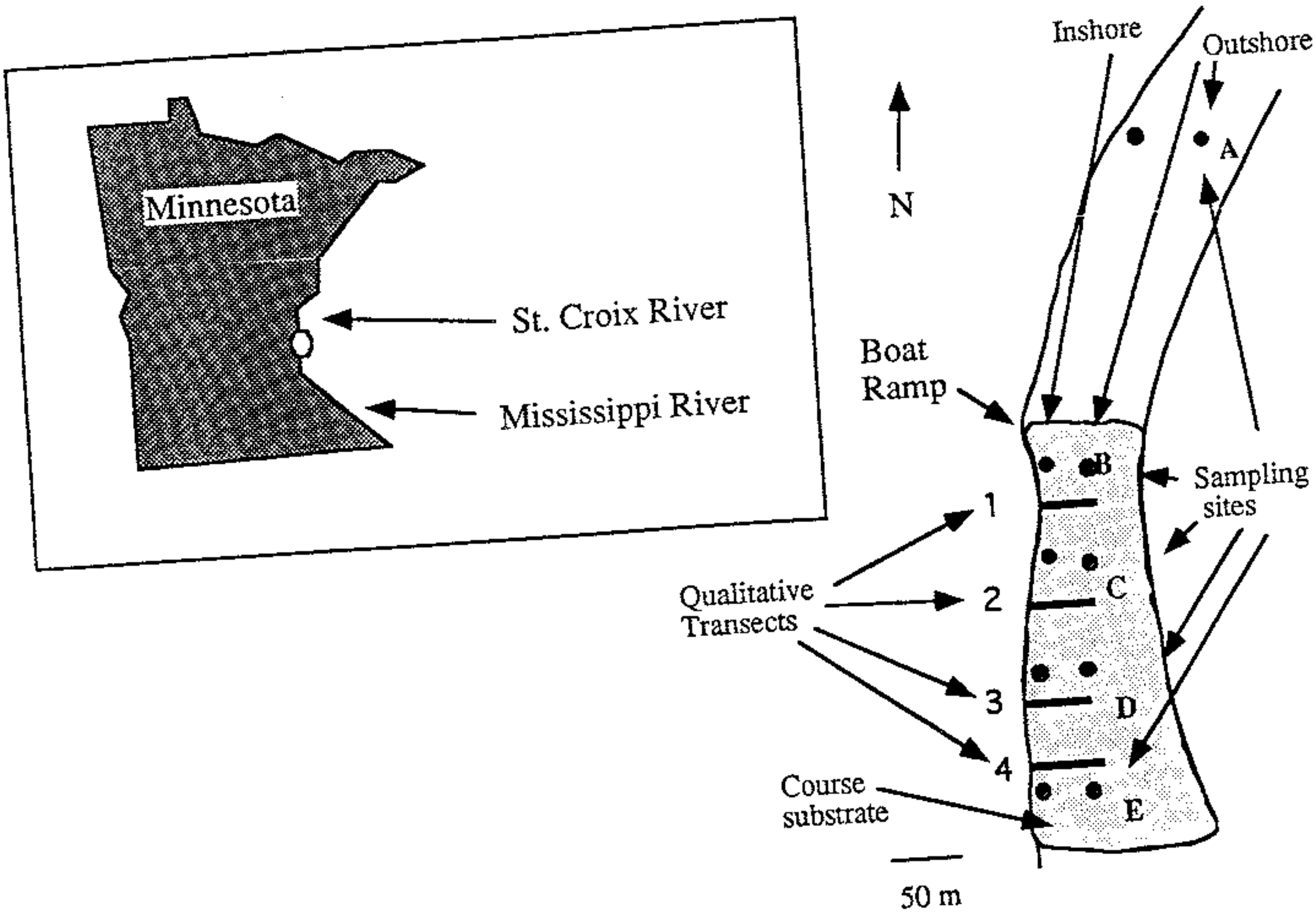


Figure 1. Map of study area.

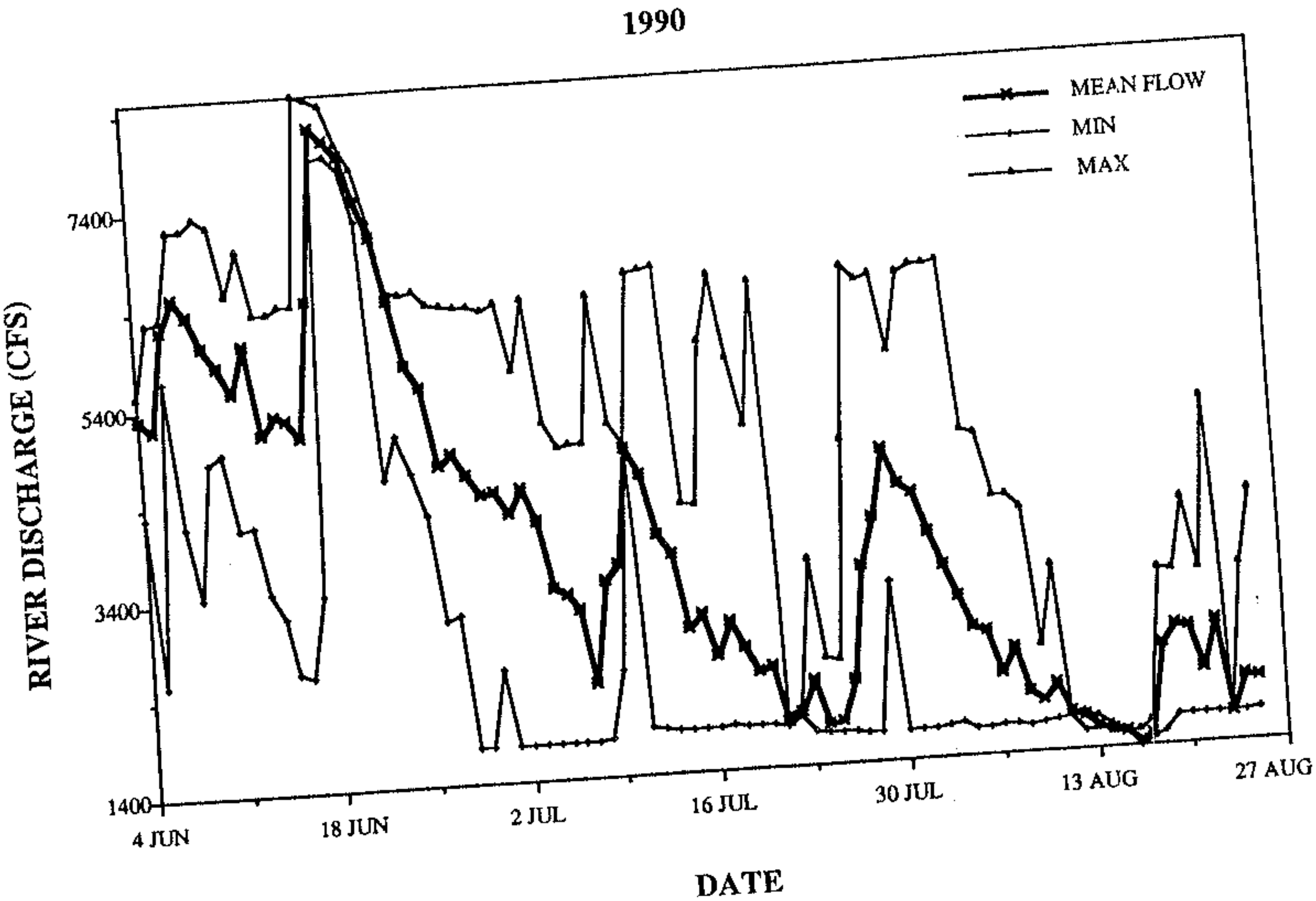


Fig. 2. River discharge at the USGS gaging station at St. Croix Falls, WI.

Fig. 3 DEPTH MAP OF SAMPLING AREA
(DEPTH PROFILES ARE IN METERS)

