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POPULATION DYNAMICS OF UNIONID MUSSELS IN LAKE PEPIN, UPPER MISSISSIPPI RIVER, MINNESOTA AND WISCONSIN

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ABSTRACT

Hart, Rick Alan, Ph.D., Department of Zoology, College of Science and Mathematics, North Dakota State University, April 1999. Population Dynamics of Unionid Mussels in Lake Pepin, Upper Mississippi River, Minnesota and Wisconsin. Major Professor: Dr. James W. Grier.

To assess the effects of commercial harvest on *A. plicata* (Say 1817) populations and colonization by *D. polymorpha* (Pallas 1771), population densities and survival of unionid mussels were estimated. From 1990-97, 7 mussel beds were quantitatively sampled to determine mussel densities. Additionally, to measure survival rates, 240 *A. plicata* mussels were marked in each of 3 beds in Lake Pepin. The 3 beds were chosen based on known *D. polymorpha* densities, with each bed having a density of, 0-10, 25-100, or >250 *D. polymorpha*/m^2. For a reference sample, 240 *A. plicata* were marked where no *D. polymorpha* were present in the Otter Tail River, MN. Also, 79 *D. polymorpha* colonized *Fusconaia flava* (Rafinesque 1820) and 240 colonized *Elliptio dilatata* (Rafinesque 1820) mussels were marked in Lake Pepin, while 240 *F. flava* and 113 *Lasmigona costata* (Rafinesque 1820) were marked in the Otter Tail River. Densities of *A. plicata* showed significant declines ($p<0.05$) at 5 of the 7 mussel beds sampled. Densities of non-harvested mussels remained constant in all but one bed. We attribute these declines to commercial harvesting. Mean annual survival of marked *A. plicata* from 1996-98 was significantly greater at beds with low densities or absence of *D. polymorpha* (98%, 99%, and 98%) compared to those heavily colonized (76%) ($\chi^2_{df=3}=93.93$, $p<0.0001$). Survival rates of Otter Tail River *L. costata* and *F. flava* were greater than 99%, while survival of *E. dilatata* and *F.*

flava from Lake Pepin equaled 95% and 90%, respectively. Differences in survivorship of *A. plicata* and *F. flava* were attributed to the high densities of *D. polymorpha*. These survival rates were used in simulations of *A. plicata* populations under varying levels of harvest and *D. polymorpha* colonization. Sensitivity analysis revealed population growth to be most sensitive to alterations in adult survival. Simulations predict that the current levels of mortality attributed to *D. polymorpha* may result in local population extirpations in less than 50 years. Models simulating harvesting revealed that a 5% take of adults may result in population decline of 50% in less than 40 years. This research provided estimates of mean annual survivorship of several mussel species and made new and important contributions to the study of freshwater mussel life-history and population dynamics.

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GENERAL INTRODUCTION

An Explanation of the Dissertation Organization

I separated the dissertation into three individual papers, with each prepared for submission to peer-reviewed biological journals. Because it is anticipated that the papers will be submitted to journals under multiple authorship, I used plural personal pronouns throughout the manuscripts. A literature review precedes the papers.

Mussel Research in the Upper Mississippi River

The mussel communities of the Upper Mississippi River have been researched since the end of the 1800s (Smith 1898). These studies were part of a much broader program initiated by the United States Fish Commission to assess the status of the mussel communities harvested for the manufacturing of pearl buttons (Smith 1898). During the early 20th century, the button manufacturing industry was noted to be a multi-million dollar industry employing over 8,000 people and having gross annual revenues of over $5,000,000. The mussel harvesting that supplied this industry yielded over $800,000 worth of raw shell material and $100,000 worth of natural pearls annually, while employing over 10,000 mussel harvesters (Smith 1919). Therefore, the mere thought of a reduction in the numbers of available mussels for manufacturing was of grave economic concern both to the industry itself and for the economy of at least 20 Mississippi River basin states (Smith 1898, 1919; Southall 1925).

Concern spawned by the potential over-exploitation of the mussel beds initiated the establishment of a biological station in Fairport, Iowa in 1909 (Smith

1919). Research conducted at this biological station produced a wealth of information concerning the life-histories, habitats, and distributions of freshwater mussels. This research is still valuable today, stimulating additional studies of mussel life-history and host fish identification (Watters and O'Dee 1998).

The mussel populations declined (Smith 1919, Southall 1925), and a system for mussel propagation was developed to aid in the recovery of the depleted stocks (Smith 1919). While the pearl button industry was the main reason for declining mussel populations, harvest was not the sole factor leading to the depletion of the mussel beds. Pollution and sedimentation were becoming a widespread problem at some of the mussel beds as early as the late 1800s (Smith 1898, Ellis 1931) and were responsible for the reduction in mussel populations (Ellis 1931). Shortly after declines in the mussel populations became apparent, the manufacturing industry collapsed because plastic buttons were being developed (Williams et al. 1993). Declines in mussel research accompanied the dwindling mussel industry, and new studies were not initiated until concern over habitat modifications, commercial navigation, and pollution in the Mississippi River became apparent (Fuller 1978, Thiel 1981, Miller and Payne 1991).

Recently, several species of freshwater mussels are again being commercially harvested for their use in the cultured pearl industry (Finke 1966, Williams et al. 1993). Mussel shells are now used in the development of pearl nuclei, which when inserted into oysters produce a cultured pearl (Williams et al. 1993). Consequently, there is a renewed interest in the possibility that over-harvesting of certain mussel species may be occurring in portions of the Upper

Mississippi River.

A new threat to freshwater mussels, a non-indigenous species, has also become apparent in the Mississippi River. The exotic zebra mussel, *Dreissena polymorpha* (Pallas 1771) was first discovered in the Laurentian Great Lakes in the 1980s (Hebert et al. 1989) and has since become the dominant benthic organism in some portions of the Lakes (Hebert et al. 1989). *D. polymorpha* are currently well established in the Mississippi River (Tucker et al. 1993), and there is concern that their colonization may cause mortality of native mussels, thus resulting in lowered indigenous mussel population densities (Ricciardi et al. 1998).

We established 2 research goals: 1) to obtain a better understanding of the basic population characteristics and dynamics of a major but poorly known group of freshwater organisms, the unionid mussels; and 2) to provide information and recommendations for management projections and strategies for selected fresh water mussel populations.

These goals were attained by developing the following 3 research objectives: 1) to describe and compare mussel community characteristics in terms of density and diversity at selected mussel beds within Lake Pepin; 2) to determine the occurrence and degree of *D. polymorpha* colonization of unionids at selected sites in Lake Pepin, Minnesota and Wisconsin; and 3) to conduct population viability analysis, incorporating computer simulations, for the commercially harvested mussel species, *Amblema plicata* (Say 1817).

By monitoring the biological components of ecosystems such as mussels, environmental disturbances in the form of harvesting and non-indigenous species competition can be quantified (Green et al. 1989, Hart 1994). This study was conducted integrating conservation biology and population modeling as they relate to the effects of commercial harvesting and non-indigenous species competition.

Literature Cited

Ellis, M. M. 1931. A survey of conditions affecting fisheries in the Upper Mississippi River. United States Bureau of Fisheries 5:1-18.

Finke, A. 1966. Report of a mussel survey in Pools 4A (Lake Pepin), 5, 6, 7, and 9 of the Mississippi River during 1965. Wisconsin Department of Natural Resources, Madison, WI.

Fuller, S. L. H. 1978. Freshwater mussels of the Upper Mississippi River: Observations at selected sites within the 9-foot cannel navigation project on behalf of the U. S. Army Corps of Engineers. Academy of Natural Science, Philadelphia, PA.

Green, R. H., R. C. Bailey, S. G. Hinch, J. L. Metcalfe, and V. H. Young. 1989. Use of freshwater mussels (Bivalvia: Unionidae) to monitor the nearshore environment of Lakes. Journal of Great Lakes Research 15:635-644.

Hart, D. D. 1994. Building a stronger partnership between ecological research and biological monitoring. Journal of the North American Benthological Society 13:110-116.

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.

Miller, A. C., and B. S. Payne. 1991. Effects of increased commercial navigation traffic on freshwater mussels in the Upper Mississippi River: 1989 studies. Technical Report EL-91-3, U.S. Army Corps of Engineers Waterways Experiment Station, Vicksburg, MS.

Ricciardi, A., R. J. Neves, and J. B. Rasmussen. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. Journal of Animal Ecology 67:613-619.

Smith, H. H. 1898. The mussel fishery and pearl-button industry of the Mississippi River. United States Bureau of Fisheries 18:289-314.

Smith, H. M. 1919. Freshwater mussels. A valuable national resource without sufficient protection. United States Bureau of Fisheries 43:1-5.

Southall, J. B. 1925. Mussel survey of Lake Pepin in 1924. With a discussion of the effects of the system of the alternate closure of sections of the lake to the taking of mussels. United States Bureau of Fisheries 57:1-3.

Thiel, P. A. 1981. A survey of unionid mussels in the Upper Mississippi River (Pools 3 through 11). Technical Bulletin Number 124. Department of Natural Resources, Madison, WI.

Tucker, J. K., C. H. Theiling, K. K. Blodgett, and P. A. Thiel. 1993. Initial occurrences of zebra mussels (*Dreissena polymorpha*) on freshwater mussels (Family Unionidae) in the Upper Mississippi River. Journal of Freshwater Ecology 8:245-251.

Watters, G. T., and S. H. O'Dee. 1998. Metamorphosis of freshwater mussel glochidia (Bivalvia: Unionidae) on amphibians and exotic fishes. American Midland Naturalist 139:49-57.

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.

LITERATURE REVIEW

The extinction of plant and animal species is a natural process in geological time, yet some biologists are concerned that the rate of extinctions has increased due to anthropogenic perturbations (Caughley and Gunn 1996). Historically, the causes of extinction have been studied and theorized by biologists. More recently though, the study of the mechanisms which can stem the rate of these declines and elicit recovery of species from the brink of extinction has been termed "conservation biology" (see Caughley and Gunn 1996 and references contained therein).

