Journal of the Iowa Academy of Science: JIAS

Volume 112 | Number 3-4 Article 4

2005

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Jour. Iowa Acad. Sci. 112(3,4):28–35, 2005

Discordant Harmonies in Fingernail Clam Populations (*Musculium transversum*) of Mississippi River Backwater Lakes

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The populations of *Musculium transversum* from 8 backwater lakes have been studied over a 29-year period based upon over 440 grab samples. These lakes in Navigation Pool 9 of the Upper Mississippi River (UMR) range in size from 2 to 255 hectare surface area, mean depths from 0.2 to 0.9 meters, with mean water exchange times from 0.5 to almost 57 hours. Samples from the 1989–91 period suggested summer *Musculium* populations had declined to about 9 percent of their mid-1970 levels. Deterministic models have attempted to explain this decline. More recent sampling suggests a substantial recovery of *Musculium* populations (mid-summer mean of 560 m^{-2} in 2002). Simple stochastic models, with realistic levels of POISSON and NORMAL variables, may provide a better explanation of population fluctuations than previously used deterministic models.

INDEX DESCRIPTORS: fingernail clams, population decline, Mississippi River.

Backwater lakes of the Upper Mississippi River have often had the highest productivity in the entire river system (see Carlander 1954, Eckblad et al. 1977, Eckblad et al. 1984, Jahn and Anderson 1986, Eckblad 1986). Construction of locks and dams in the 1930's helped stabilize water levels in these backwaters, especially during periods of low flow. Lock and Dam 9 on the Upper Mississippi River, 1042 km (647.9 miles) above the mouth of the Ohio River, impounds a 50.4 km reach of river that includes a variety of backwater lakes and running sloughs, as well as the main navigation channel and its channel border (Fig. 1). At normal pool elevation (189 m above mean sea level) there are approximately 11,730 ha of aquatic and 9,310 ha of terrestrial habitat in Pool 9.

The benthic macroinvertebrates of backwater lakes have included populations of fingernail clams (*Musculium transversum*), burrowing mayflies (*Hexagenia* sp.), midges (Chironomidae), and segmented worms (Oligochaeta). Fingernail clam population densities for the Upper Mississippi have been reported at over 5,000 m^{-2} (Gale 1969), and have constituted over 58% of the benthic biomass (Eckblad et al. 1977). Gizzard shad, carp, buffalo, suckers, channel catfish, bullheads, and perch are among the fish known to forage on fingernail clams, and these benthic mollusks are also an important source of food for migratory waterfowl, particularly the lesser scaup and canvasback (Anderson et al. 1978). *Musculium* have a somewhat unusual reproductive biology in that they are hermaphroditic, may engage in selfing, are ovoviviparous, and carry shelled-embryos within the pregnant adult (Gale 1969).

Previous studies reported a decline in *Musculium* populations in the late 1980's in these and other backwater lakes of the Upper Mississippi River (Eckblad and Lehtinen 1991, Wilson et al. 1995). Explanations for these declines have included sediment toxicity (e.g., Frazier et al. (1996) suggest high concentrations of un-ionized ammonia (NH_3) in sediment pore water), extended periods of low flow and low water levels (Sparks 1980), and possible virus infections similar to what has been reported in marine bivalves (Comps and Masso 1978, Elston 1979). Thus far there appears to be no widespread acceptance of a single deterministic model to explain *Musculium* declines. For example, Canfield et al. (1998) found no correlations between sediment chemistry and benthic communities in a study of 23 pools in the Upper Mississippi River.

The title of this article, imitative of a book title (Botkin 1990), is intended to suggest that viewing fingernail clam populations as part of a natural balance, i.e. 'harmony', in a river system is a failure to recognize the non-equilibrium dynamics of this ecosystem. Rivers change over essentially all time scales, and its communities of organisms should be expected to reflect this change. In complex systems it can be very difficult to identify single causal factors to explain changes especially when they are influenced by chance events (Likens 2001). Whereas useful deterministic models may require an unrealistically large number of parameters, stochastic models can help in describing complex systems as they can often be implemented with explicit knowledge of only a limited number of variables (Murdoch 1994).

METHODS

Fingernail clams were sampled from backwater lakes of Navigation Pool 9 of the UMR using a 232-cm^2 Ponar grab. Samples were sieved through a U.S. Sieve No. 30 (533 μm) and preserved in 70% ethanol to which Rhodamin-B vital stain had been added; this stain was especially helpful in identifying live fingernail clams. Six samples were taken along central transects in each of the lakes. Most sampling was conducted during mid-summer (late June to early July). During the 29-year period reported herein (1973–2002) a total of over 440 grab samples were taken to estimate *Musculium* populations. Since 1990, we have been measuring *Musculium* shell-lengths, and have determined the number and size of shelled-embryos within adult individuals.