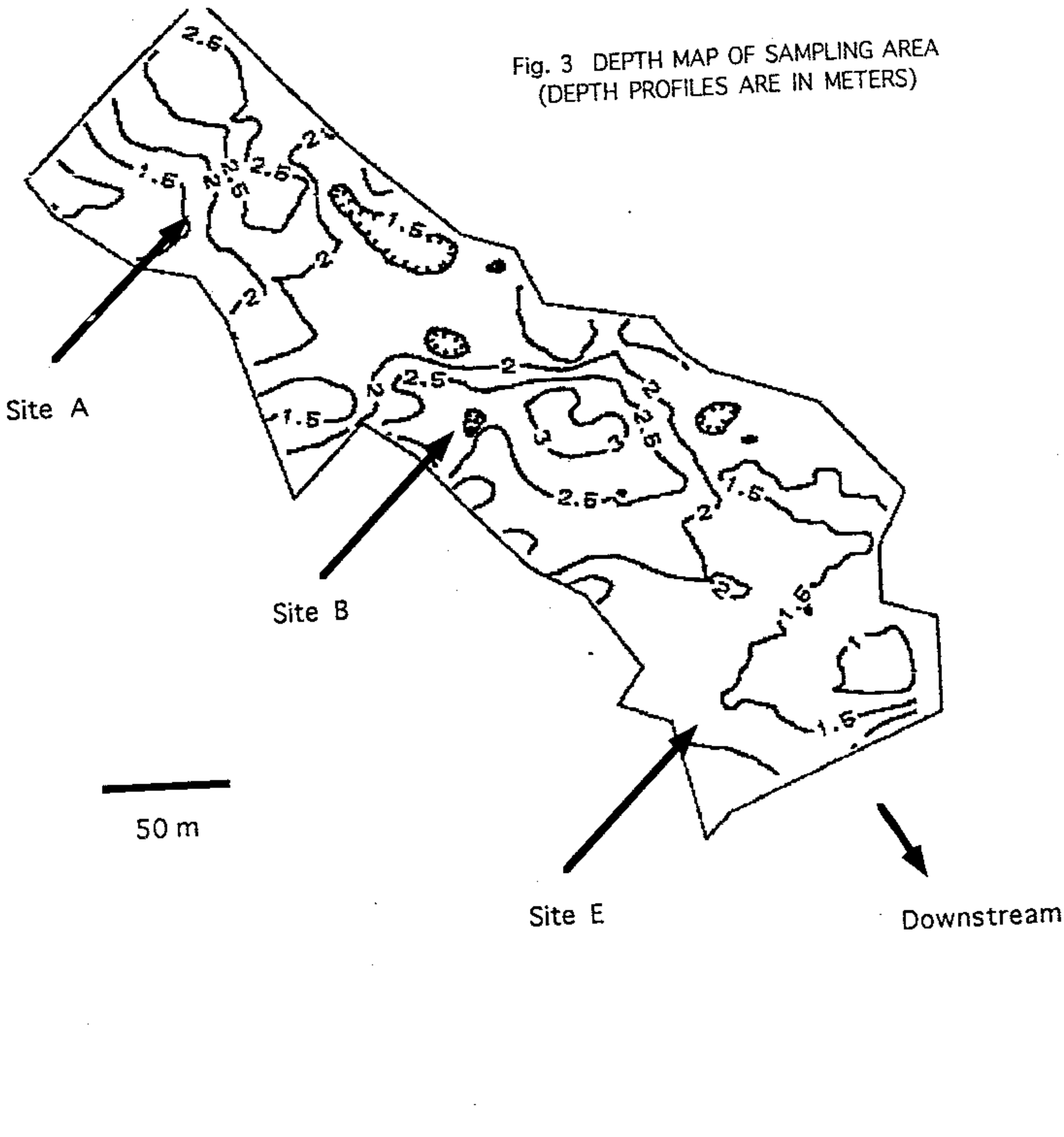
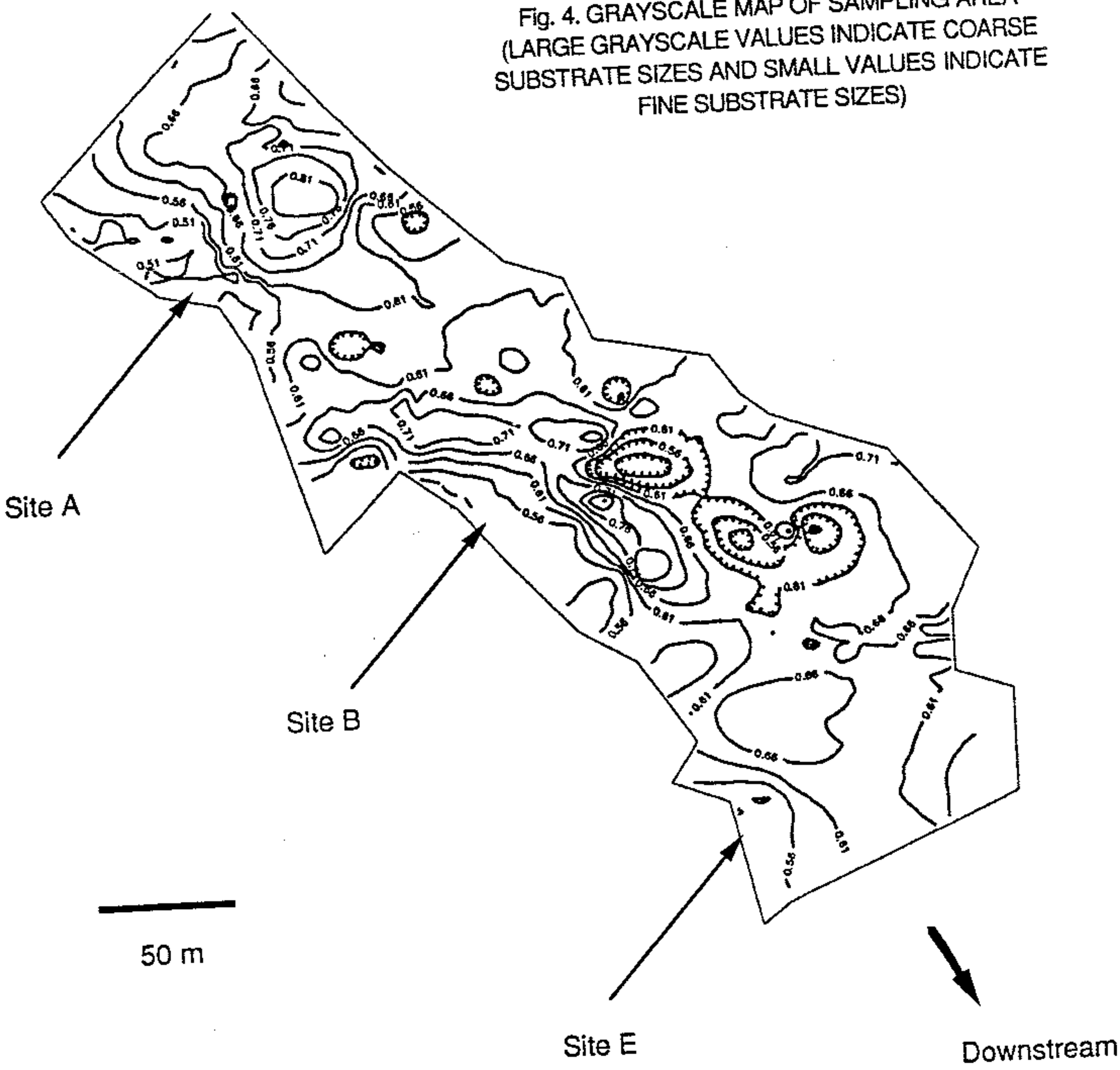


Fig. 4. GRAYSCALE MAP OF SAMPLING AREA (LARGE GRAYSCALE VALUES INDICATE COARSE SUBSTRATE SIZES AND SMALL VALUES INDICATE FINE SUBSTRATE SIZES)



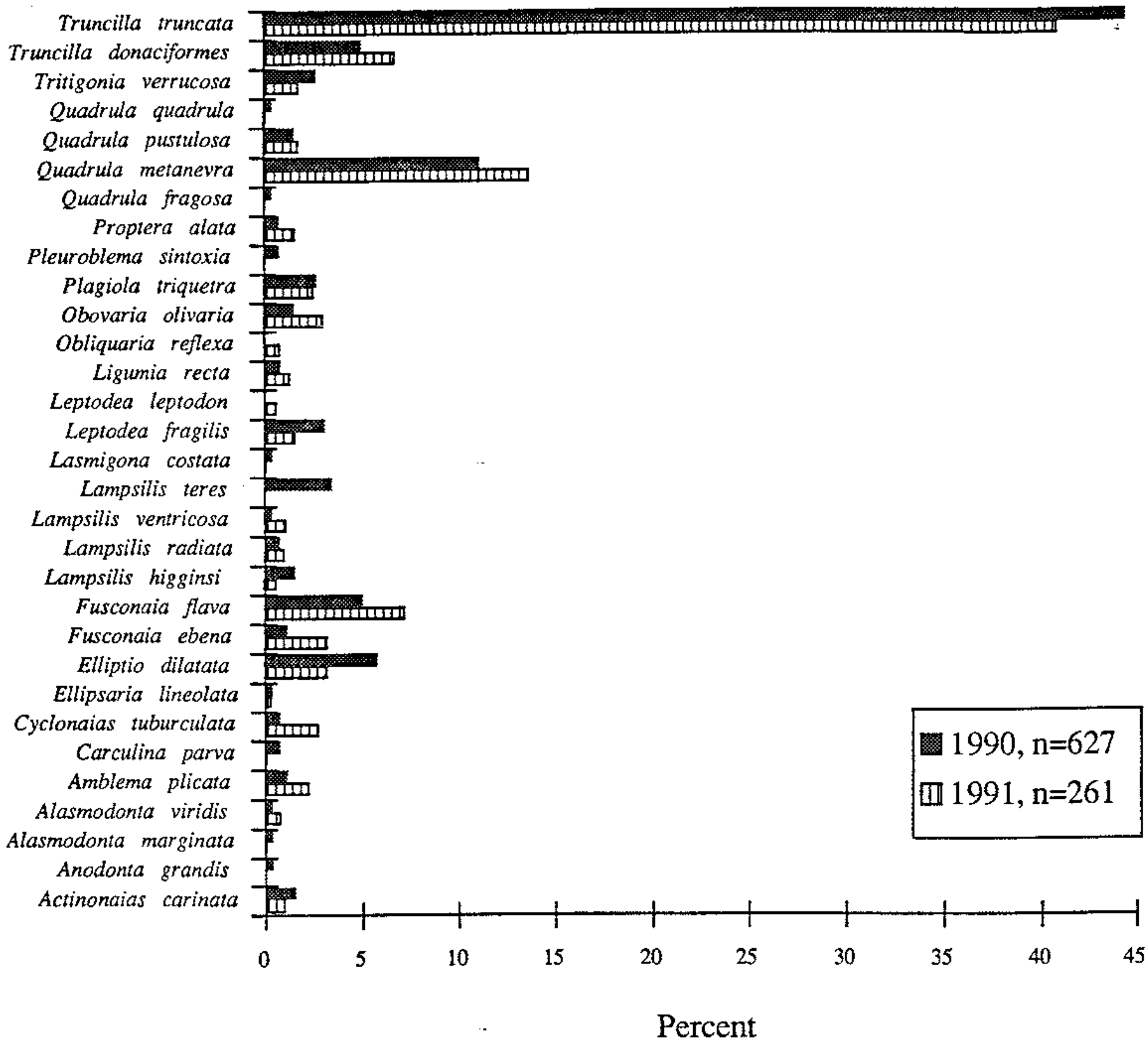


Fig. 5. Mussel community composition at Franconia, MN.