This new discipline came into being in the 1980s when biologists integrated several theoretical concepts. These concepts included, but were not limited to, the study of metapopulations and the biology of small populations (Caughley and Gunn 1996). The concept of metapopulations became firmly established when Levins (1968) coined the term. While the idea of local populations, i.e., metapopulations of a given species, was not entirely new when he used the term, Levins (1968) synthesized the concept. Levins (1968) noted that a metapopulation can be thought of as any population that is a population of local populations which are established by colonists, survive for a while, send out migrants, and eventually disappear. Levins' (1968) development of mathematical models described how the theory worked, relative to the dynamics of the metapopulation. While Levins' (1968) model has been characterized by some as being simplistic in nature (Harris 1991), it does offer the researcher the ability to explore qualitative changes in population structure (Caughley and Gunn 1996).

Naturally occurring rare species may commonly live as small groups in habitat patches; therefore, these species may have narrow habitat preferences making them susceptible to extinctions, especially in the face of habitat fragmentation. These types of plants or animals are usually regarded as the classic rare species and are most often found in relatively low population numbers (Hunter 1996). The study of these small populations has become more common in the field of conservation biology.

It has been found that if population densities are stationary yet low, their survival is still uncertain (Lacy et al. 1995). The uncertainty of their survival is attributed to insufficient genetic diversity necessary for them to evolve in the face of changing conditions. Small populations are also more susceptible to random, environmental occurrences that may remove some members of the population (Lacy et al. 1995). Research on these small populations has led to the development of the population viability analysis (PVA) (Soulé 1987).

PVAs are primarily conducted to identify and evaluate the importance of factors that may place the survival of a particular population at risk (Soulé 1987). Computer programs within PVAs are used to simulate the effects that alterations in demographic and environmental parameters may have on extinction rates, as well as the retention of genetic diversity, of the studied populations (Soulé 1987).

Various types of simulations have been developed for the study of population behavior. Models that have been used extensively for PVA include analytical models, deterministic single-population models, stochastic single-population models, and metapopulation models (Beissinger and Westphal 1998).

The following models, as described by Beissinger and Westphal (1998) and Grier (1991), provide some examples of the historical and current trends in population modeling.

Analytical models have often been used to explore a particular system's behavior rather than to make quantitative predictions. Conversely, the predictive and more commonly used deterministic models are generally thought of as easy to use and are often employed in the PVA process. These models usually use matrix analysis or life tables to estimate the growth rate of a particular population under a given set of demographic parameters (Grier 1991, Krebs 1994, Beissinger and Westphal 1998). A drawback to these models is the assumption that demographic rates are constant throughout the simulation. This assumption is often violated and, therefore, has resulted in the development of stochastic models that introduce random events into the simulation model (Beissinger and Westphal 1998).

The introduction of stochasticity into simulations increases the reality of the model by incorporating chance events. The incorporation of randomness into the simulation may have large effects on population growth, most especially for small populations (Grier 1991, Lacy et al. 1995). Beissinger and Westphal (1998) noted that the aforementioned models do not allow for the exchange of immigrants and emigrants between sub-populations. This shortfall has been overcome by the recent advent of metapopulation models (Lacy et al. 1995, Beissinger and Westphal 1998 and references contained therein).

These models allow for the exchange of individuals between patches of suitable habitats, which adds an additional dimension to the simulation (Price and

Gilpin 1996). These simulations appear to offer a more realistic approach because they allow the investigator to alter the underlying patterns of the landscape, therefore changing the habitat quality a metapopulation may inhabit. The alterations can then be evaluated to determine how they affect dispersal of immigrants and emigrants into other habitat patches (Beissinger and Westphal 1998).

On a cautionary note, PVA models need to be considered as a tool and not the end point in a particular species recovery (Beissinger and Westphal 1998). Beissinger and Westphal (1998) also stress that PVA can be helpful in decision making concerning the screening of various hypotheses for the causation of population declines and in assessing various management options. Unfortunately, PVAs and their accompanying computer simulations do not have the capability to predict for certain when a species will go extinct under given conditions (Beissinger and Westphal 1998). Therefore, the computer simulations used in PVAs should not be considered a substitute for well-designed field studies that may determine extinction causation or validate a particular PVA simulation. The simulations should be considered as an additional tool to stem the rate of population and species extinctions (Beissinger and Westphal 1998).

The study of conservation biology and the resulting PVAs emerged from the desire to stem extinctions caused by anthropogenic distrubances such as habitat fragmentation or over harvest. Recently though, a new problem confronting conservation biologists is the continued introduction of non-indigenous species into new habitats (Hunter 1996). With the increase in human travel throughout the world, the rate of non-indigenous species introductions has greatly accelerated from the 1800s to present (Hunter 1996).

Non-indigenous species usually act in a much different manner than do other perturbations to natural communities (Hunter 1996). Conventional disturbances more common to communities, i.e., habitat fragmentation, pollution, or harvesting, usually act on a more gradual time scale. Conversely, some non-indigenous species impacts have been documented to act in a more rapid fashion. Non-indigenous species may negatively impact native fauna primarily because the indigenous species do not have any natural defenses against them (Hunter 1996).

The introduction of the fire ant, *Solenopsis invicta,* into the southern United States in the 1940s is a classic example of the havoc that can be created from the introduction of alien species. It is believed these ants were introduced into southern Alabama when a cargo vessel from Brazil delivered its ant-containing ballast to the port.

Fire ants spread through areas of the southern U.S. killing virtually every small animal they encountered, thus causing population declines of several species (Sikes and Arnold 1986, Allen et al. 1997). Currently, they inhabit nine southern states, being found in some areas with densities as great as 7.8 million ants per acre, or 179 individuals per square foot. These large colonies of ants have been noted to be extremely aggressive, attacking anything that poses a threat to the colony. Allen et al. (1997) reported that high densities of fire ants were responsible for lowered recruitment of white-tailed deer fawns into some Texas populations. While Allen et al. (1997) were the first to document direct deleterious effects of fire ants on large mammalian fauna, populations of small mammals species have been decimated in some areas where dispersing or foraging ants are present in large numbers (Smith et al. 1990).

Another non-indigenous species that acts in a manner somewhat similar to fire ants, i.e., directly and aggressively killing native fauna, is the sea lamprey, *Petromyzon marinus*. The parasitic sea lamprey, which is native to the North Atlantic Ocean, entered portions of the Great Lakes in the late 1800s and early 1900s and eventually colonized the entire Great Lakes region in the mid-to-late 1930s (Smith and Tibbles 1980). The fish now appears to be a permanent member of the aquatic community and is a great concern for conservation biologists.

The combination of sea lampreys and commercial fishery harvests led to a collapse of the lake trout, *Salvelinus namaycush,* fishery by the mid-to-late 1950s in most of the Great Lakes (Hansen et al. 1995). As the trout population diminished, sea lamprey attacks on other species of fish increased and ultimately led to great changes in the aquatic biota of the Great Lakes (Hansen et al. 1995). This collapse of the lake trout populations led to the closing of fishing seasons in Lake Superior in 1962 (Hansen et al. 1994). Only after some control measures of the sea lamprey were deemed successful was the lake reopened to fishing (Hansen et al. 1994). While sea lamprey control has been somewhat successful in reducing this non-indigenous species, another invader, the zebra mussel, or *Dreissena polymorpha*, was introduced into the Great Lakes in the late 1980s.

The mechanisms for the impacts of the exotic zebra mussel are much different than the fire ants and sea lampreys. Fire ants and sea lamprey impacts are primarily direct in that they seem to act on only one community member at a time. Conversely, zebra mussel effects are both direct and indirect to the native fauna. Zebra mussels directly impact native fauna by completely covering the substrate of the colonized lake or river (MacIsaac 1996). In some impacted areas, they literally encrust benthic organisms, such as native mussels and crayfish, leading to starvation, suffocation, and loss of mobility (MacIsaac 1996). Indirect effects include the colonization of historical spawning beds of fish species such as walleye, *Stizostedion vitreum* (Fitzsimmons et al. 1995), and alterations of entire food webs in the aquatic community due to the filtration of zoo- and phytoplankton from the water column (Padilla et al. 1996, Pace et al. 1998).

Recently, tools such as population viability analysis incorporating computer modeling offer hopeful possibilities in the study of non-indigenous species impacts. Therefore, in this research we used freshwater mussels as a model to incorporate some aspects of conservation biology and computer simulations to investigate the potential impact that a particular non-indigenous species, the zebra mussel, may have on populations of indigenous mussels.

Freshwater mussels are important components of aquatic ecosystems, where they function in the cycling of nutrients, in stream bed stabilization, and as a food source for several species of fish and mammals (McMahon 1991). Yet, mussels are one of North America's most imperiled groups of fauna. Williams et al. (1993) reported that of the 297 known taxa of freshwater mussels, 213 are listed as endangered, threatened, or of special concern.

The main causes for the decline in mussel populations are habitat destruction caused by the construction of dams, stream channelization, siltation, over-harvesting, and competition with non-indigenous species (Williams et al. 1993). Since post European settlement of North America, the Upper Mississippi River system has experienced all of these environmental disturbances to some degree.

The Upper Mississippi River underwent extensive changes in the 1930s when the U.S. Army Corps of Engineers installed the lock and dam system that is now in place. These dams and similar dams, and their resulting impoundments on other river systems have resulted in the extirpation of 30 to 60% of the original mussel fauna residing in the impacted areas (Williams et al. 1992, Layzer et al. 1993, Williams et al. 1993, Watters 1996). Habitats upstream of the dams become prone to increased sedimentation, while downstream habitats may experience accelerated bed cutting, due to lowered bed loads, thus making these areas unsuitable for several mussel species (Stansbery 1970, Salmon and Green 1983).