Musculium populations are also being sampled as part of the Long Term Resource Monitoring Program (LTRMP) which is

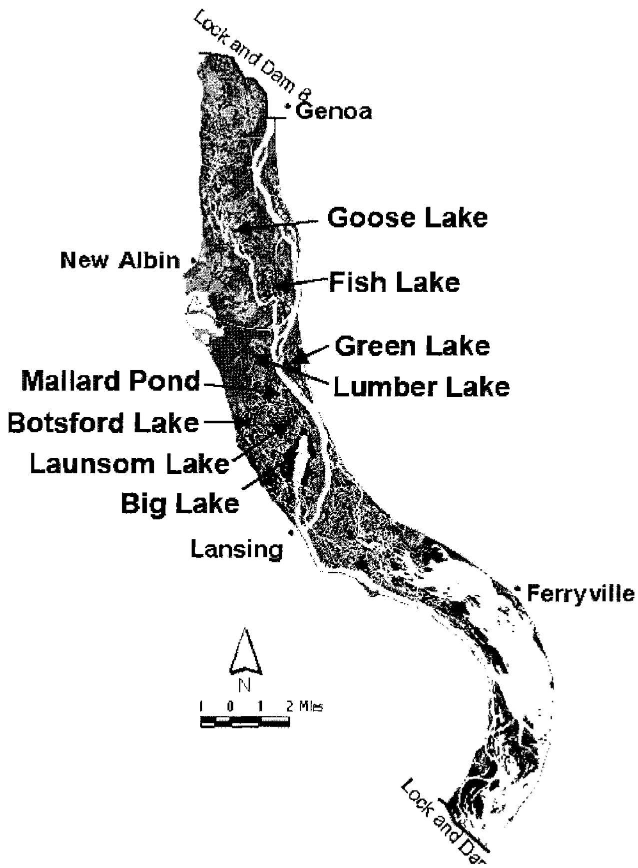

Fig. 1. Map of Pool 9 of the Upper Mississippi River showing the 8 backwater lakes (Goose Lake, Fish lake, Green Lake, Lumber Lake, Mallard Pond, Botsford Lake, Launsom Lake, Big Lake).

implemented by the Upper Midwest Environmental Sciences Center (UMESC), a U. S. Geological Survey science center, in cooperation with the five Upper Mississippi River System (UMRS) States of Illinois, Iowa, Minnesota, Missouri, and Wisconsin. Sample data for early summer samples from Lake Pepin (Pool 4) and Pool 13 from 1995 to 2002 were made available by Jennifer Sauer of the UMESC, La Crosse, Wisconsin. Lake Pepin is about 100 river miles upstream from Pool 9 and Pool 13 is about 140 river miles downstream from Pool 9.

Musculium sample numbers are reported using box-and-whisker plots in order to represent both central tendency and the amount of variation present. The 'box' represents the interquartile-range (i.e., middle 50% of the samples), and 'whiskers' extend to the maximum and minimum values; outlier values are plotted individually when they occur more than (1.5)(interquartile-range) away from the interquartile-range. Computer simulation models to represent *Musculium* populations were developed using *STELLA* from High Performance Systems, Inc.

FINGERNAIL CLAM POPULATIONS

Musculium populations from backwater lakes of Pool 9 showed a general pattern of decline in numbers by the late 1980's, low numbers in the early 1990's, followed by increased numbers after the mid-1990's (Fig. 2–9). Launsom Lake showed increased

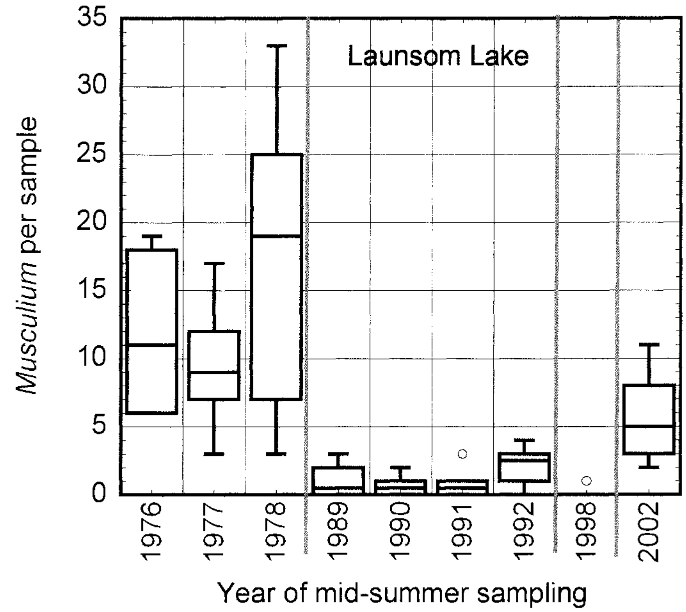

Fig. 2. Launsom Lake *Musculium* populations 1976–2002. Launsom Lake has a surface area of 84.7 ha, and is located at river mile 668.0 in Pool 9 of the Upper Mississippi River. Box-and-whisker plots based upon 6 ponar grab samples.

populations in 2002 from the early 1990's, but populations are still below their mid-1970 levels (Fig. 2). Lumber Lake showed increased populations from the early 1990's, and the 2002 population was at or above the mid-1970 levels (Fig. 3). Fish Lake had population numbers higher than the early 1990's, and

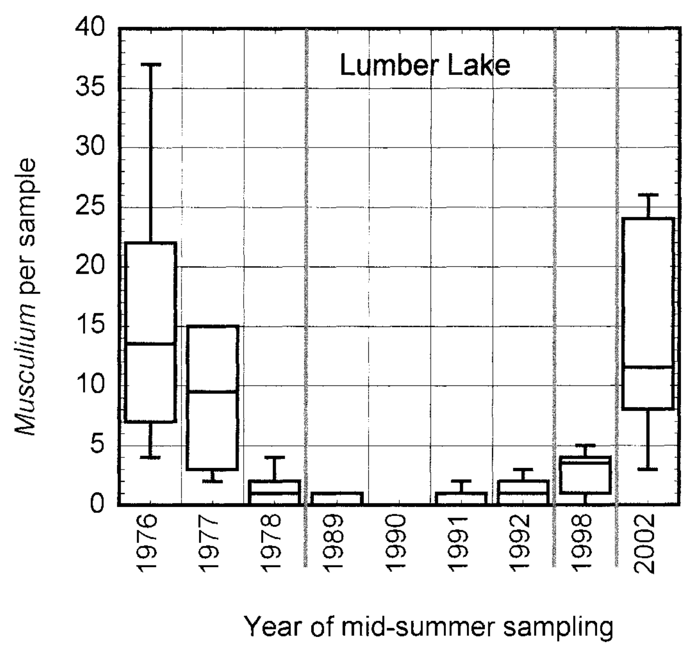

Fig. 3. Lumber Lake *Musculium* populations 1976–2002. Lumber Lake has a surface area of 1.8 ha, and is located at river mile 670.2 in Pool 9 of the Upper Mississippi River. Box-and-whisker plots based upon 6 ponar grab samples.