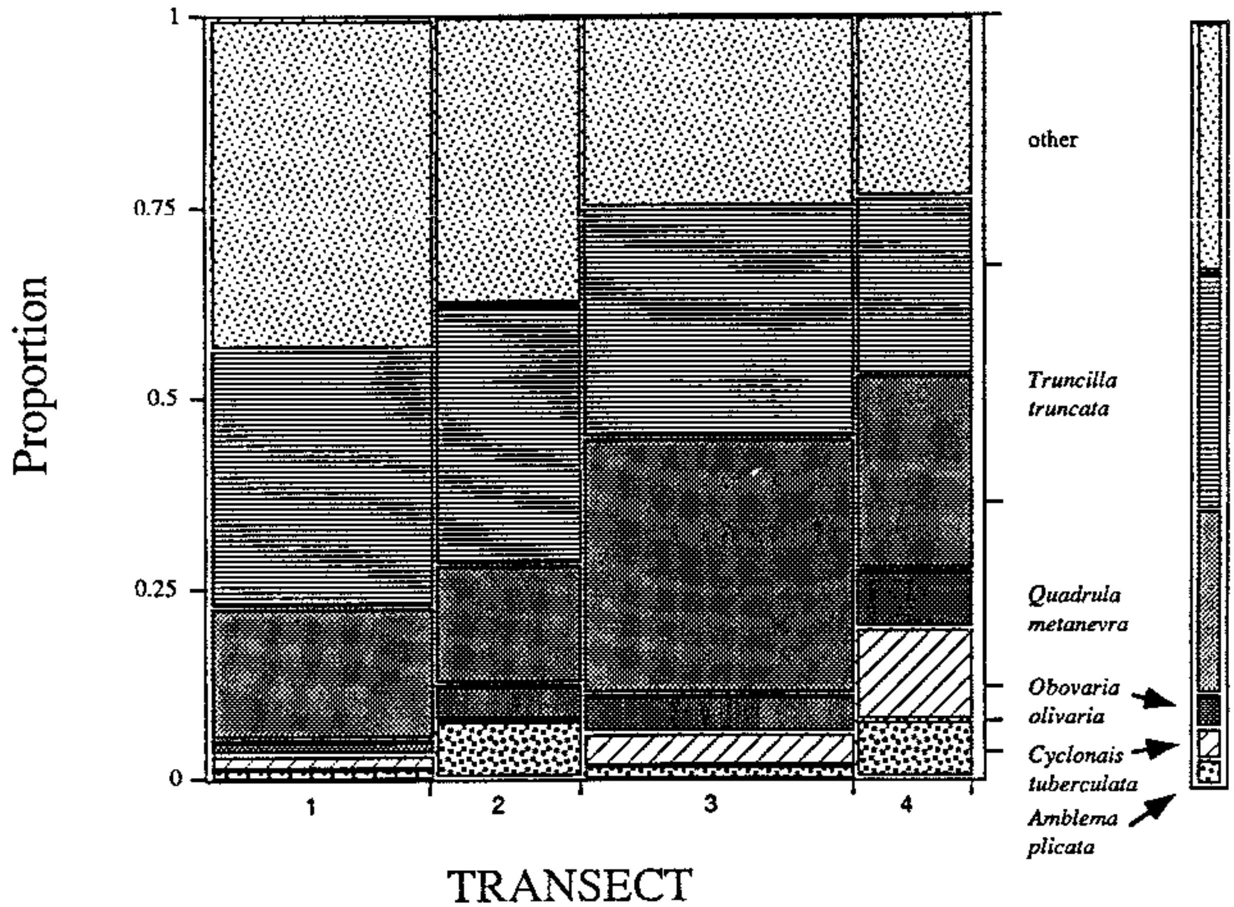


Fig. 6. Changes in mussel community structure parallel to the flow of the river based on qualitative sampling 1990.

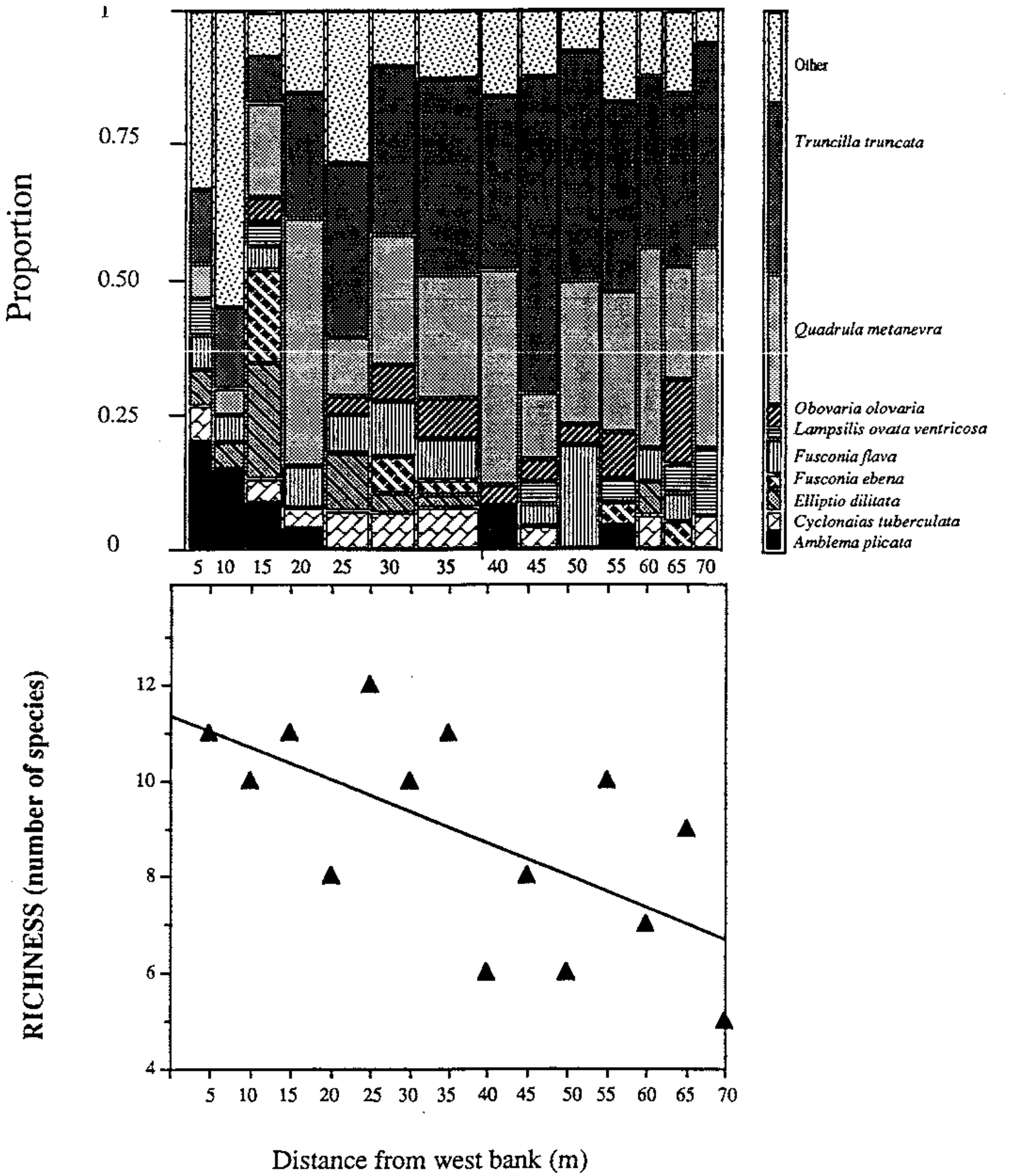


Fig. 7. Changes in mussel community structure perpendicular to the flow of the river, based on qualitative samples taken in 1990.