Wilson and Danglade (1914) reported that the benthic habitats in the mid-lake areas of Lake Pepin, Upper Mississippi River, Minnesota and Wisconsin, consisted primarily of coarse gravel. More recently and coincidental with an increase in agriculture activity, the mid-lake areas of Lake Pepin have been characterized as completely silt covered (Ellis 1931) and devoid of mussels (Thiel 1981). This increase in the sediment load and the loss of mussels in these habitats are most likely the result of agricultural runoff (Ellis 1931, Thiel 1981).

While habitat destruction has been suggested to cause wide scale losses of mussel species, the commercial harvesting of mussels has been implicated in the localized loss and declines of populations (Williams et al. 1993). Early freshwater mussel surveys were primarily concerned with locating large mussel beds suitable for harvest for the pearl button industry (Wilson and Danglade 1914). Freshwater mussels within these beds were then harvested and their shells made into pearl buttons (Smith 1898). In the early 1900s, mussels were harvested in such large numbers from Lake Pepin that they were transported to button factories by the railroad car load (Southall 1925). Southall (1925) reported that such large harvests ultimately resulted in significant declines in population size and structure. These declines precipitated the establishment of harvesting restrictions within Lake Pepin, which included such measures as alternate closures of some areas of the lake and an increase in research to quantify the impacts of harvesting on the resident mussels (Southall 1925). A mussel propagation program was also initiated in Lake Pepin beginning in 1912 and continuing into the 1920s. The intent of this project was to offset harvesting pressures by successfully rearing and stocking young mussels into portions of the lake (Southall 1925). Harvesters working in areas that had recently been reopened in Lake Pepin in the 1920s were collecting up to 2,000 pounds of mussels daily.

Research on the Lake Pepin mussel populations diminished by the 1940s because of the development of plastics for the manufacturing of buttons, thus making the harvesting of mussels unnecessary. After the collapse of the pearl button industry due to the advent of inexpensive plastics, mussel research on Lake Pepin did not occur with any regularity until the 1960s when the demand for mussel shells increased for the Japanese cultured pearl industry (Finke 1966). In the 1960s, several species of thick-shelled, freshwater mussel species such as *Amblema plicata* (Say 1817), *Megalonaias nervosa* (Rafinesque 1820), and many others were used in the manufacturing of pearl nuclei for the cultured pearl industry (Williams et al. 1993).

While it has been reported that controlled harvests may not deplete mussel stocks, over-harvesting can adversely affect unionid populations (Smith 1919). Some populations of mussels no longer legally collected may still be experiencing the impacts of being harvested during the early 1900s (Thiel 1981). Fuller (1978) speculated that the butterfly mussel, *Ellipsaria lineolata*, the mucket, *Actinonaias ligamentina*, and the yellow sandshell, *Lampsilis teres,* are present only in low numbers due, in part, to past over-harvest. Fuller's (1978) data may not be comparable to previous work as his data were collected using qualitative methods. While there is concern that over-harvesting may be occurring in some mussel populations, a more recent threat to the viability of mussel populations is competition with the recently introduced zebra mussel (*Dreissena polymorpha* Pallas 1771).

Freshwater mussel populations may decline due to the colonization of zebra mussels (Gillis and Mackie 1994, Schloesser et al. 1998). Gillis and Mackie (1994) reported that colonization of zebra mussels on unionids in Lake St. Clair increased from 143 zebra mussels per unionid in 1989 to 642 zebra mussels per unionid in 1990. They believed this infestation caused a dramatic decline in native mussel density and species richness (Gillis and Mackie 1994, Schloesser et al. 1996).

Zebra mussels affect unionids by covering any exposed area of the native mussel's shell, eventually causing death due to increased vulnerability to parasitism, interference with locomotion, and starvation (Gillis and Mackie 1994).

The Mississippi River system contains a large number of federal- and state-listed threatened and special concern mussel species (Williams et al. 1993), with these species being primarily in peril due to human disturbances such as habitat destruction and over-harvesting (Williams et al. 1993). Therefore, it is probable that if *D. polymorpha* impact unionids in this river system like they have in other water bodies, more populations of North American mussels will become extirpated from their historical habitats (Gillis and Mackie 1994, Ricciardi et al. 1998, Schneider et al. 1998).

Literature Cited

Allen, R. G., S. Demarai, and R. S. Lutz. 1997. Effects of red imported fire ants on recruitment of white-tailed deer fawns. Journal of Wildlife Management 61:911-916.

Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62:821-841.

Caughley, G., and A. Gunn. 1996. Conservation Biology in Theory and Practice. Blackwell Science, Cambridge, MA.

Ellis, M. M. 1931. A survey of conditions affecting fisheries in the Upper Mississippi River. United States Bureau of Fisheries 5:1-18.

Finke, A. 1966. Report of a mussel survey in Pools 4A (Lake Pepin), 5, 6, 7, and 9 of the Mississippi River during 1965. Wisconsin Department of Natural Resources, Madison, WI.

Fitzsimmons, J. D., J. H. Leach, S. J. Nepszy, and V. W. Cairns. 1995. Impacts of zebra mussel on walleye *(Stizostedion vitreum*) reproduction in western Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 52:578-586.

Fuller, S. L. H. 1978. Freshwater mussels of the Upper Mississippi River: Observations at selected sites within the 9-foot channel navigation project on behalf of the U.S. Army Corp of Engineers. Academy of Natural Science, Philadelphia, PA.

Gillis, P. L., and G. L. Mackie 1994. Impact of the zebra mussel, *Dreissena polymorpha*, on populations of Unionidae (Bivalvia) in Lake St. Clair. Canadian Journal of Zoology 72:1260-1271.

Grier, J. W. 1991. Population modeling: An introduction and overview. In Proceedings Midwest Raptor Management Symposium and Workshop. National Wildlife Federation, Washington, DC.

Hansen, M. J., M. P. Ebener, R. G. Schorfhaar, S. T. Schram, D. R. Schreiner, and J. H. Selgeby. 1994. Declining survival of lake trout stocked during 1962-1986 in U.S. waters of Lake Superior. North American Journal of Fisheries Management 14:395-402.

Hansen, M. J., R. G. Schorfhaar, J. W. Peck, J. H. Selgeby, and W. W. Taylor. 1995. Abundance indices for determining the status of lake trout restoration in Michigan waters in Lake Superior. North American Journal of Fisheries Management 15:830-837.

Harris, S. 1991. Local extinction in a metapopulation context: An empirical evaluation. Biological Journal of the Linnean Society 42:73-88.

Hunter, M. L. 1996. Fundamentals of Conservation Biology. Blackwell Science, Cambridge, MA.

Krebs, C. J. 1994. Ecology: The Experimental Analysis of Distribution and Abundance, fourth edition. HarperCollins College Publishers, New York, NY.

Lacy, R. C., K. A. Hughes, and P. S. Miller. 1995. VORTEX: A stochastic simulation of the extinction process. Version 7 users manual. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Layzer, J. B., M. E. Gordon, and R. M. Anderson. 1993. Mussels: The forgotten fauna of regulated rivers. A case study of the Caney Fork River. Regulated Rivers: Research and Management 8:63-71.

Levins, R. 1968. Evolution in Changing Environments: Some Theoretical Explorations. Monograph in Population Biology, Princeton University Press, Princeton, NJ.

MacIsaac, H. J. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. American Zoologist 36:287-299.

McMahon, R. F. 1991. Mollusca: Bivalvia. In Ecology and Classification of North American Freshwater Invertebrates. J. H. Thorpe and A. C. Covich, eds. Academic Press, San Diego, CA.

Pace, M. L., S. E. G. Findlay, and D. Fischer. 1998. Effects of an invasive bivalve on the zooplankton community of the Hudson River. Freshwater Biology 39:103-116.

Padilla, D. K., S. C. Adolph, K. C. Cottingham, and D. W. Schneider. 1996. Predicting the consequences of dreissenid mussels on a pelagic food web. Ecological Modeling 85:129-144.

Price, M. V., and M. Gilpin. 1996. Modelers, mammalogists, and metapopulations: Designing Stephens' kangaroo rat reserves. In Metapopulation and Wildlife Conservation. D. R. McCullough, ed. Island Press, Washington, DC.

Ricciardi, A., R. J. Neves, and J. B. Rasmussen. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. Journal of Animal Ecology 67:613-619.

Salmon, A., and R. H. Green. 1983. Environmental determinants of unionid clam distribution in the Middle Thames River, Ontario. Canadian Journal of Zoology 1:832-838.

Schloesser, D. W., W. P. Kovalak, G. D. Longton, K. L. Ohnesorg, and R. D. Smithee. 1998. Impact of zebra and quagga mussels (*Dreissena* spp.) On freshwater unionids (Bivalvia: Unionidae) in the Detroit River of the Great Lakes. American Midland Naturalist 140:299-313.

Schloesser, D. W., T. F. Nalepa, and G. L. Mackie. 1996. Zebra mussel infestation of unionid bivalves (Unionidae) in North America. American Zoologist 36:300-310.

Schneider, D. W., S. D. Ellis, and K. S. Cummings. 1998. A transportation model assessment of the risk to native mussel communities from zebra mussel spread. Conservation Biology 12:788-800.

Sikes, P. J., and K. A. Arnold. 1986. Red imported fire ant (*Solenopsis invicta*) predation on cliff swallow (*Hirundo pyrrhonata*) nestlings in east-central Texas. Southwestern Naturalist 31:105-106.

Smith, B. R., and J. J. Tibbles. 1980. Sea lampreys (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: History of invasion and control, 1936-78. Canadian Journal of Fisheries and Aquatic Sciences 37:1780-1801.

Smith, H. M. 1898. The mussel fishery and pearl-button industry of the Mississippi River. Bulletin of the United States Fish commission. 18:289-314.

Smith, H. M. 1919. Freshwater mussels, a valuable national resource without sufficient protection. United States Bureau of Fisheries 43:1-5.

Smith, T. S., S. A. Smith, and D. J. Schmidly. 1990. Impact of fire ant (*Solenopsis invicta*) density on northern pygmy mice (*Baiomys taylori*). Southwestern Naturalist 35:158-162.