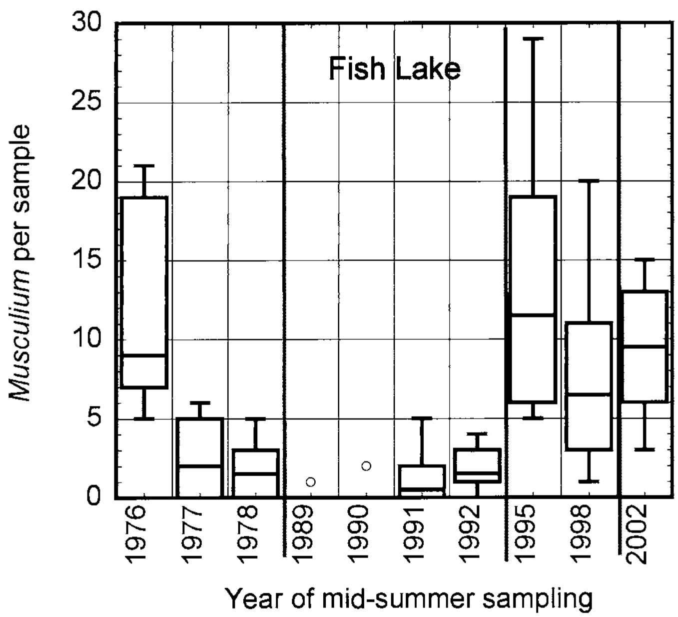

Fig. 4. Fish Lake *Musculium* populations 1976–2002. Fish Lake has a surface area of 27.4 ha, and is located at river mile 672.7 in Pool 9 of the Upper Mississippi River. Box-and-whisker plots based upon 6 ponar grab samples.

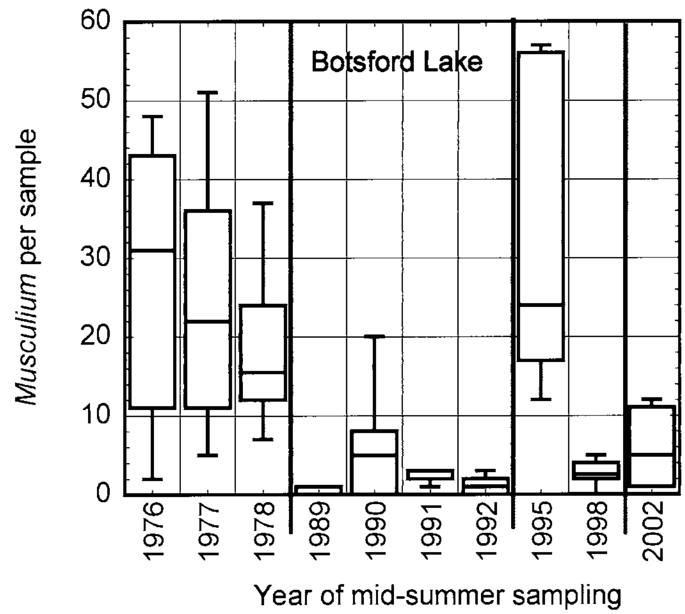

Fig. 6. Botsford Lake *Musculium* populations 1976–2002. Botsford Lake has a surface area of 39.7 ha, and is located at river mile 667.3 in Pool 9 of the Upper Mississippi River. Box-and-whisker plots based upon 6 ponar grab samples.

sampling from 1995 and 1998 showed that populations had already recovered to or above their mid-1970 levels (Fig. 4). Mallard Pond showed increased populations from the early 1990's, and the 2002 population was at or above the mid-1970 levels (Fig. 5). Botsford Lake *Musculium* populations had increased by the 1995 sampling, and populations were below the mid-1970 levels in the most tecent sampling (Fig. 6). Big Lake populations showed increased numbers from the lows of the early 1990's, and numbers in 2002 were at or higher than reported in the mid-1970's (Fig. 7). Goose Lake populations declined to very

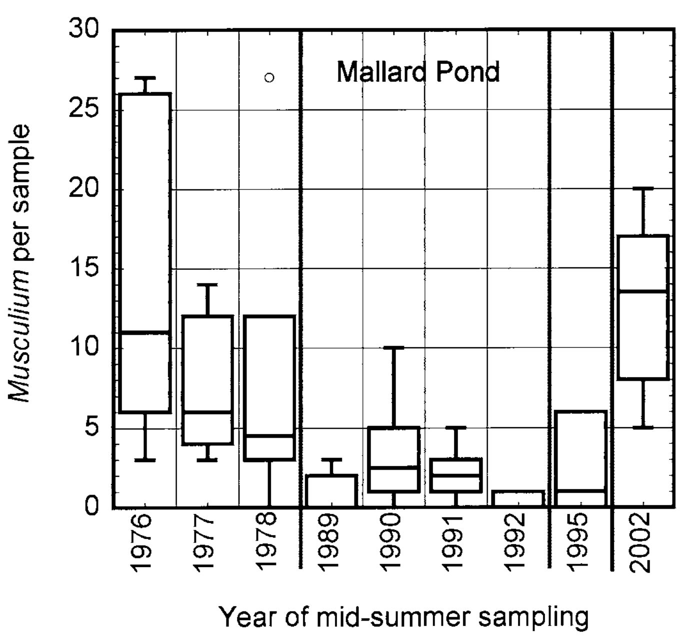

Fig. 5. Mallard Pond *Musculium* populations 1976–2002. Lumber Lake has a surface area of 4.0 ha, and is located at river mile 669.4 in Pool 9 of the Upper Mississippi River. Box-and-whisker plots based upon 6 ponar grab samples.