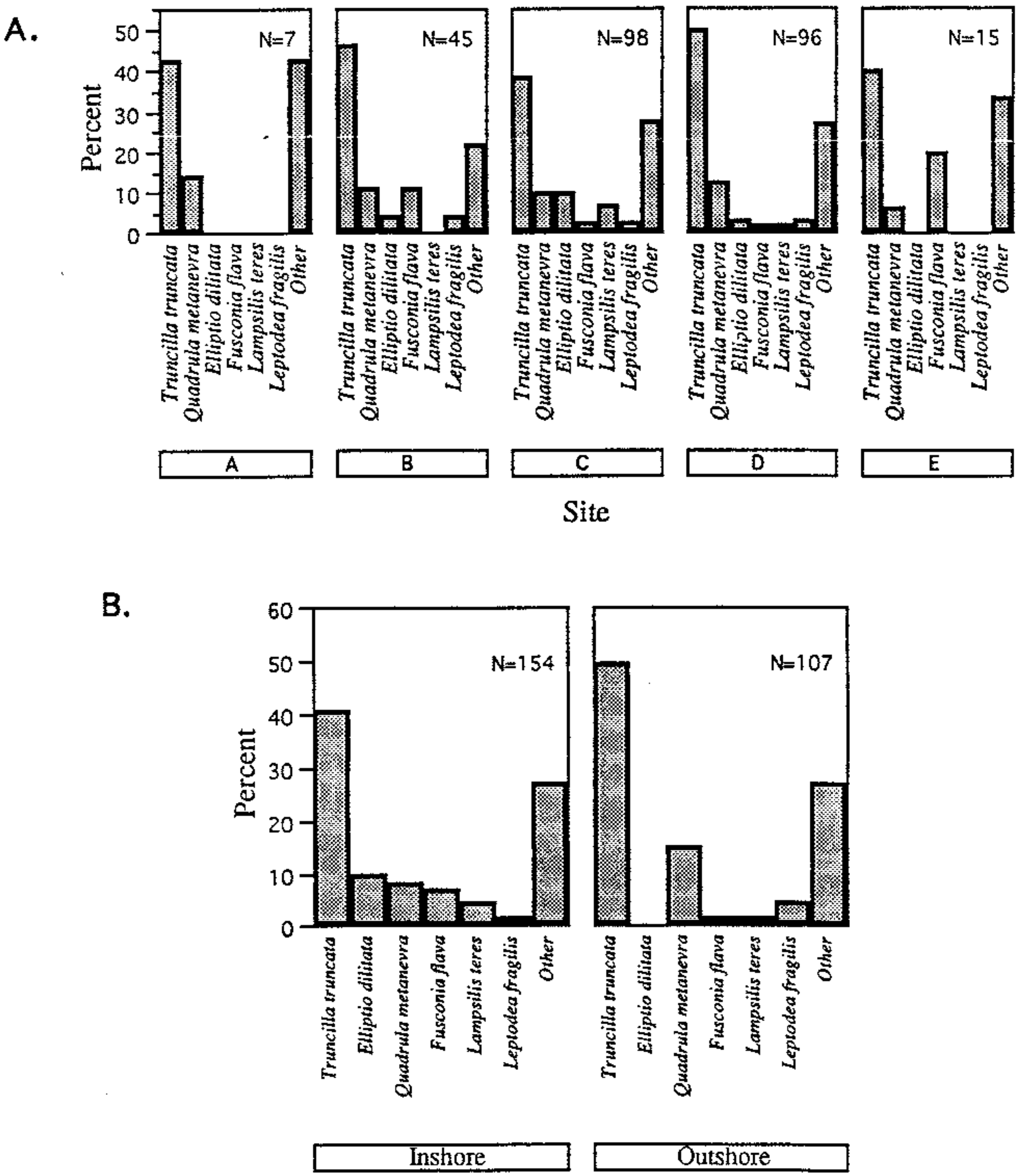


Fig. 8. Changes in mussel community structure (1991) parallel (A) and perpendicular (B) to the flow of the river.

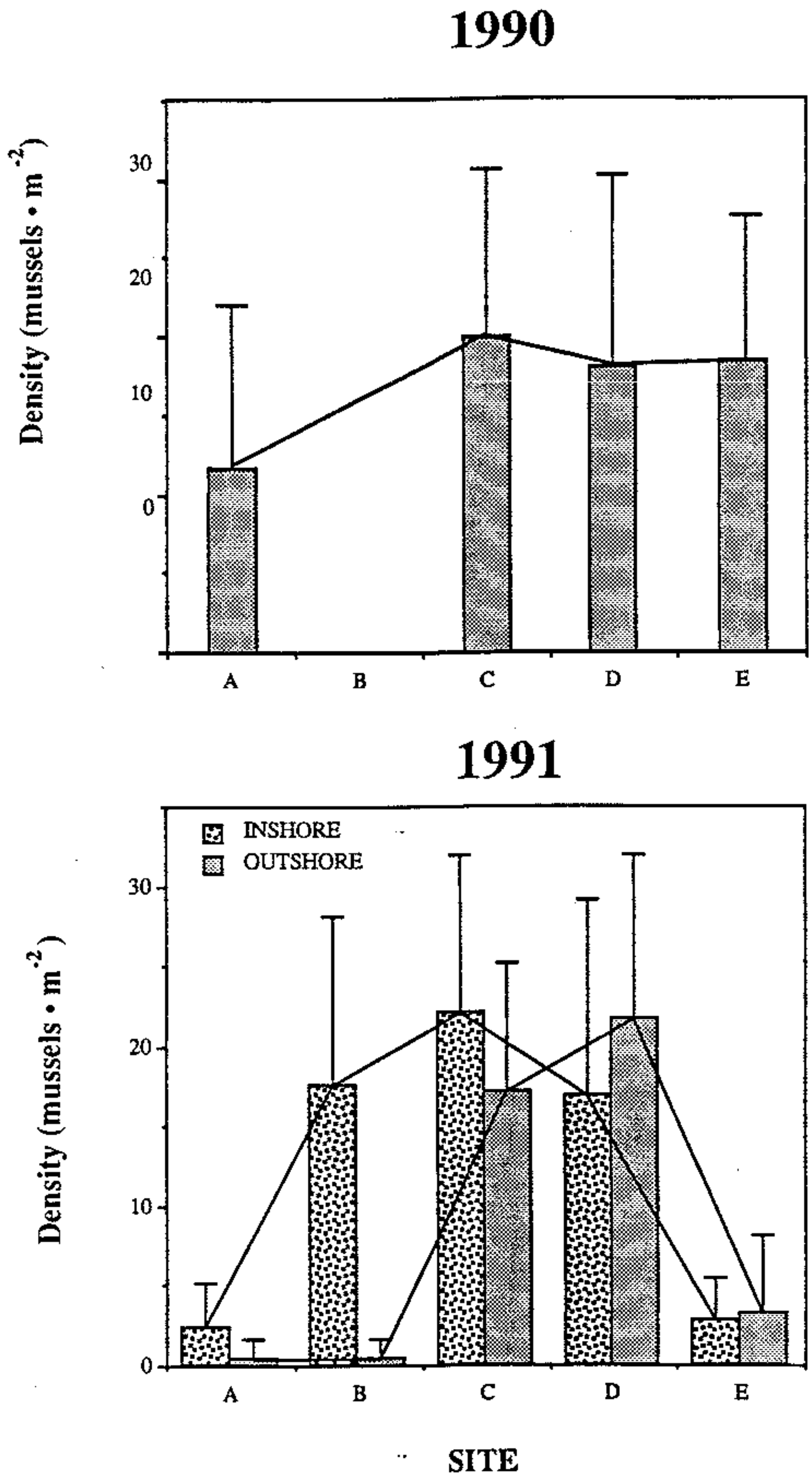


Fig. 9. Mean mussel density at various sites at Franconia, MN. Vertical bars indicate 1 standard deviation.

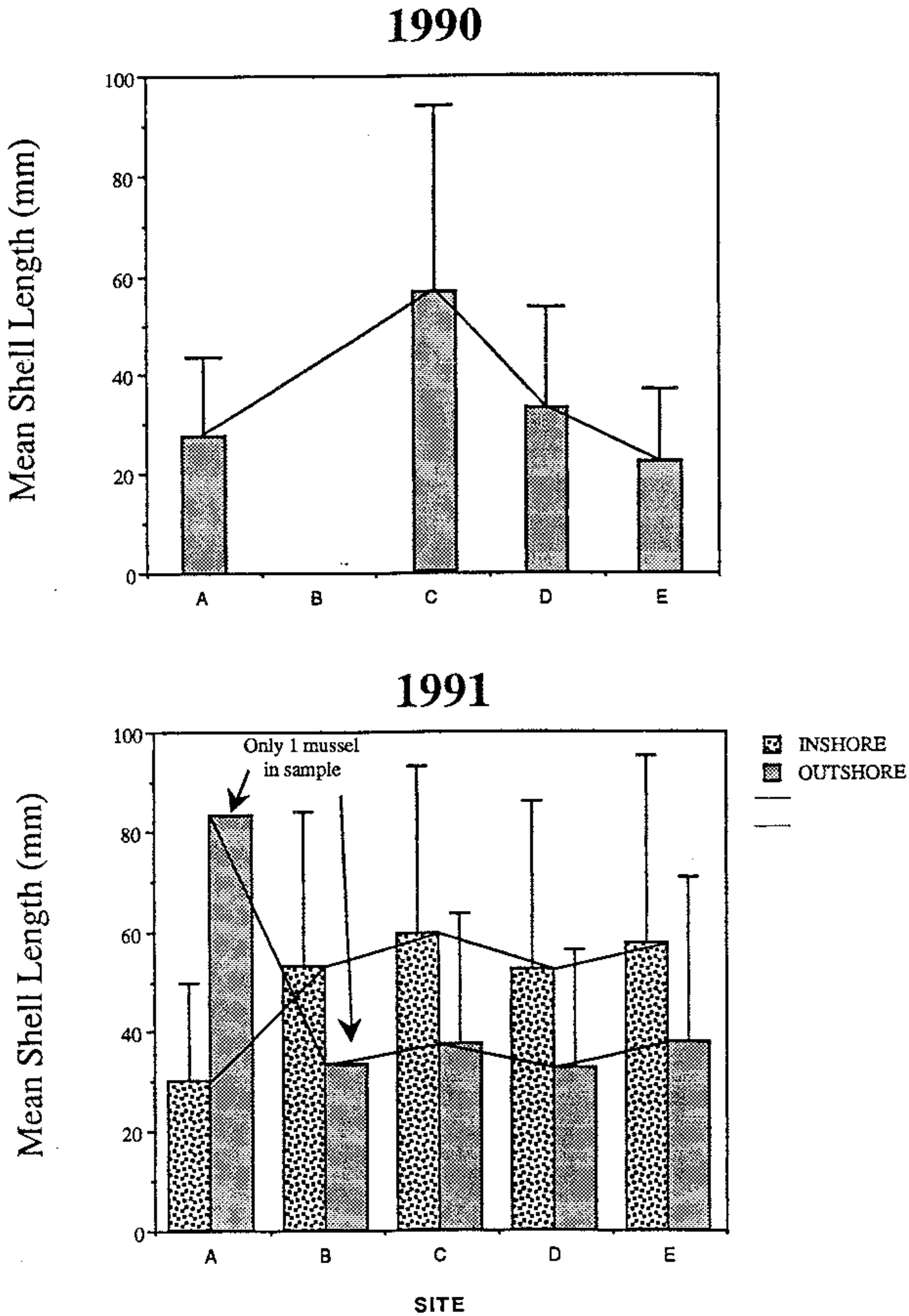
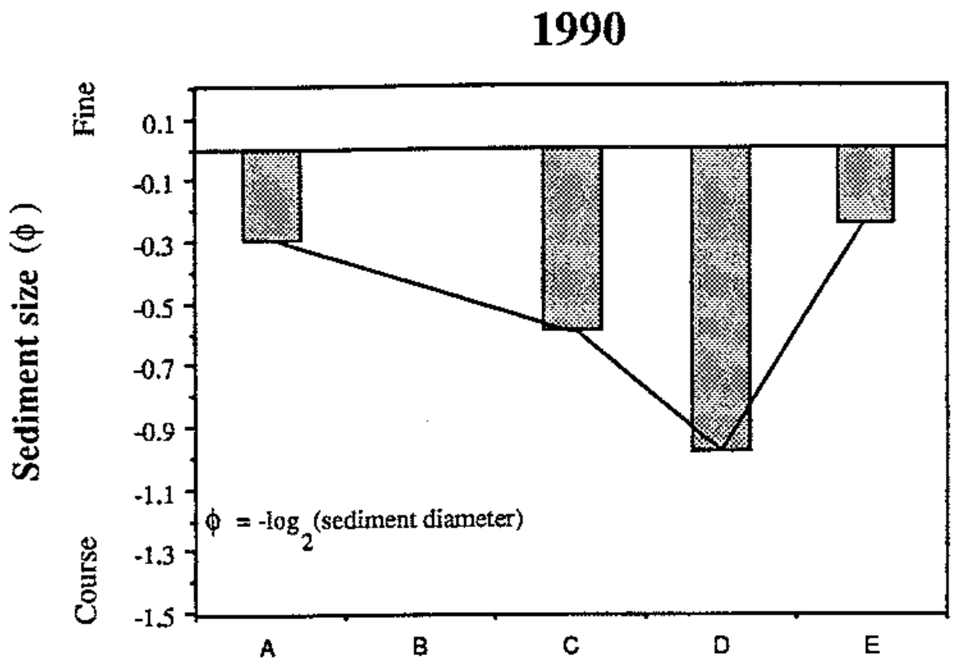