Soulé, M. E. 1987. Viable Populations for Conservation. Cambridge University Press, New York, NY.

Southall, J. B. 1925. Mussel survey of Lake Pepin in 1924. With a discussion of the effects of the system of the alternate closure of sections of the lake to the taking of mussels. United States Bureau of Fisheries 57:1-3.

Stansbery, D. H. 1970. Eastern freshwater mollusks (I); the Mississippi and St. Lawrence River systems. Malacologia 10:9-22.

Thiel, P. A. 1981. A survey of unionid mussels in the Upper Mississippi River (Pools 3 through 11). Technical Bulletin Number 124. Department of Natural Resources, Madison, WI.

Watters, G. T. 1996. Small dams as barriers to freshwater mussels (Bivalvia: Unionoida) and their hosts. Biological Conservation 75:79-85.

Williams, J. D., S. L. H. Fuller, and R. Grace. 1992. Effects of impoundments on freshwater mussels (Mollusca: Bivalvia: Unionidae) in the main channel of the Black Warrior and Tombigbee rivers in Western Alabama. Bulletin of the Alabama Museum of Natural History 13:1-10.

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 E. Danglade. 1914. The mussel fauna of central and northern Minnesota. United States Bureau of Fisheries 803:1-26.

PAPER 1. CHANGES IN FRESHWATER MUSSEL COMMUNITIES IN LAKE PEPIN, UPPER MISSISSIPPI RIVER, MINNESOTA AND WISCONSIN

ABSTRACT

Density and size demography of unionid mussel populations were quantitatively measured at 7 mussel beds in Lake Pepin, Upper Mississippi River, Minnesota and Wisconsin, beginning in 1990. Densities of the commercially harvested threeridge mussel, *Amblema plicata* (Say 1817), declined at 5 of the 7 mussel beds sampled. The most dramatic decline occurred at the Hok Si La, Minnesota mussel bed where average densities of *A. plicata* equaled about 22 mussels/m^2 in 1993, declining to less than 6/m^2 from 1995-97 ($F=14.940_{df=4}$, $P<0.0001$). Densities of non-harvested mussel species remained stationary at all but 1 bed during this research. Shell height distributions for *A. plicata* indicate that there is little or no recent recruitment evident within the sampled mussel beds of Lake Pepin. These data implicate commercial harvest as a contributing factor in the decline of *A. plicata*. During this study, zebra mussels (*Dreissena polymorpha* Pallas 1771) became established in Lake Pepin. The greatest density of *D. polymorpha* was found at the King's Coulee, Minnesota, site. Densities of *D. polymorpha* have been steadily increasing within this bed since 1995, reaching average densities of over 4,000 mussels/m^2 in 1997.

INTRODUCTION

Lake Pepin, Upper Mississippi River, historically harbored a diverse freshwater mussel assemblage (Wilson and Danglade 1914, Southall 1925, Ellis 1931), most of which inhabited a large bed near the outlet of the lake. A decline in native mussel population densities in Lake Pepin began in the early 1900s and has been attributed to commercial harvest, water pollution, and habitat degradation (Southall 1925, Ellis 1931, Fuller 1978, Thiel 1981).

The harvesting of freshwater mussels from lakes and streams in the United States, beginning in the 1890s, was primarily for the manufacture of pearl buttons. More recently, mussels have been harvested, their shells cut into cubes, and then tumbled into pearl nuclei. These nuclei are then inserted into oysters which form cultured pearls. Because various species of mussels residing in Lake Pepin are valuable, and therefore harvested for the cultured pearl industry, there is concern that over-harvesting may be occurring. Fuller (1978) and Williams et al. (1993) speculated that declines in certain populations of mussels can be directly related to over-harvesting, with these mussels now present in low numbers due to their inability to recover from historical harvesting pressures.

While harvesting removes individuals of select species, a more recent threat to all unionid mussels species is caused by the introduction of the zebra mussel, *Dreissena polymorpha* (Pallas 1771). With the recent introduction of *D. polymorpha* into Lake Pepin, there is a concern that it may cause declines in native mussel populations in the Upper Mississippi River as it has in other regions of North America (Ricciardi et al. 1995, 1998).

Because of concern that over-harvest of certain species of unionid mussels may be occurring within Lake Pepin, a long-term monitoring study of the selected freshwater mussel beds was initiated in 1990. Monitoring was initiated to provide quantitative data to allow for the assessment of harvesting. An added dimension of this monitoring program became necessary with the increase of *D. polymorpha* densities within the lake. Therefore, this research was conducted to assess the impacts of harvest on threeridge mussels, *A. plicata*, within Lake Pepin and to determine the intensity of the recent invasion of *D. polymorpha*.

METHODS

Study Sites

Lake Pepin, on the border between Minnesota and Wisconsin, is a natural lake within the Mississippi River. The lake begins at approximately river mile (RM) 787 and extends to about RM 763.5 near Read's Landing, Minnesota (Fig. 1.1). This lake is formed by a natural sand dam that is created where the Chippewa River drops its bed load at the confluence with the Mississippi River.

Seven unionid mussel beds were sampled from 1990 to 1997 in Lake Pepin, Minnesota (Fig. 1.1). Sampled beds located within Lake Pepin were located near Fredrich's Point at RM 784.2, Methodist Point at RM 779.2, Hok Si La at RM 776, Erickson's Point at RM 775.5, Waterman's at RM 774, King's Coulee at RM 767.2, and at the outlet of Lake Pepin along the Wisconsin shore at Lacupolis, RM 764.5.

Mussel Sampling

All mussel sampling was conducted by divers using scuba. Mussel beds thought suitable for sampling were investigated by divers during reconnaissance dives during the initial phases of the study. Divers initially estimated mussel density, species composition, and substrate composition. If mussel density was greater than about 5 mussels/m^2, the bed was deemed suitable for intensive quantitative mussel sampling.

Quantitative quadrat samples were collected at all 7 beds. At each bed, 3 subsites were randomly chosen for sampling. At each subsite, 10 randomly

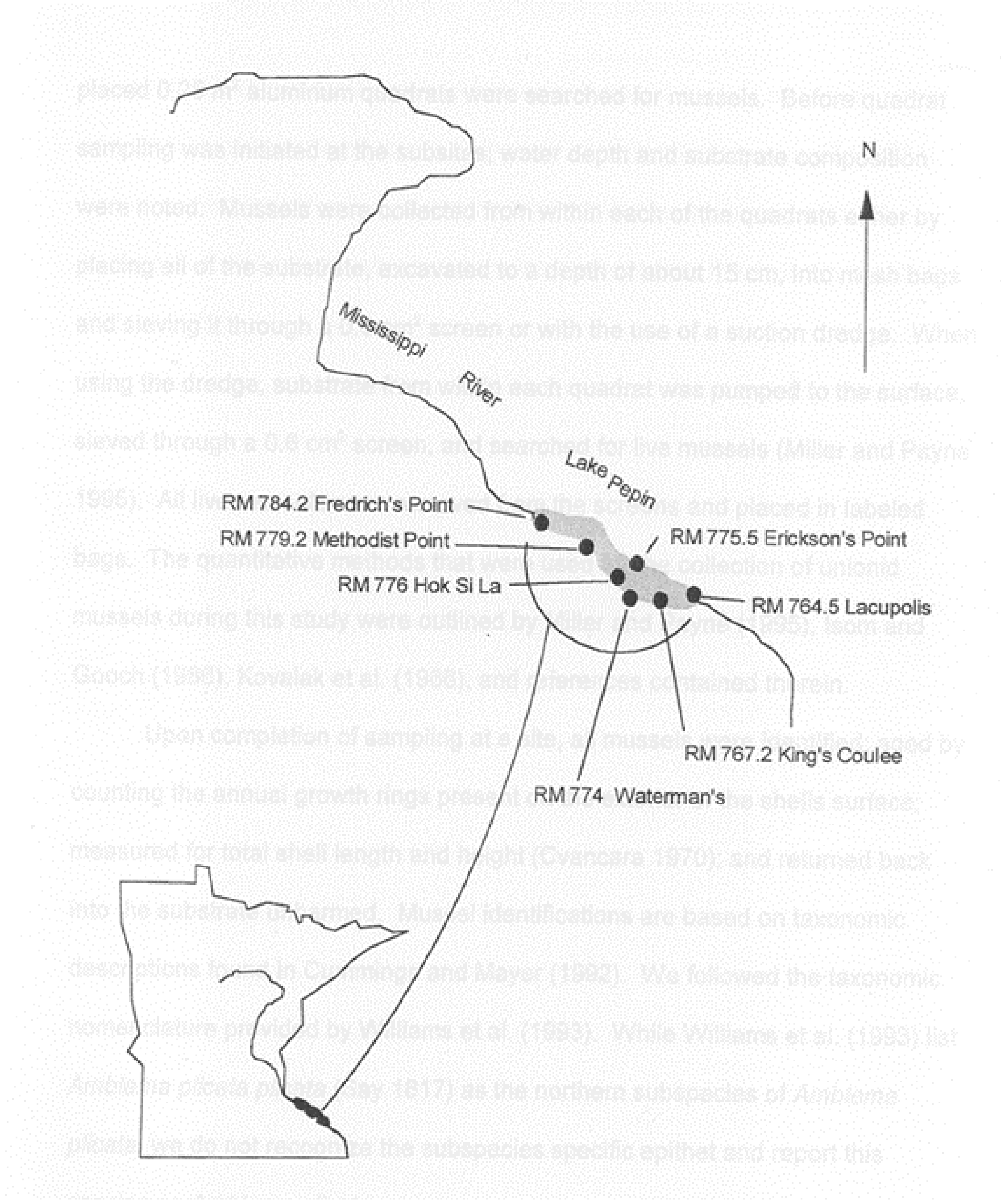

Figure 1.1. Lake Pepin location and quantitiative sampling sites.

placed 0.25 m^2 aluminum quadrats were searched for mussels. Before quadrat sampling was initiated at the subsites, water depth and substrate composition were noted. Mussels were collected from within each of the quadrats either by placing all of the substrate, excavated to a depth of about 15 cm, into mesh bags and sieving it through a 0.6 cm^2 screen or with the use of a suction dredge. When using the dredge, substrate from within each quadrat was pumped to the surface, sieved through a 0.6 cm^2 screen, and searched for live mussels (Miller and Payne 1995). All live mussels were removed from the screens and placed in labeled bags. The quantitative methods that were used for the collection of unionid mussels during this study were outlined by Miller and Payne (1995), Isom and Gooch (1986), Kovalak et al. (1986), and references contained therein.