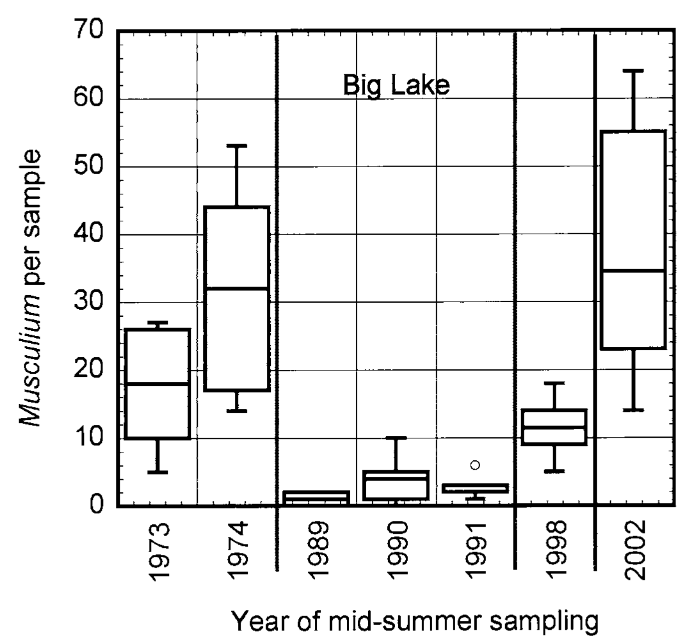

Fig. 7. Big Lake *Musculium* populations 1973–2002. Big Lake has a surface area of 255.7 ha, and is located at river mile 666.2 in Pool 9 of the Upper Mississippi River. Box-and-whisker plots based upon 6 ponar grab samples.

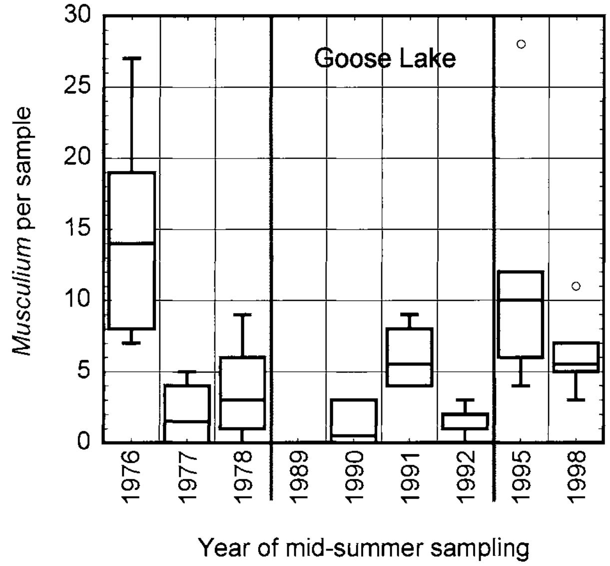

Fig. 8. Goose Lake *Musculium* populations 1976–1998. Goose Lake has a surface area of 20.4 ha, and is located at river mile 675.2 in Pool 9 of the Upper Mississippi River. Box-and-whisker plots based upon 6 ponar grab samples.

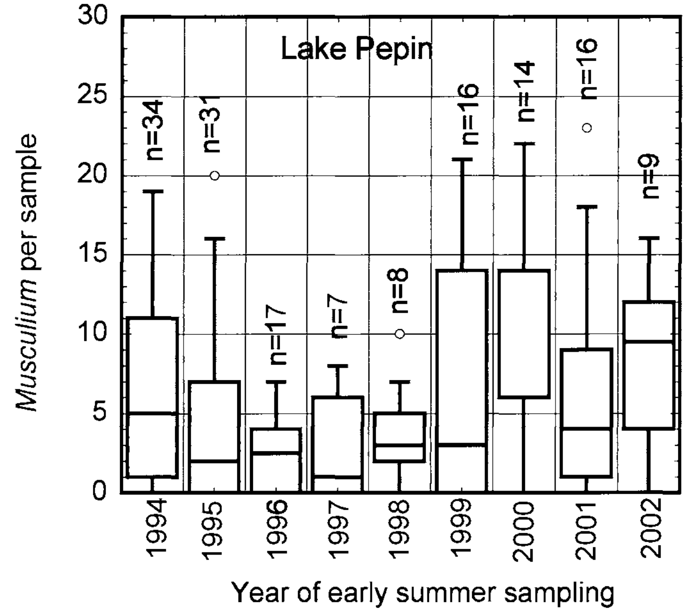

Fig. 10. Lake Pepin *Musculium* populations based upon Long Term Resource Monitoring Program (LTRMP) Macroinvertebrate Database. Number of ponar grab samples per year for each box-and-whisker plot is shown. The median of 6 in 2000 is also the lower value of the interquartile range.

low numbers in the late 1980's, but showed recovery to their mid-1970's level by the late 1990's (Fig. 8). Green Lake populations showed very low numbers in the 1989–91 period but had increased to mid-1970's levels by 1992.