Fig. 10. Mean shell lengths of mussels collected from various sites at Franconia, MN. Vertical bars are 1 standard deviation.



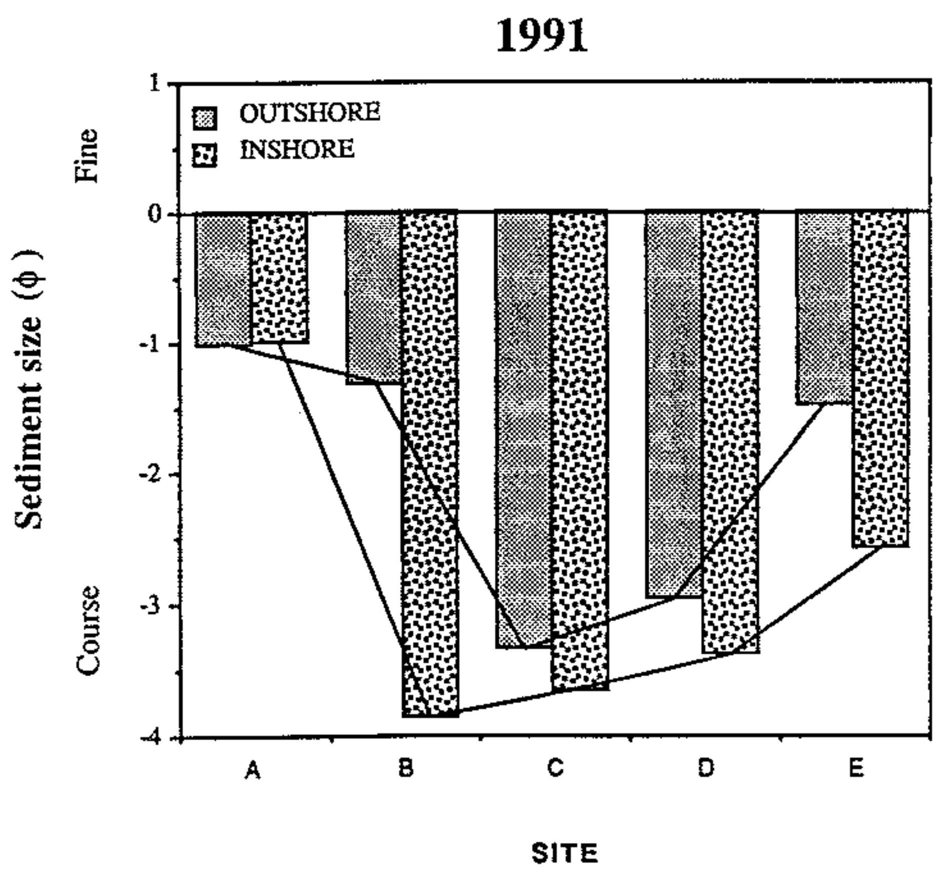
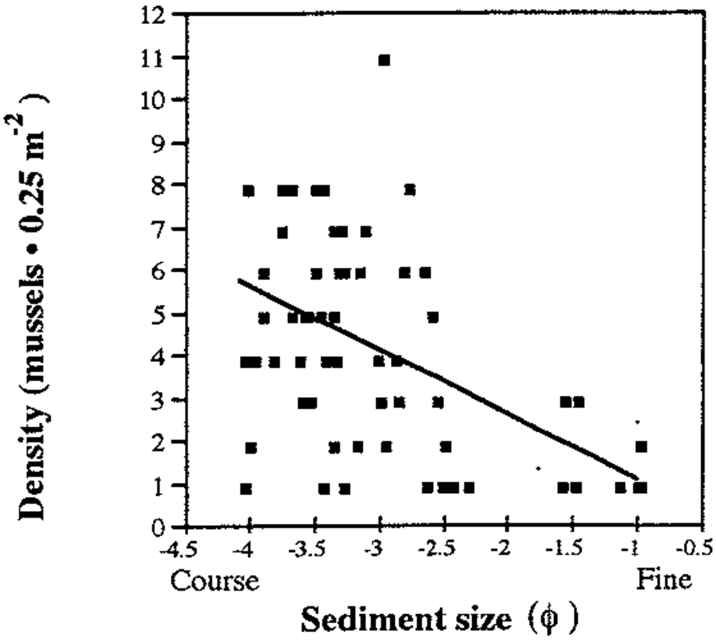


Fig. 11. Mean sediment sizes from various sampling sites at Franconia, MN. (Note: different methods of sediment collection were used in 1990 and 1991 resulting in the different y-axis scales)

A



B

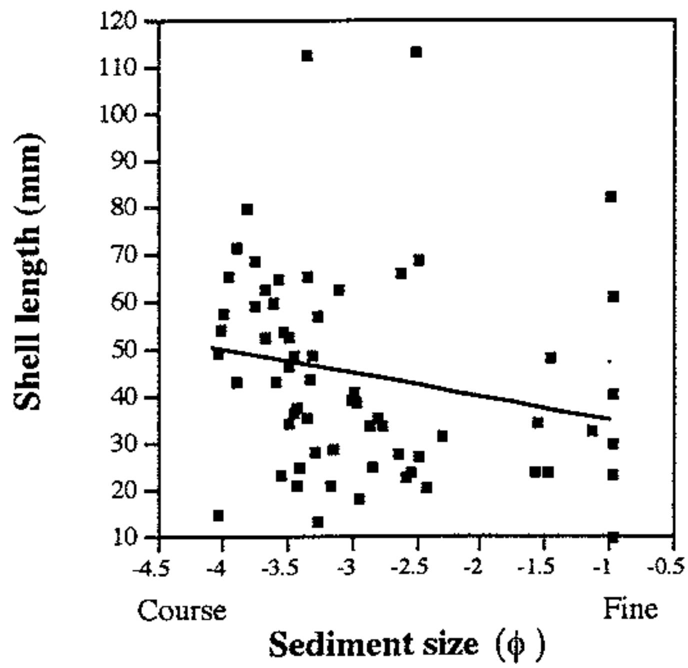


Fig. 12. Relationship between sediment size and mussel density (A) and mussel size (B) based on 100 samples taken in 1991.