Upon completion of sampling at a site, all mussels were identified; aged by counting the annual growth rings present on the exterior of the shells surface; measured for total shell length and height (Cvancara 1970); and returned back into the substrate unharmed. Mussel identifications are based on taxonomic descriptions found in Cummings and Mayer (1992). We followed the taxonomic nomenclature provided by Williams et al. (1993). While Williams et al. (1993) list *Amblema plicata plicata* (Say 1817) as the northern subspecies of *Amblema plicata*, we do not recognize the subspecies specific epithet and report this species as *Amblema plicata*.

A one-way analysis of variance and a post-hoc Tukey's multiple comparison technique were used to detect changes in mussel density over the course of this study. Relationships between *A. plicata* mussel age, shell length, and shell height were analyzed with the use of regression analysis (Zar 1984). Linear, power, logarithmic, and exponential regression equations were investigated, and the equations expressing the best-fit to the data are presented (Smock 1980).

RESULTS

Mussel Population Density and Size Demography

Twenty-nine species of unionid mussels were collected from the 7 mussel beds over the 8 years of this study. The Lacupolis bed had the highest species richness when compared to the other sites. This bed had 29 species compared to only 12 living species at Methodist Point (Table 1.1). Total mussel density for all species in the community ranged from a high of $>70/m^2$ at the Lacupolis bed in 1993 to $< 8/m^2$ at the Waterman's bed in 1996.

Since the mussel beds were not originally selected on a random basis and because the main goal of the research was to quantify changes within versus among mussel beds, I did not conduct statistical analysis on the differences between beds. Therefore, the analysis of mussel community changes are on a bed-by-bed basis, presented with the most upstream beds and progressing sequentially to the most downstream bed. Also, while there may have been numerous mussel species collected from a particular bed, I only conducted statistical analysis on those members of the community that were present in sufficient enough numbers to warrant analysis. The dominant mussel species in most of the mussel communities were the threeridge, *A. plicata*, the wabash pigtoe, *Fusconaia flava* (Rafinesque 1820), and the three-horn wartyback, *Obliquaria reflexa* Rafinesque 1820. The Lacupolis bed, which had the most mussel species of all beds studied, had an additional species that was statistically analyzed, the spike, *Elliptio dilatata* (Rafinesque 1820). Most of the other mussel

Table 1.1. Unionid mussel species collected in quantitative and qualitative samples from Lake Pepin, Minnesota and Wisconsin.

	Sites[1]						
Mussel Species	1	2	3	4	5	6	7
Subfamily Ambleminae							
Megalonaias nervosa	x	x	x		x		x
Tritogonia verrucosa							x
Quadrula quadrula	x						x
Quadrula metanevra					x		x
Quadrula pustulosa	x	x	x	x	x	x	x
Amblema plicata	x	x	x	x	x	x	x
Fusconaia flava	x	x	x	x	x	x	x
Cyclonaias tuberculata							x
Pleurobema coccineum					x		x
Elliptio dilatata			x	x	x	x	x
Subfamily Anodontinae							
Utterbackia imbecillis	x	x	x	x	x		x
Pyganodon grandis		x	x			x	x
Stophitus undulatus			x		x		x
Alasmidonta marginata							x
Lasmigona complanata							x
Lasmigona costata							x
Subfamily Lampsilinae							
Obliquaria reflexa	x	x	x	x	x	x	x
Actinonaias ligamentina							x
Ellipsaria lineolata							x
Obovaria olivaria				x			x
Truncilla truncata	x	x	x	x	x	x	x
Truncilla donaciformis							x
Leptodea fragilis	x	x		x			x
Potamilus ohiensis	x	x	x	x	x	x	x
Potamilus alatus	x		x	x	x	x	x

Table 1.1 (continued).

Mussel Species	Sites[1] 1	2	3	4	5	6	7
Subfamily Lampsilinae							
Toxolasma parvus	x		x	x	x	x	x
Ligumia recta			x	x	x	x	x
Lampsilis siliquoidea	x	x	x	x	x	x	x
Lampsilis cardium	x	x	x	x	x	x	x
Total number of species collected	14	12	16	15	17	13	29

[1] Site 1 = Fredrich's Point, site 2 = Methodist Point, site 3 = Hok Si La, site 4 = Erickson's Point, site 5 = Waterman's, site 6 = King's Coulee, and site 7 = Lacupolis.

beds also had populations of the exotic zebra mussel, *D. polymorpha*, present in large enough numbers to warrant analysis.

Fredrich's Point, Minnesota

Fourteen species of mussels were collected from quantitative samples at Fredrich's point (Table 1.1). When population density was calculated for all of the mussel species residing in the community, there was no significant difference from 1995-97, $F=2.677_{df=2}$, $p=0.073$, (Fig. 1.2, Table 1.2). The apparent stability for this mussel community was also evident when individual mussel species populations were analyzed.

Densities of commercially harvested and protected mussel species did not show any appreciable changes in population density from 1995-97. Densities of the commercially valuable *A. plicata* did not show any signs of population changes from 1995-97 ($F=0.809_{df=2}$, $P=0.448$) (Fig. 1.2, Table 1.2). Legal-sized *A. plicata*, those greater than 70 mm in shell height, and individuals of sub-legal size did not show any significant changes in population densities, $F=0.617_{df=2}$, $p=0.541$, and $F=0.792_{df=2}$, $p=0.456$, respectively (Fig. 1.2). Size distributions of *A. plicata* indicate that there may be low levels of juvenile recruitment into the population. While individuals smaller than about 40 mm in shell height were collected throughout the 3 years this bed was sampled, they do not compose a large portion of the population (Fig. 1.3).

Densities of *Fusconaia flava* declined in 1997 compared to 1996, yet there was no significant difference in densities between 1995 and 1997 ($F=7.065_{df=2}$, GiF

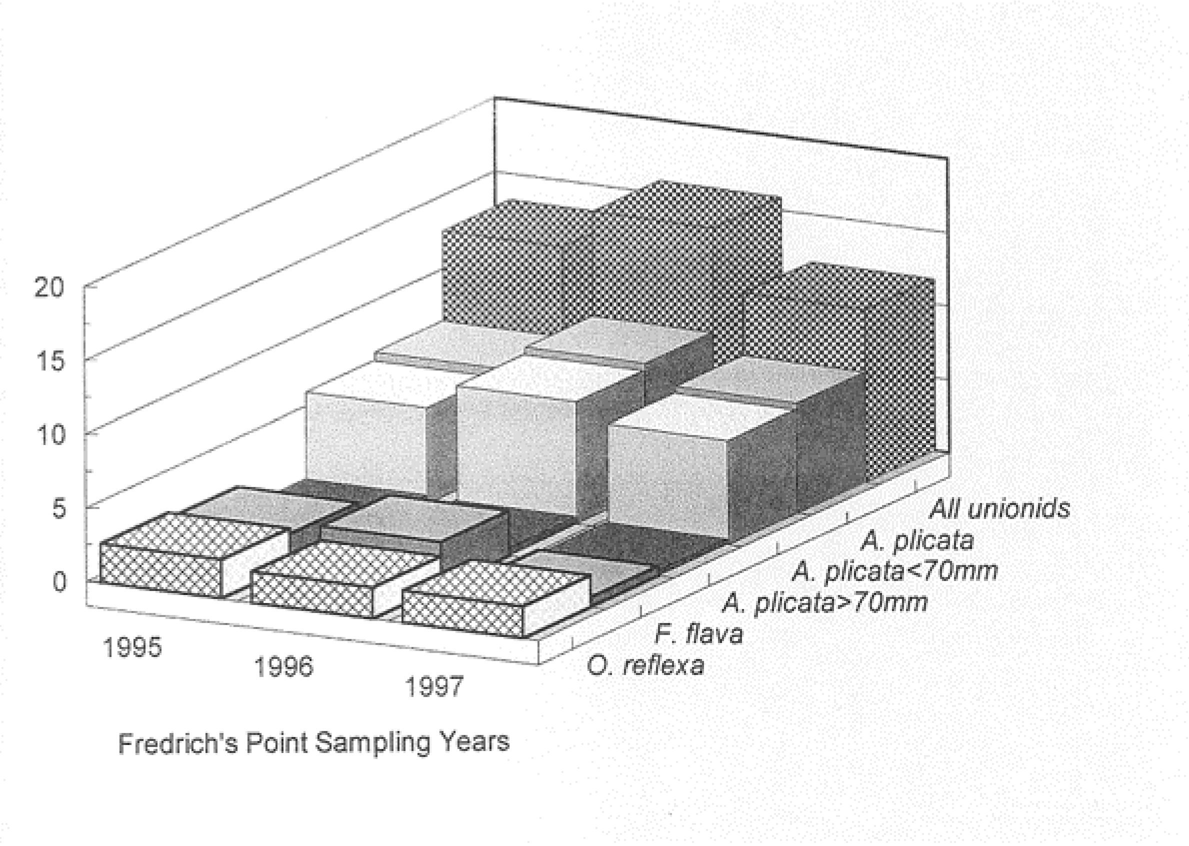

Figure 1.2. Mean unionid mussel densities measured at Fredrich's Point, Minnesota, 1995-97.

Fredrich's Point Sampling Years

Table 1.2. Lake Pepin unionid mussel density comparisons: means, standard errors, and multiple comparisons.