Early summer sample data from both Lake Pepin (Pool 4) and Pool 13 (LTRMP) over the 8-year period from 1995 to 2002 also show variable *Musculium* populations (Fig. 10–13). Median sample numbers of *Musculium* from Lake Pepin populations ranged from 1 to 9 during this period (Fig. 10). Median numbers show a similar range from backwaters of Pool 13, but the greater variation is displayed in the number of outlier values plotted (Fig. 11). Higher median *Musculium* numbers from Pool 13 were

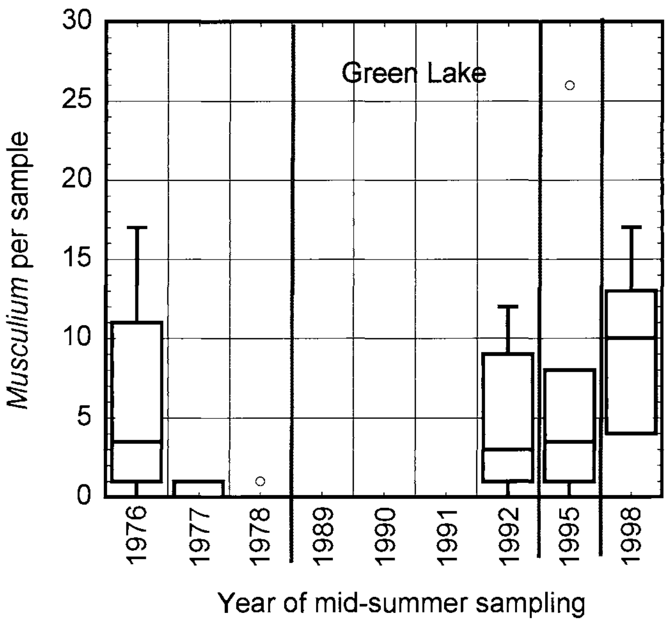

Fig. 9. Green Lake *Musculium* populations 1976–1998. Green Lake has a surface area of 12.9 ha, and is located at river mile 670.0 in Pool 9 of the Upper Mississippi River. Box-and-whisker plots based upon 6 ponar grab samples.

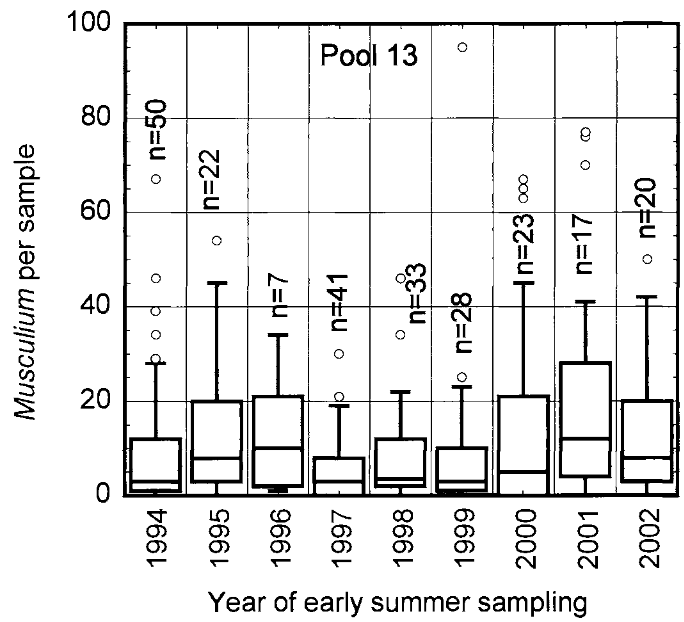

Fig. 11. Pool 13 backwater *Musculium* populations based upon Long Term Resource Monitoring Program (LTRMP) Macroinvertebrate Database. Number of ponar grab samples per year for each box-and-whisker plot is shown.

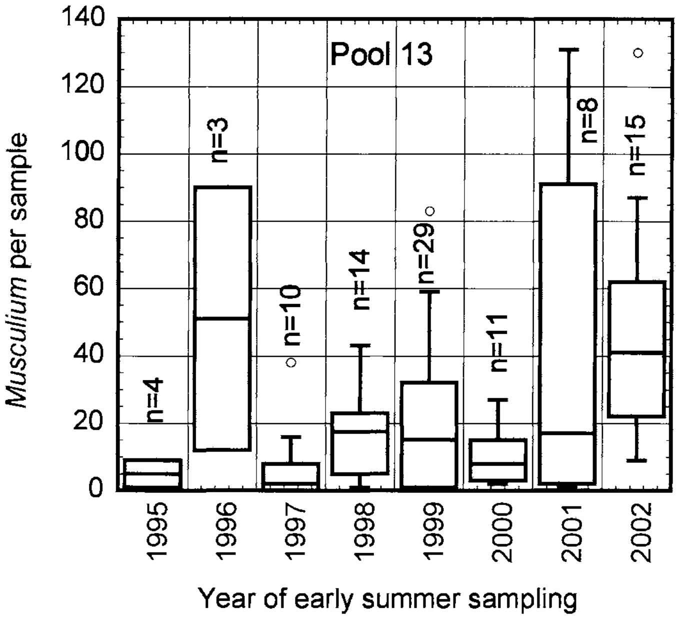

Fig. 12. Pool 13 ***Musculium*** populations based upon Long Term Resource Monitoring Program (LTRMP) Macroinvertebrate Database samples classified as having 50% or more fingernail clam shells in the washed sample. Number of ponar grab samples per year for each box-and-whisker plot is shown.