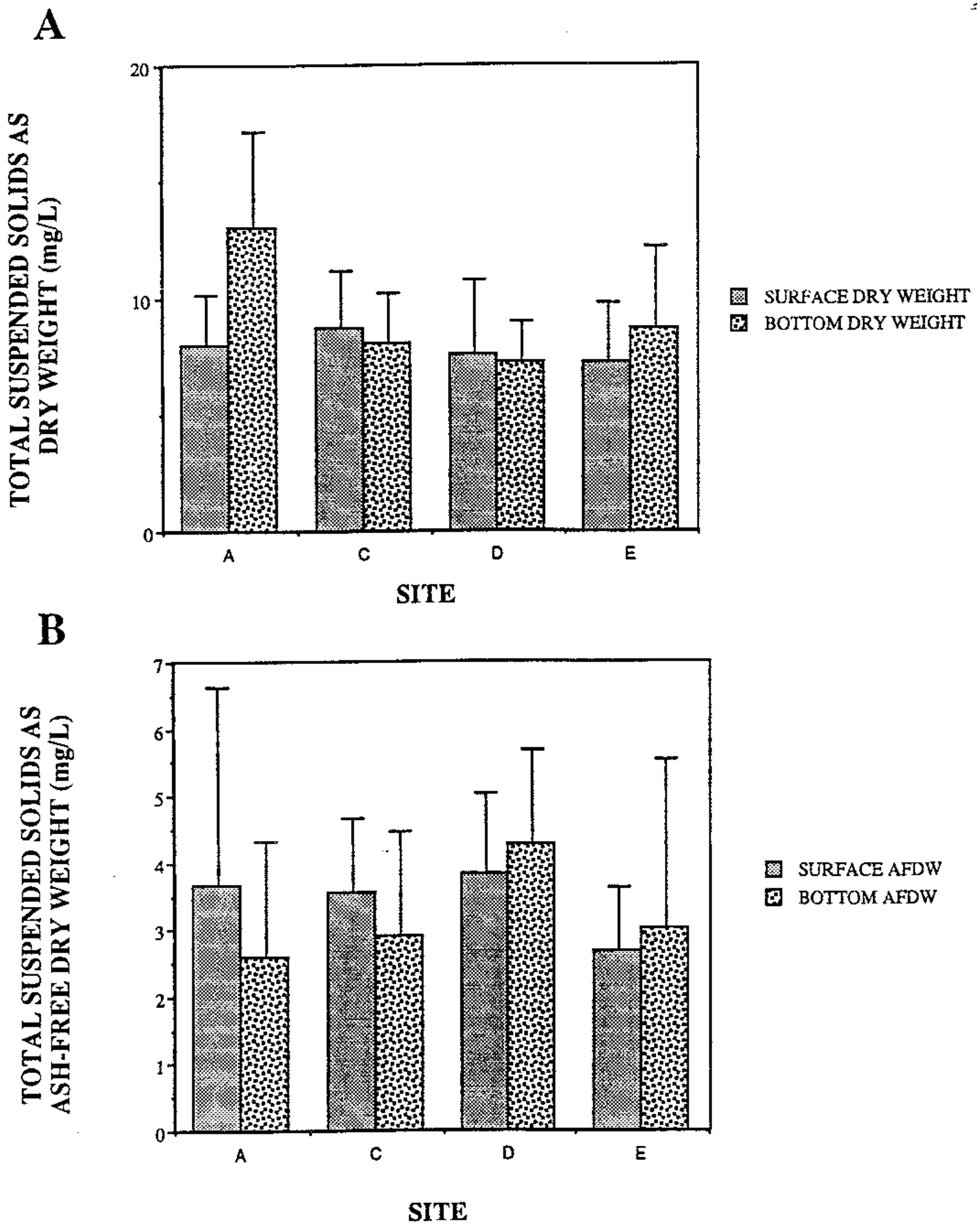


Fig. 13. Variation in suspended solids as dry weight (A) and ash-free dry weight (B) from samples taken on July 31, 1990. Vertical lines indicate 1 standard deviation.

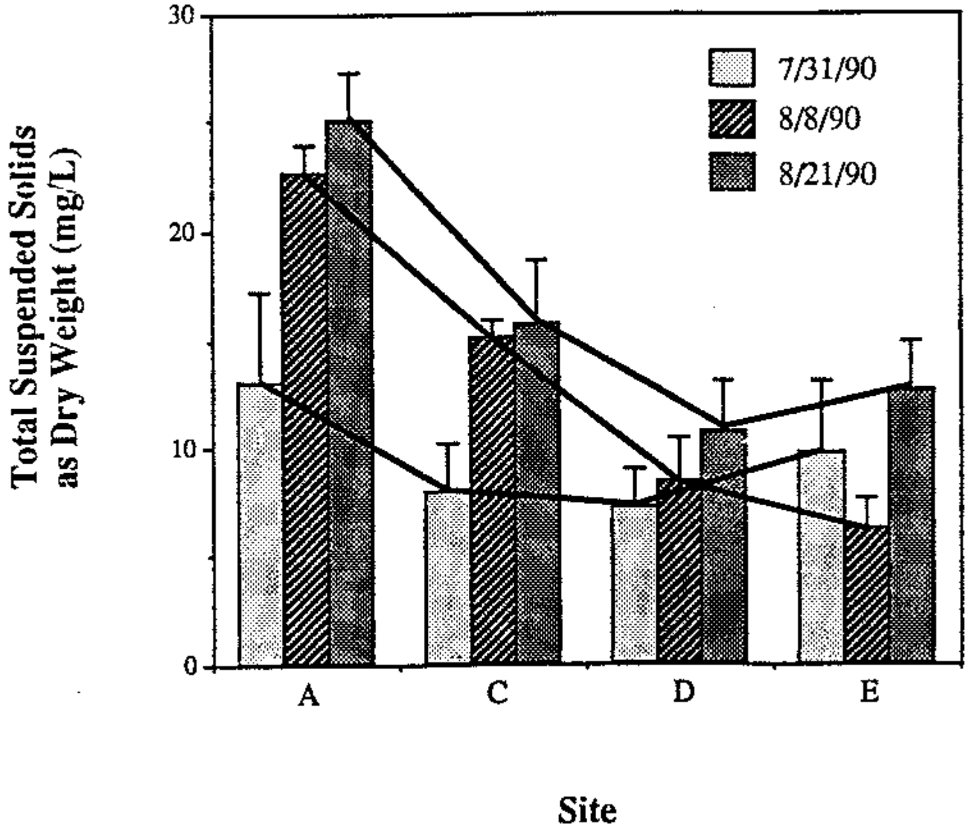
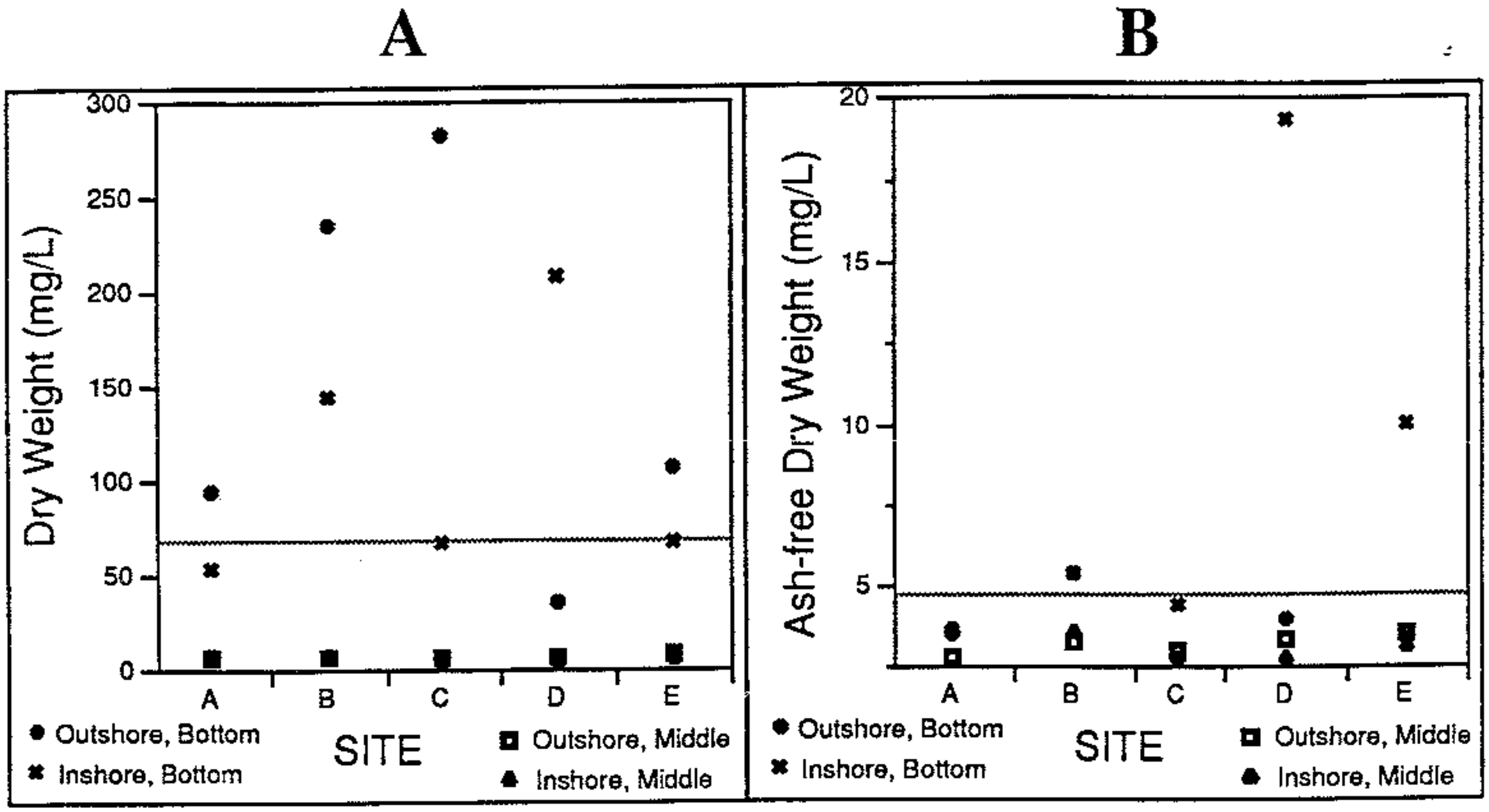


Fig. 14. Total suspended solids as dry weight sampled above the bottom of the St. Croix River - Franconia, MN for 3 dates in1990.



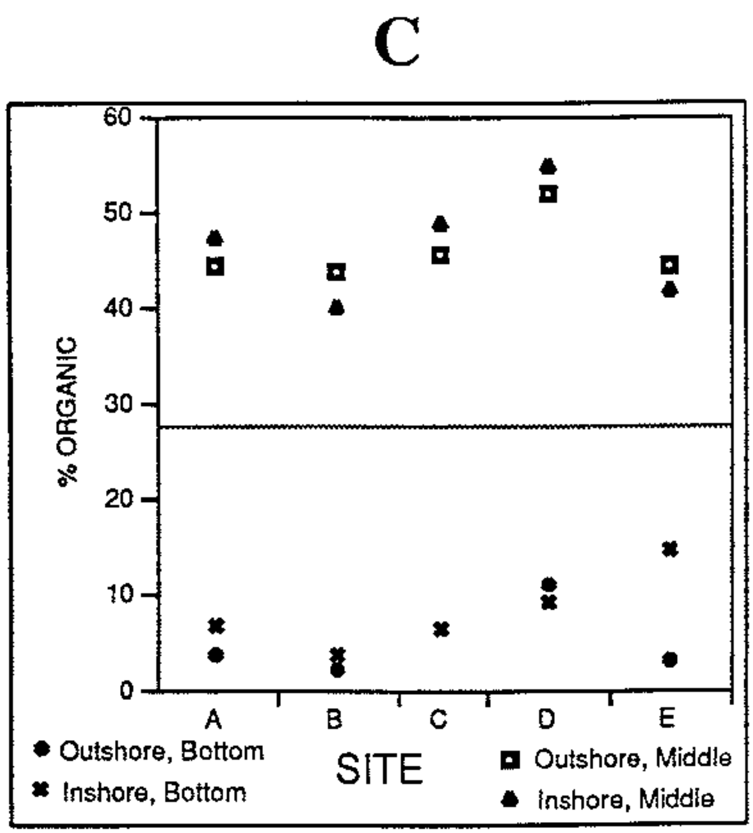


Fig. 15. Variation in suspended solids as dry weight (A) ash-free dry weight (B) and organic matter (C) in samples taken August 15, 1991.