Site and Species	1990		1991		1993		1994		1995		1996		1997	
	Mean(SE) ^{2}	Mult. ^{1} comp.	Mean (SE) ^{2}	Mult. ^{1} comp.	Mean (SE) ^{2}	Mult. ^{1} comp.	Mean (SE) ^{2}	Mult. ^{1} comp.	Mean (SE) ^{2}	Mult. ^{1} comp.	Mean (SE) ^{2}	Mult. ^{1} comp.	Mean (SE) ^{2}	Mult. ^{1} comp.
Fredrich's Point														
All unionids									13.2 (1.69)	A	15.9 (1.17)	A	11.7 (1.02)	A
A. plicata									7.07 (0.83)	A	8.8 (1.11)	A	7.5 (0.76)	A
A. plicata > 70 mm									0.7 (0.34)	A	0.5 (0.25)	A	0.4 (0.16)	A
A. plicata < 70 mm									6.5 (0.83)	A	8.27 (1.03)	A	7.1 (0.76)	A
F. flava									2.3 (0.68)	AB	3.07 (0.71)	A	0.7 (0.25)	B
O. reflexa									2.7 (0.48)	A	2.13 (0.71)	A	2.2 (0.43)	A
Methodist Point														
All unionids					27.1 (2.4)	A			25.7 (1.87)	AB	19.6 (1.69)	B	11.3 (0.98)	C
A. plicata					15.3 (1.99)	A			15.7 (1.34)	A	9.5 (1.01)	B	5.1 (0.66)	C
A. plicata > 70 mm					0.53 (0.25)	A			0.8 (0.35)	A	0.27 (0.19)	A	0.4 (0.16)	A
A. plicata < 70 mm					14.8 (2.0)	A			14.8 (1.27)	A	9.6 (1.04)	B	4.8 (0.66)	C
F. flava					6.3 (0.93)	A			5.6 (0.44)	A	4.4 (0.78)	A	3.7 (0.59)	A
O. reflexa					4.3 (0.90)	A			3.47 (0.81)	AB	4.8 (0.82)	A	1.5 (0.34)	B

Table 1.2 (continued).

	1990		1991		1993		1994		1995		1996		1997	
Site and Species	Mean(SE) ^{2}	Mult. ^{1} comp.	Mean (SE) ^{2}	Mult. ^{1} comp.	Mean (SE) ^{2}	Mult. ^{1} comp.	Mean (SE) ^{2}	Mult. ^{1} comp.	Mean (SE) ^{2}	Mult. ^{1} comp.	Mean (SE) ^{2}	Mult. ^{1} comp.	Mean (SE) ^{2}	Mult. ^{1} comp.
Hok Si La														
All unionids	30.4 (5.69)	A			29.2 (4.3)	A			11.2 (1.53)	B	11.6 (1.24)	B	6.8 (0.65)	B
A. plicata	16.8 (3.76)	AB			21.8 (4.67)	A			6.0 (1.28)	BC	5.0 (0.76)	C	3.3 (0.56)	C
A. plicata > 70 mm	9.6 (3.59)	A			4.1 (1.17)	B			0.8 (0.35)	C	0.6 (0.34)	C	0.8 (0.23)	C
A. plicata < 70 mm	7.2 (0.99)	A			17.6 (3.53)	B			5.2 (1.09)	AC	4.4 (0.78)	AC	2.5 (0.49)	AC
F. flava	7.6 (1.83)	A			3.5 (0.83)	BC			4.1 (0.68)	AC	4.3 (0.85)	AC	1.7 (0.33)	B
O. reflexa	0.8 (0.53)	AB			0.27 (0.19)	A			0.27 (0.19)	A	1.4 (0.47)	B	0.53 (0.20)	AB
Erickson's Point														
All unionids			23.7 (2.05)	AB			31.5 (3.03)	A			21.3 (2.69)	B		
A. plicata			18.3 (1.7)	A			19.3 (1.76)	A			12.3 (1.79)	B		
A. plicata > 70 mm			1.6 (0.45)	A			0.5 (0.34)	A			1.5 (0.41)	A		
A. plicata < 70 mm			17.6 (1.72)	A			18.8 (1.92)	A			10.3 (1.8)	B		
F. flava			2.9 (0.81)	A			3.8 (1.00)	A			2.8 (0.72)	A		
O. reflexa			1.7 (0.42)	A			4.3 (0.85)	B			2.4 (0.65)	AB		

Table 1.2 (continued).

Site and Species	1990		1991		1993		1994		1995		1996		1997	
	Mean(SE) [2]	Mult. [1] comp.	Mean (SE) [2]	Mult. [1] comp.	Mean (SE) [2]	Mult. [1] comp.	Mean (SE) [2]	Mult. [1] comp.	Mean (SE) [2]	Mult. [1] comp.	Mean (SE) [2]	Mult. [1] comp.	Mean (SE) [2]	Mult. [1] comp.
Waterman's														
All unionids			19.6 (3.00)	A			16.6 (1.77)	AB			8.8 (1.16)	C	10.8 (1.34)	BC
A. plicata			11.8 (2.40)	A			11.8 (1.65)	AB			4.8 (0.87)	C	6.4 (0.97)	BC
A. plicata > 70 mm			1.8 (0.74)	A			2.3 (0.81)	A			0.9 (0.31)	A	1.2 (0.34)	A
A. plicata < 70 mm			10 (2.08)	A			9.4 (1.66)	AC			3.9 (0.89)	B	5.1 (0.81)	BC
F. flava			2.8 (0.66	A			2.3 (1.09)	A			1.5 (0.41)	A	2.0 (0.53)	A
King's Coulee														
All unionids									15.7 (1.36)	A	15.2 (1.81)	A	13.2 (1.33)	A
A. plicata									7.9 (1.08)	A	6.9 (1.08)	A	4.9 (0.78)	A
A. plicata > 70 mm									0.93 (0.31)	A	0.8 (0.35)	A	0.5 (0.32)	A
A. plicata < 70 mm									6.9 (1.08)	A	5.9 (0.95)	A	4.4 (0.78)	A
F. flava									2.5 (0.56)	A	4.7 (0.90)	A	4.5 (0.81)	A
O. reflexa									0.93 (0.31)	A	0.4 (0.22)	A	0.93 (0.37)	A

Table 1.2 (continued).

Site and Species	1990 Mean(SE) [2]	1990 Mult. [1] comp.	1991 Mean (SE) [2]	1991 Mult. [1] comp.	1993 Mean (SE) [2]	1993 Mult. [1] comp.	1994 Mean (SE) [2]	1994 Mult. [1] comp.	1995 Mean (SE) [2]	1995 Mult. [1] comp.	1996 Mean (SE) [2]	1996 Mult. [1] comp.	1997 Mean (SE) [2]	1997 Mult. [1] comp.
Lacupolis														
All unionids					70.56 (4.79)	A			36.1 (4.36)	B	30.1 (2.86)	B	34.7 (4.10)	B
A. plicata					18.5 (2.74)	A			16.8 (2.74)	A	7.7 (1.47)	B	10.9 (2.23)	AB
A. plicata > 70 mm					2.3 (0.77)	A			1.2 (0.48)	A	2.0 (0.76)	A	0.13 (0.13)	A
A. plicata < 70 mm					13.9 (2.64)	AB			15.6 (2.60)	AC	5.4 (1.09)	B	11.1 (2.23)	AB
F. flava					9.7 (1.48)	A			2.7 (0.62)	B	1.6 (0.41)	B	1.6 (0.53)	B
E. dilatata					9.9 (1.35)	A			7.1 (1.08)	A	8.9 (1.38)	A	6.8 (1.09)	A

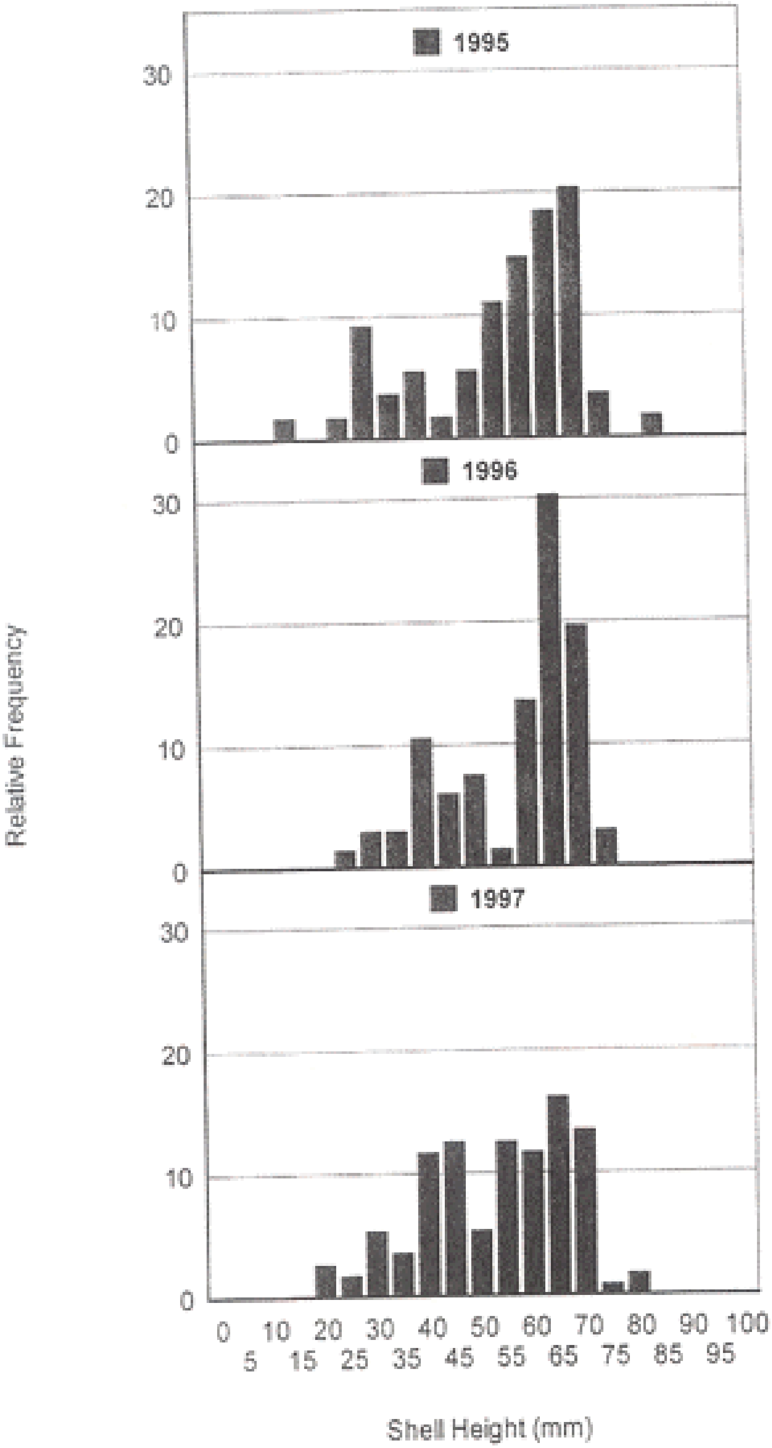

Figure 1.3. Fredrich's Point. *A. plicata* shell height distributions, 1995-97.