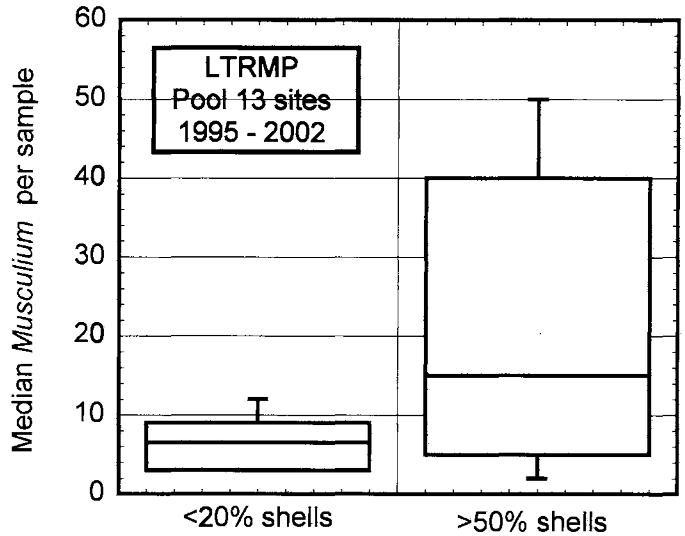

Fig. 13. Summary Pool 13 ***Musculium*** from Long Term Resource Monitoring Program (LTRMP) Macroinvertebrate Database with samples over the 8-year period (1995–2002) classified based upon the percentage of fingernail clam shells in the washed samples. During this period the median ***Musculium*** numbers ranged from 1 to 50, and the mean number of samples per year was about 24 (for sites <20% shells) and about 12 (for sites >50% shells).

present when sample sites were classified based upon the percentage of fingernail clam shells in the washed samples (Fig 12). Summary values based upon the 8-year period (1995–2002), with Pool 13 samples classified based upon the percentage of fingernail clam shells in the washed samples, had a median of 7 and 15 (Fig. 13).

About 41% of the *Musculium* from mid-summer sampling in 2002 had shell-lengths > 4.0 mm and of these about 19% were pregnant, i.e. carrying shell-embryos (Fig. 14). In two lakes sampled in both mid-summer and again in the autumn (22 Sept 2002), there were 19 out of 150 adults were carrying shelled embryos (= 13% pregnancy) in mid-summer, and 36 out of 77 adults were carrying shelled embryos (= 47% pregnancy) in autumn (Fig. 15). In both mid-summer and autumn the median number of embryos per pregnant adult was about 7.

SIMULATION MODELS OF FINGERNAIL CLAMS

A simple model was designed to represent Fingernail Clams as being increased by Births and decreased by Deaths (Fig. 16). These in turn respond to BirthFraction and AveLifetime, which are inversely related to FractionOfCapacity. As FractionOfCapacity increases to and exceeds 1, both BirthFraction and AveLifetime will decrease. There are two independent stochastic variables in the model. ClutchSize responds as a discrete POISSON variable, and CarryingCapacity responds as a continuous NORMAL variable. If ClutchSize has a mean of 7, and CarryingCapacity a mean of 500 (with variance = 100), the range of values for these variables is displayed in Fig 17. If both stochastic variables happen to be low, populations will decline, when both are high populations will increase. In runs of 1000 simulations of a 70-year period (1940–2010), it was recorded that a 50% or more change in population size occurred with the following frequencies: about 50% of the runs had this magnitude

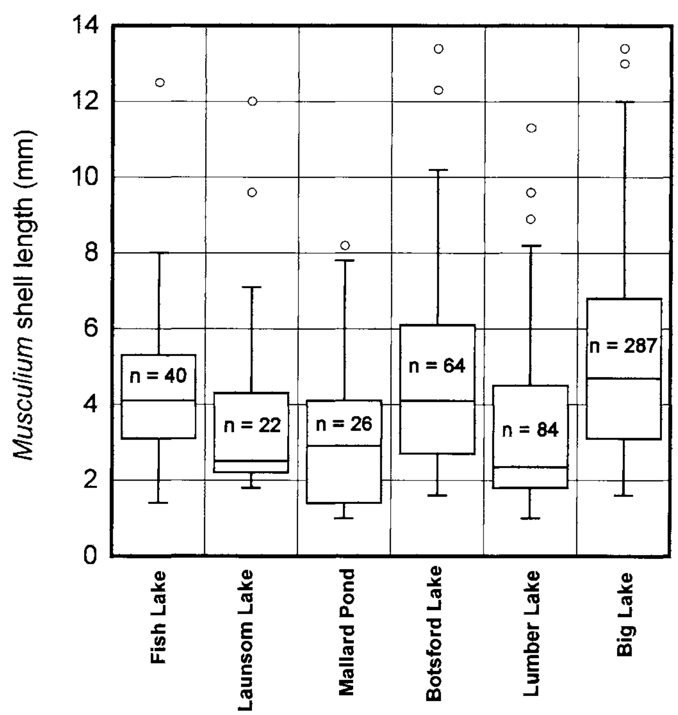

Fig. 14. ***Musculium*** shell lengths from six backwater lakes of Pool 9 sampled mid-summer in 2002. Number of ***Musculium*** measured for each lake shown within the box plot. Adult ***Musculium*** (> 4 mm shell-length) constituted 41% of the population and 19% of the adults were carrying shelled-embryos.