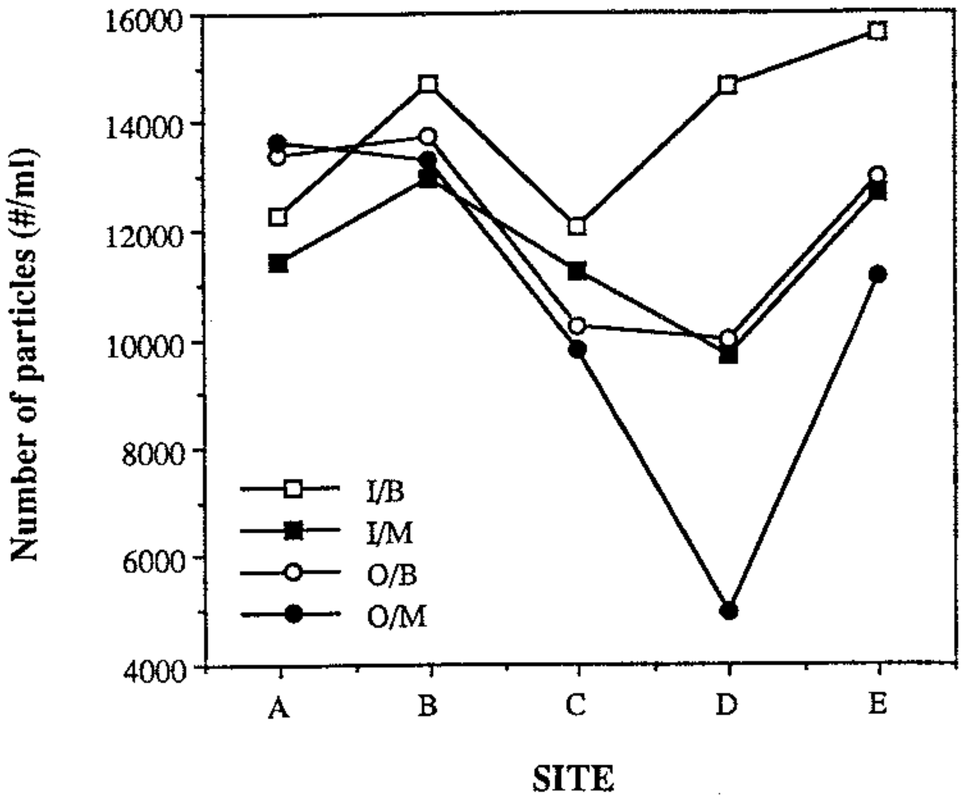


Figure 16. Mean number of particles suspended in the water column from various sites in the St. Croix River at Franconia, MN. I indicates samples taken from inshore sites, O from outshore sites, B samples at the bottom of the water column, and M taken from 0.5 m above the bottom of the water column.

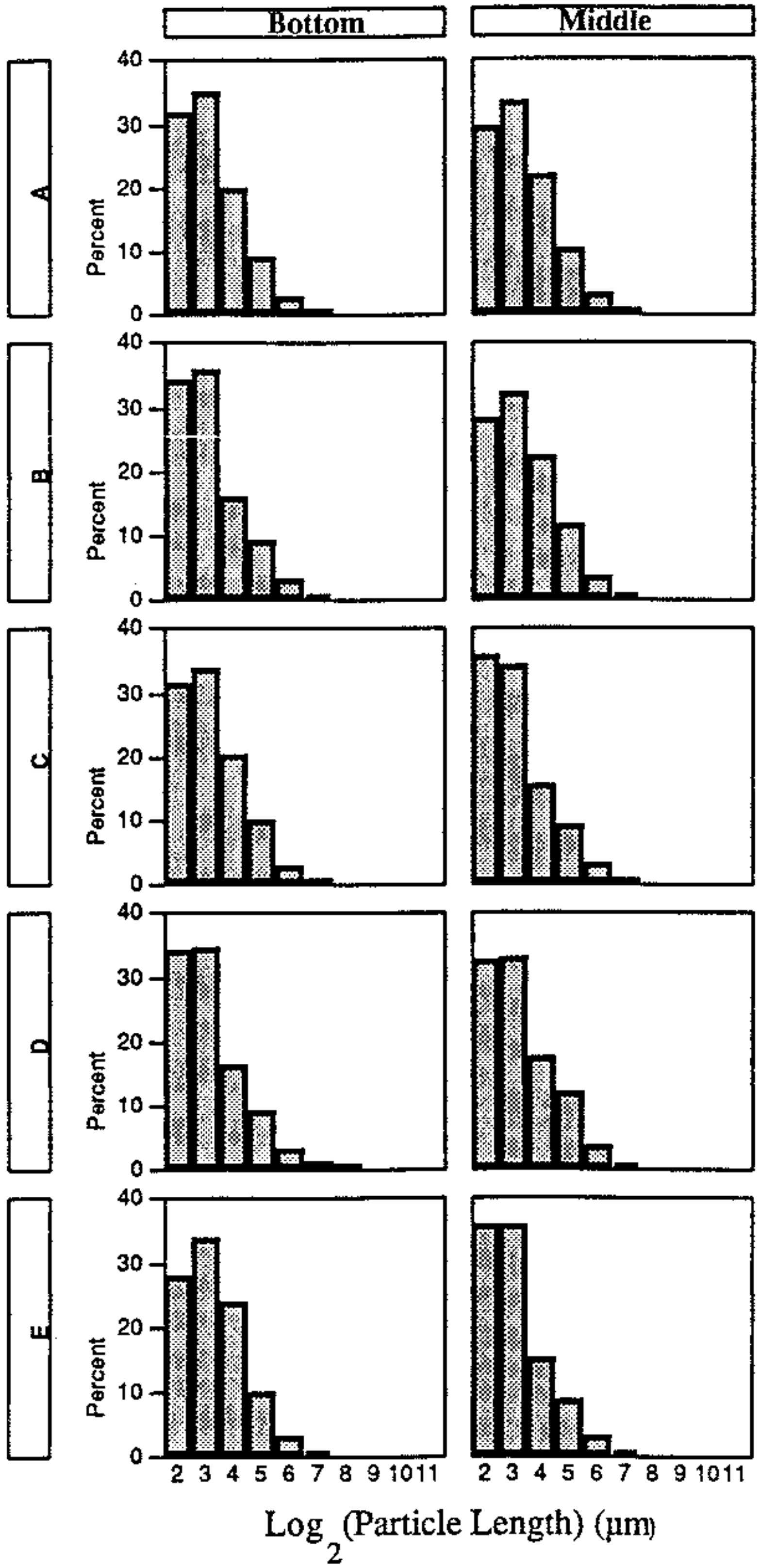


Fig. 17. Variation in the size of suspended particles in water samples taken from a number of sites on August 15, 1991 at Franconia, MN.