p=0.001) (Fig. 1.2, Table 1.2). Densities peaked with 3.07 mussels/m^2 in 1996 compared to a low of 0.7/m^2 in 1997.

While *F. flava* exhibited some declines in densities, *O. reflexa* did not. *O. reflexa* densities remained stable from 1995-96 within this mussel bed, remaining at approximately 2.5 mussels/m^2, F=0.247 $_{df=2}$, p=0.782 (Fig. 1.2, Table 1.2).

The exotic mussel species, *D. polymorpha,* was first collected from this mussel bed in 1995, yet it was only found in low numbers since that time. Densities of this non-indigenous species equaled only about 1 individual per 30 quadrats sampled throughout the study, thus hindering analysis of density for this population.

Methodist Point, Minnesota

Twelve mussel species were collected within quadrat samples from this mussel bed during the study (Table 1.1). There was a significant decline in mussel density when all of the species were combined in the initial analysis, F=23.790 $_{df=3}$, p<0.0001 (Fig. 1.4, Table 1.2). This change in density was most likely the result of declining population sizes of *A. plicata*. This population of *A. plicata* showed significant declines from 1993 through 1997 (F=21.350 $_{df=3}$, p<0.0001). Densities of this species were 15.3/m^2 in 1993 compared to 5.1/m^2 in 1997 (Fig. 1.4). Legal-sized *A. plicata* did not show signs of decline (F=0.851 $_{df=3}$, p=0.468), whereas sub-legal sized individuals did (F=20.158 $_{df=3}$, p<0.0001) (Fig. 1.4, Table 1.2). Shell height distributions for this species illustrated that there are some smaller individuals present, yet they did not compose a large portion of the population (Fig. 1.5). The distributions did, however, indicate that there had been some recruitment into the population.

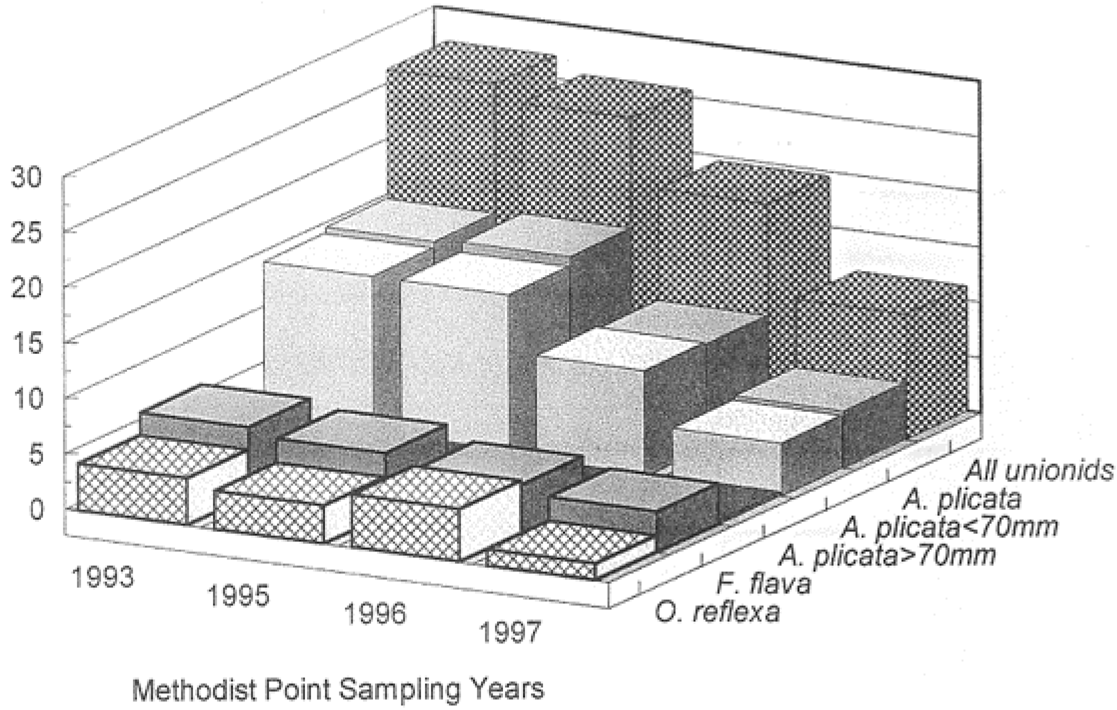

Figure 1.4. Mean unionid mussel densities measured at Methodist Point, Minnesota, 1993 and 95-97.

The non-harvested mussel species, *F. flava,* did not show any significant difference in population density over the course of this study ($F=2.638_{df=3}$, $p=0.052$) (Fig. 1.4, Table 1.2). Conversely, *O. reflexa* showed a somewhat different pattern in that population densities gradually declined from 1993 to 1997 ($F=5.808_{df=3}$, $p=0.001$) (Fig. 1.4, Table 1.2).

D. polymorpha was collected from this mussel bed beginning in 1993, yet it has only been present in low numbers through 1997. While it was collected every year during this study, the numbers did not change significantly ($F=1.431_{df=3}$, $p=0.236$) (Fig. 1.6).

Hok Si La, Minnesota

Quantitative and qualitative sampling revealed that there were 16 mussel species residing in this community (Table 1.1). Unfortunately, total mussel density, i.e., density of all of the mussels in the community combined, was found to be declining within this bed ($F=21.045_{df=4}$, $p<0.0001$) (Fig. 1.7, Table 1.2). Densities of *A. plicata* ranged from a high of 21.8/m^2 in 1993 to a low of 3.3/m^2 in 1997 ($F=14.940_{df=4}$, $p<0.0001$) (Fig. 1.7). Densities of legal-sized individuals of *A. plicata* declined during this study as well, with the numbers of harvestable individuals dropping from 9.6/m^2 in 1990 to 0.8/m^2 in 1997 ($F=12.574_{df=4}$, $p<0.0001$) (Fig. 1.7). Those individuals under legal size showed declines from 1993 to 1995-97 ($F=13.843_{df=4}$, $p<0.0001$), yet multiple comparisons revealed no difference in densities comparing 1990 to 1995-97 (Fig. 1.7, Table 1.2). Shell height distributions indicated that there had not been recent recruitment of juveniles into the population during the period this

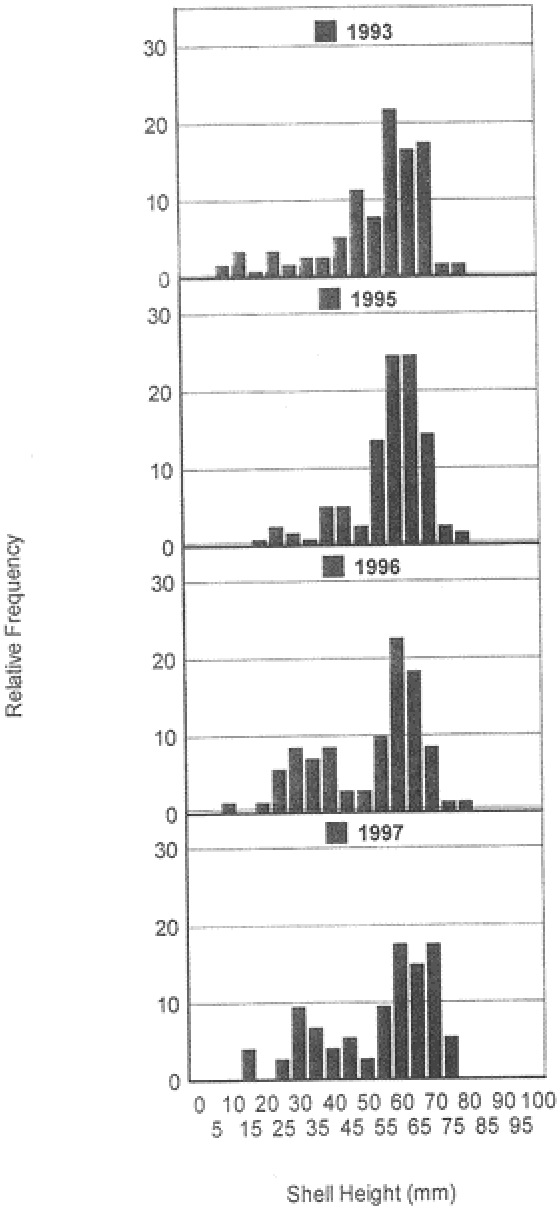

Figure 1.5. Methodist Point *A. plicata* shell height distributions, 1993 and 95-97.