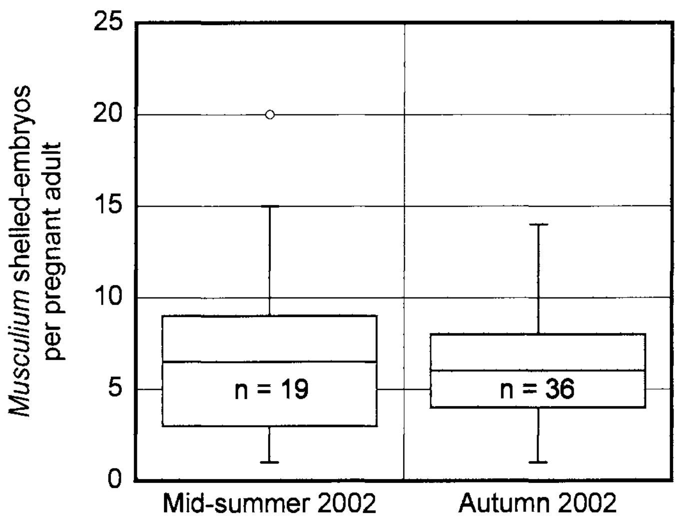

Fig. 15. Number of shelled-embryos in pregnant adult (>4 mm shell length) Musculium in samples from two Pool 9 lakes (Botsford Lake and Big Lake) during mid-summer (July 2 and 3, 2002) and during the fall (September 22, 2002). In mid-summer there were 19 out of 150 adults were carrying shelled embryos (= 13% pregnancy), and in autumn 36 out of 77 adults were carrying shelled embryos (= 47% pregnancy)

change that lasted for 5 or more years, 40% of the runs had this magnitude change that lasted for 6 or more years, and 12% of the runs had this magnitude change that lasted for 8 or more years.

DISCUSSION

The observation of declining populations, with lower numbers persisting for several years, followed by populations that increase, is a pattern that appears to describe *Musculium* populations from widely separate sections of the Upper Mississippi River. A simple simulation model, with two independent stochastic variables, produced a similar pattern in a high proportion of the simulation trials. The model also describes the likely year-to-year variation in population size, although these simulated differences are dependent upon model assumptions. For example, in the model used it was important to have a good estimate of the number of shelled-embryos per pregnant adult.

The higher population densities of live *Musculium* from samples taken from sites having empty shells in the washed samples for LTRMP data from Pool 13 was also true for the 6 backwater lakes sampled in 2002 from Pool 9. Only Big Lake had large numbers of empty shells in the washed samples. Its median *Musculium* numbers per sample were almost 4 times larger than the average for the other 5 lakes in Pool 9. It appears that these clams tend to have the greatest potential for population growth in those habitats that have in the past supported substantial populations.

The high water levels and river flows of the summer 1993 appear to be associated with the initial recovery in *Musculum* populations, after their decline of the late 1980's. Green Lake was the first backwater lake to show a *Musculium* increase following the decline of the late 1980's. Its populations began to show increases in 1992, but that followed a specific rehabilitation project for that lake which took place the previous year. This project resulted in increased water flow through the lake and reduced anaerobic conditions in the lakes sediments. Others have also suggested that flows and water depth become important variables in determining quality habitat for fingernail clams (Gale 1969, Sparks 1980, Eckblad and Lehtinen 1991).

Variation in population sizes, in contrast to a deterministic model predicting a constant population, should be expected with the presence of individual heterogeneity, spatial variation, and temporal variation (Renshaw 1991). Deterministic models that attempt a high degree of realism to describe complex systems may require too many parameters to be of practical use. For example, even restricted models that attempt to deal realistically with how *Musculium* populations are influenced by sediments (e.g., spatial and temporal variation in particle size and degree of toxicity) often require field data that are unavailable and impractical to acquire. In contrast, stochastic models can often

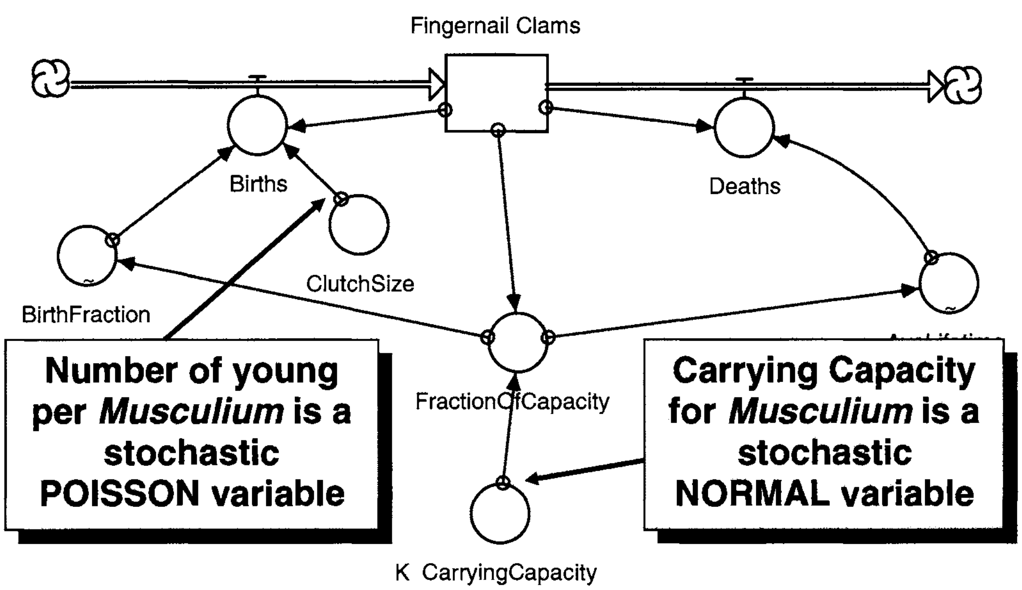

Fig. 16. Model diagram (using *STELLA*) showing two stochastic variables that can influence populations of *Musculium*.