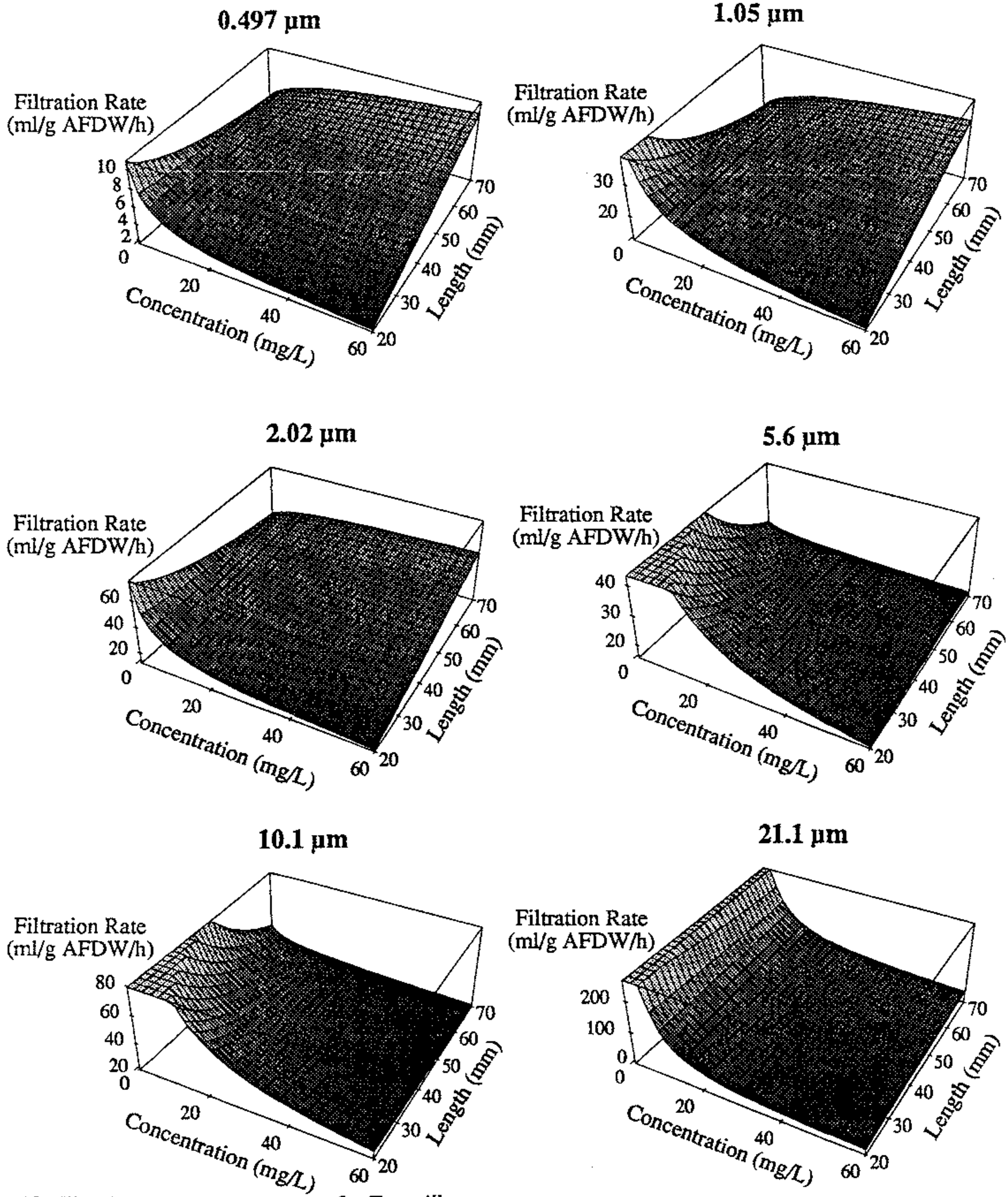


Fig. 18. Filtration rate response curves for *Truncilla truncata*.

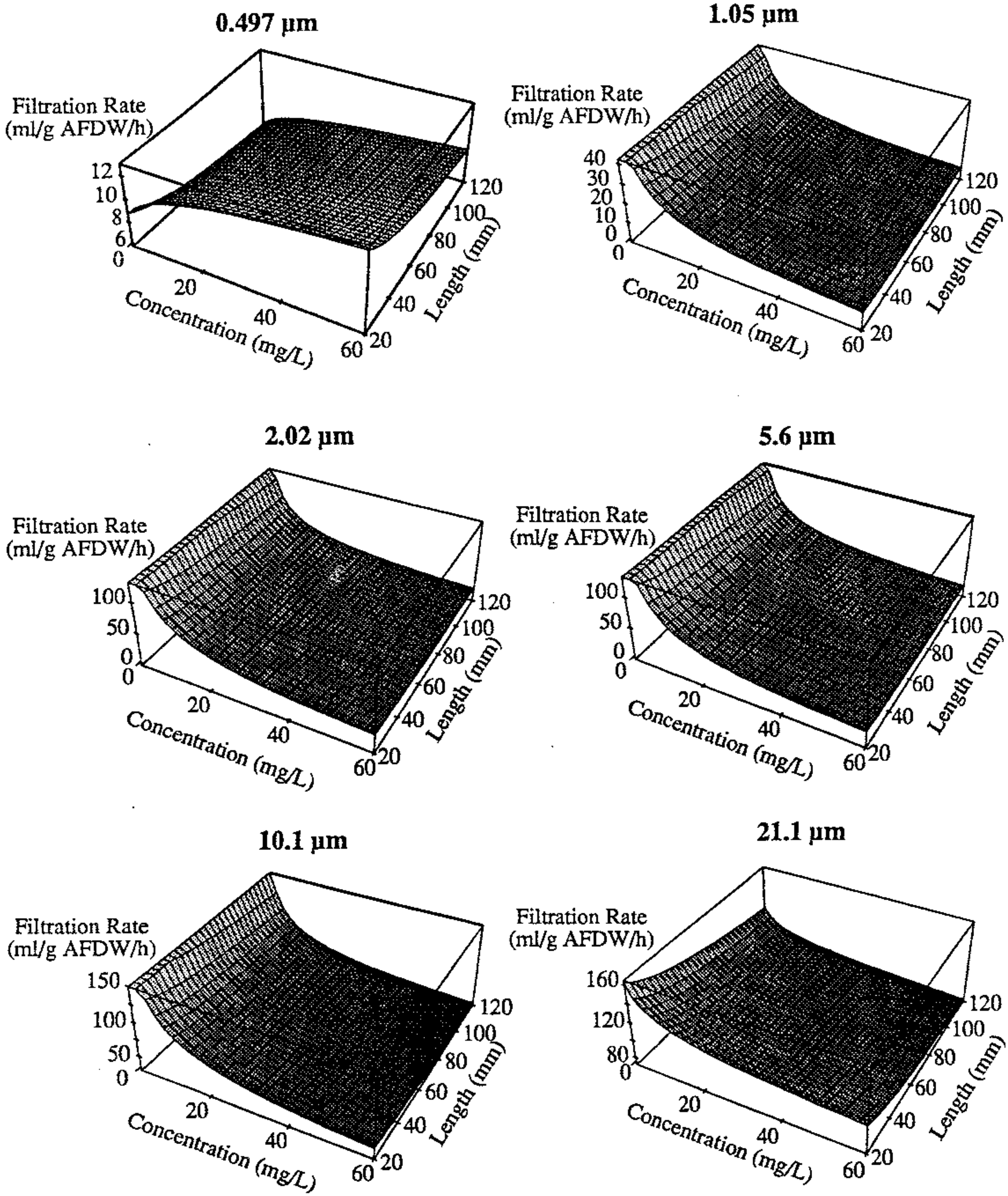


Fig. 19. Filtration rate response curves for *Quadrula metanevra*.

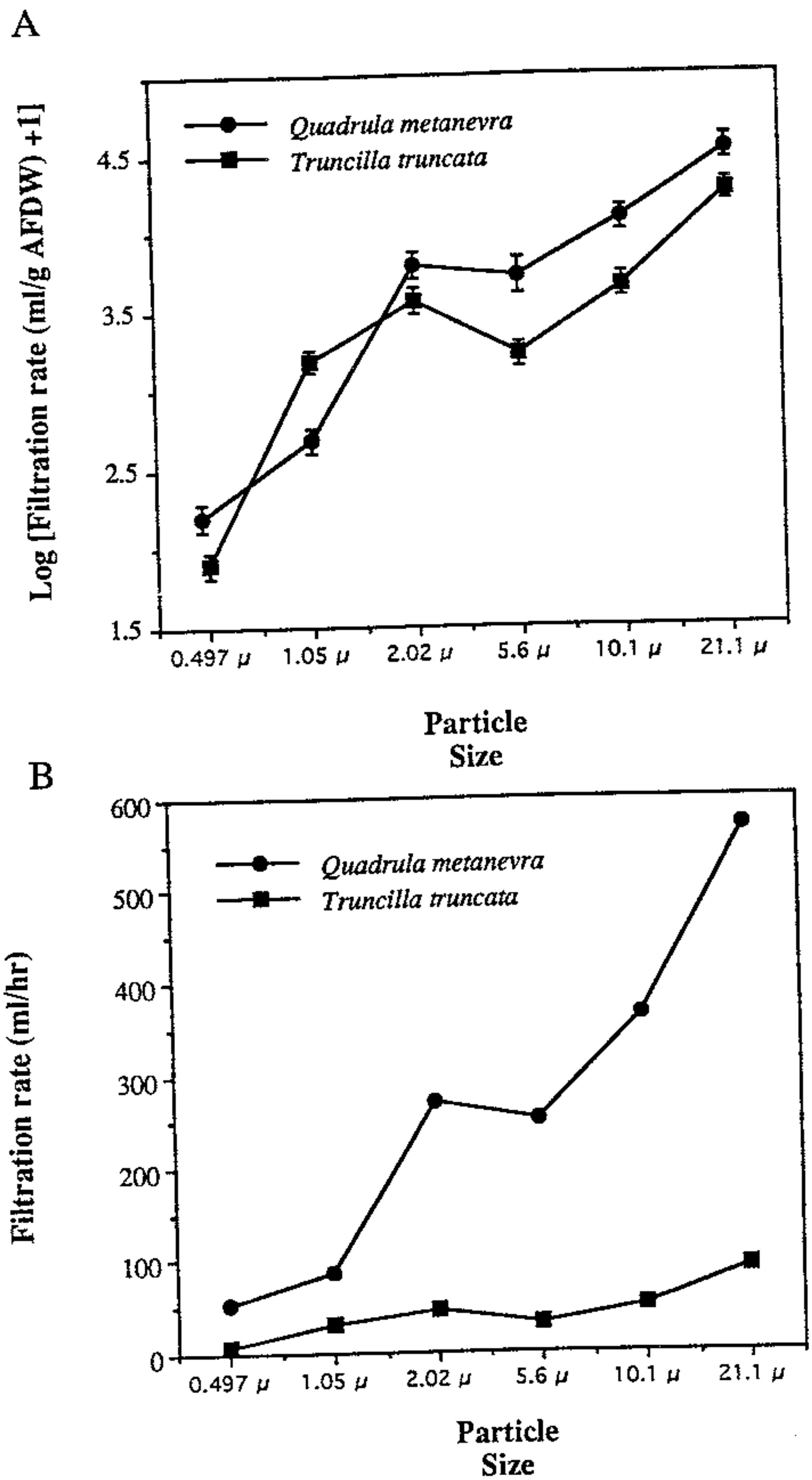


Figure 20. A. Least squares means for filtration rates for *Quadrula metanevra* and *Truncilla truncata*. Vertical lines are standard errors. B. Predicted filtration rates for mean sized animals (99.2 mm *Quadrula metanevra* and 43.1 mm *Truncilla truncata*).