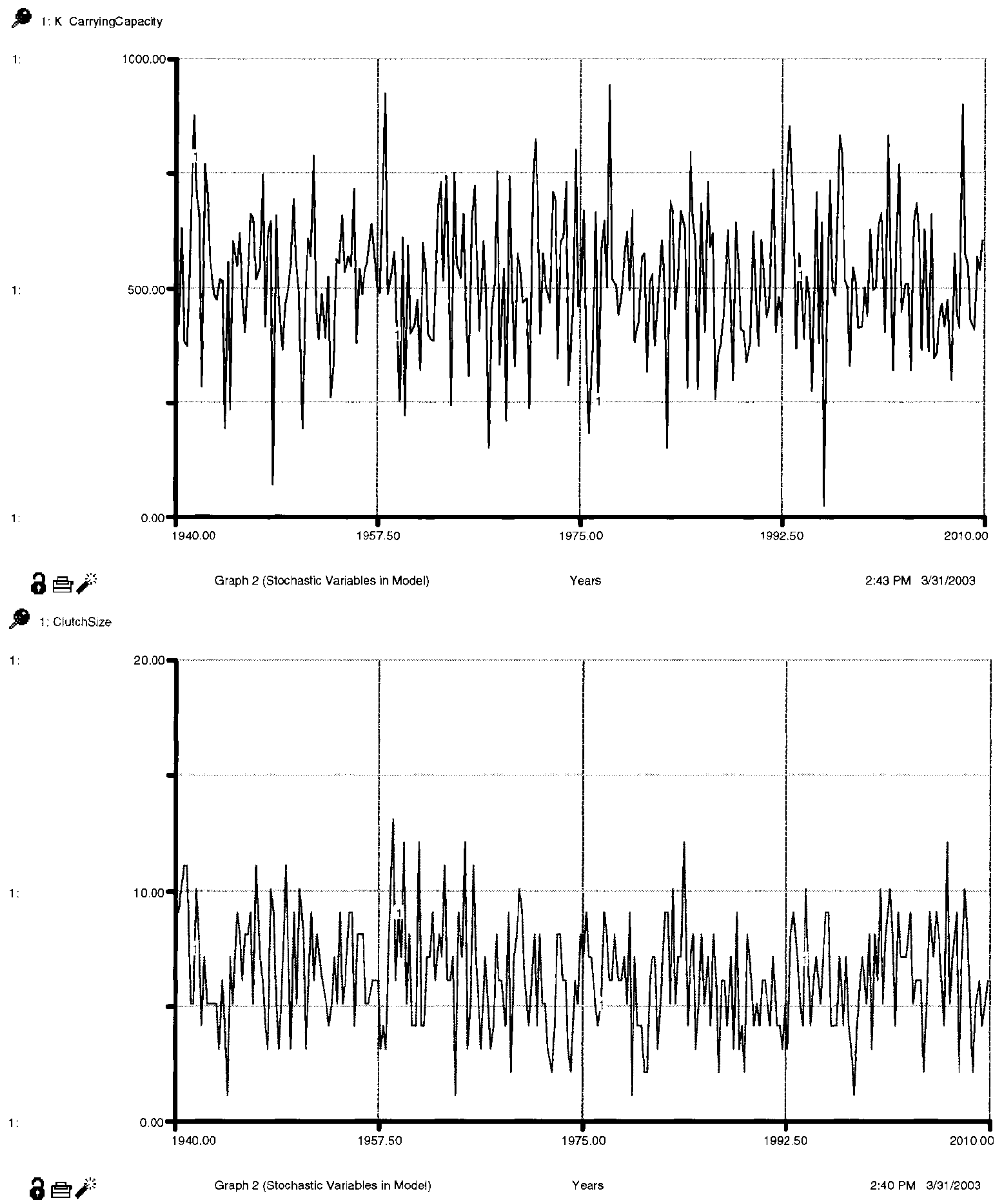

Fig. 17. Simulation over 70-years (1940–2010) showing variation in two stochastic variables in the model; Carrying Capacity (K) at top, and Clutch Size at bottom.

describe the amount of variation expected in a complex system with a smaller number of variables. Deterministic models will continue to be appropriate in the analysis of cause-effect relationships, as noted recently by Shanahan (2003), but the description of complex systems like dynamic river systems may require the tools provided by simulations using stochastic models.

ACKNOWLEDGEMENTS

Portions of this research were supported over a period of years by the National Science Foundation (GY-10703, GY-11302, EPP75-03785, SMI76-03200, SPI-7683830, SPI-8026430, REU-9000762), US Fish and Wildlife Service cooperative agreement 14-16-0003-90947, and the Luther College Faculty Research Fund. A special thanks to Greg Hanson, Karen Horn, Nancy Peterson, Kenneth Ostlie, Anne Temte, Randy Duncan, Gail Esse, Donna Rasmussen, David Welo, Chris Wheatley, Larry Reis, David Bartelt, Andrew Wold, Steven Lehtinen, Jim Lee, Anne Timm, Ryan Doorenbos, David Wente, Eric Merten, Amy Corrigan, Ryan Jepsen, Jessica Sime, Leah Campbell, Jen Weier, Erica Crowser, and Jenny Krepela for assistance in the collection and analysis of data. Also thanks to Jennifer Sauer, USGS-UMESC, for providing the LTRMP *Musculium* data.

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