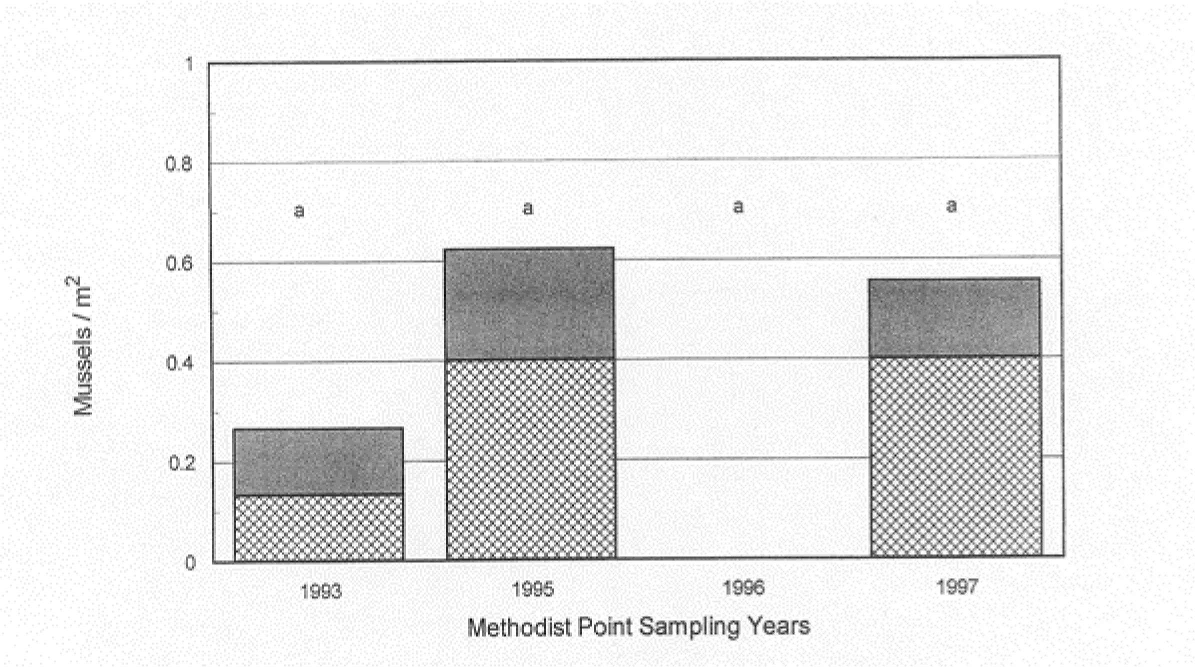

Figure 1.6. *D. polymorpha* densities + 1 standard error. Methodist Point, Minnesota. Means with a common letter are not significantly different ($p>0.05$) using an ANOVA with Tukey’s multiple comparison test.

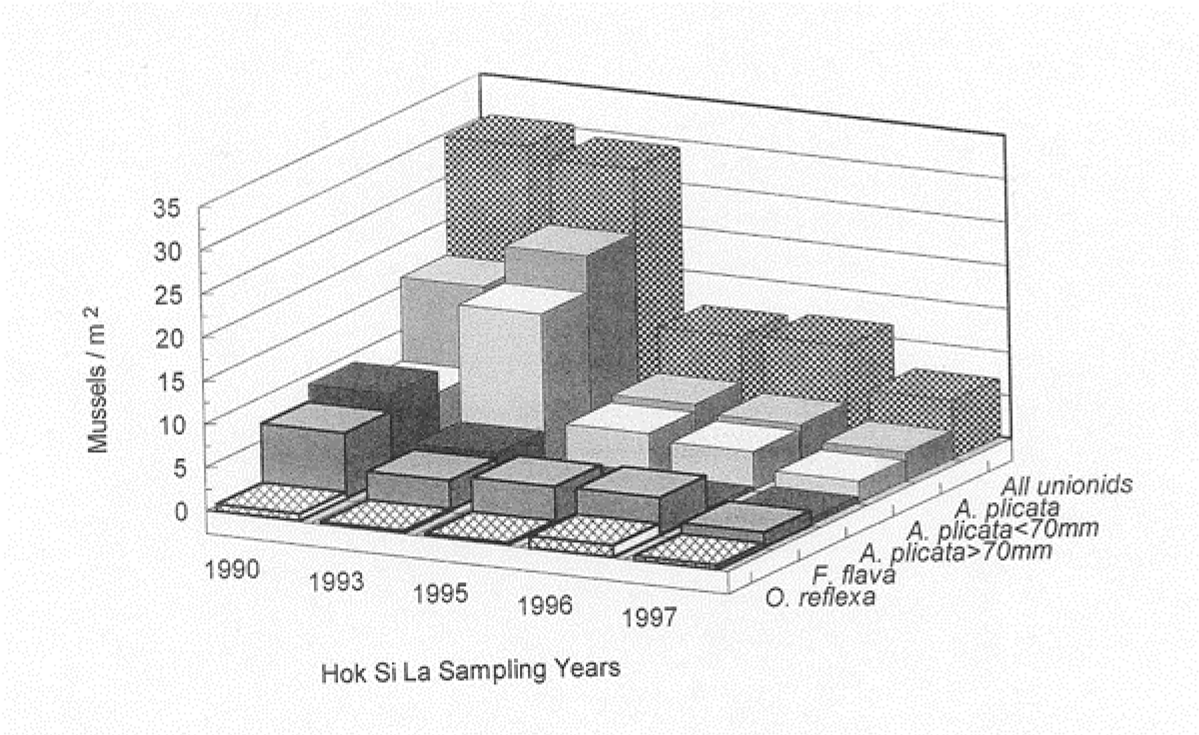

Figure 1.7. Mean unionid mussel densities measured at Hok Si La, Minnesota, 1990, 93, and 95-97.

bed was studied (Fig. 1.8).

The non-harvested *F. flava* population also showed a significant decline in numbers during select years from 1990 to 1997 ($F=6.735_{df=4}$, $p<0.0001$) (Fig. 1.7, Table 1.2). The changes in population density of O. *reflexa* were similar to those of *F. flava* in that there were some significant differences between years ($F=2.570_{df=4}$, $p=0.04$) (Fig. 1.7, Table 1.2). *O. reflexa* densities in 1990 and 1997 were equal to $0.8/m^2$ and $0.53/m^2$, respectively.

There were significant differences in densities of *D. polymorpha* at this mussel bed, with 1995 having the greatest numbers present ($F=12.119_{df=4}$, $p<0.0001$). *D. polymorpha* has recently been found in only low numbers, having significantly declined in 1997 after a peak of $50/m^2$ in 1995 (Fig. 1.9).

Erickson's Point, Wisconsin

From 1994 through 1996, 15 mussel species comprised this community (Table 1.1). In 1994 and 1996, there were differences in mussel densities found when numbers for all of the mussel species in the community were combined ($F=3.315_{df=2}$, $p=0.042$). Densities in 1994 were $31.5/m^2$, dropping to $21.3/m^2$ in 1996 (Fig. 1.10, Table 1.2).

This decline was most likely due to *A. plicata* densities also declining from 1991 and 1994, to 1996, when densities equaled $18.3/m^2$, $19.3/m^2$, and $12.3/m^2$ respectively ($F=4.472_{df=2}$, $p=0.015$) (Fig. 1.10, Table 1.2). While densities of

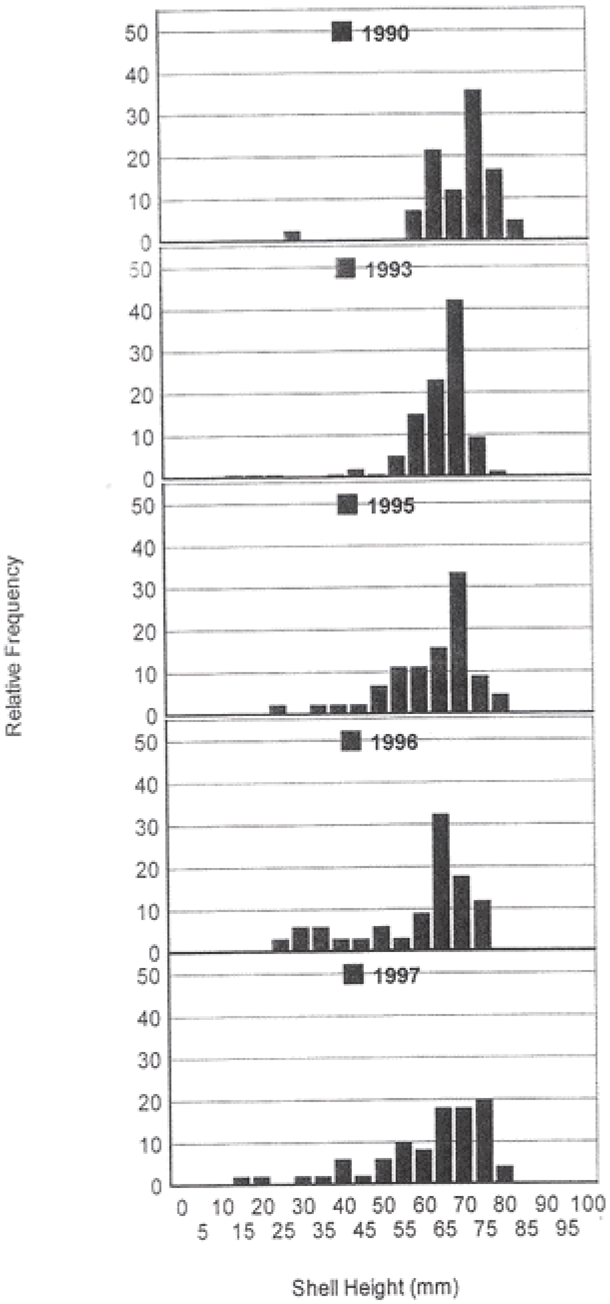

Figure 1.8. Hok Si La *A. plicata* shell height distributions, 1990, 93, and 95-97.

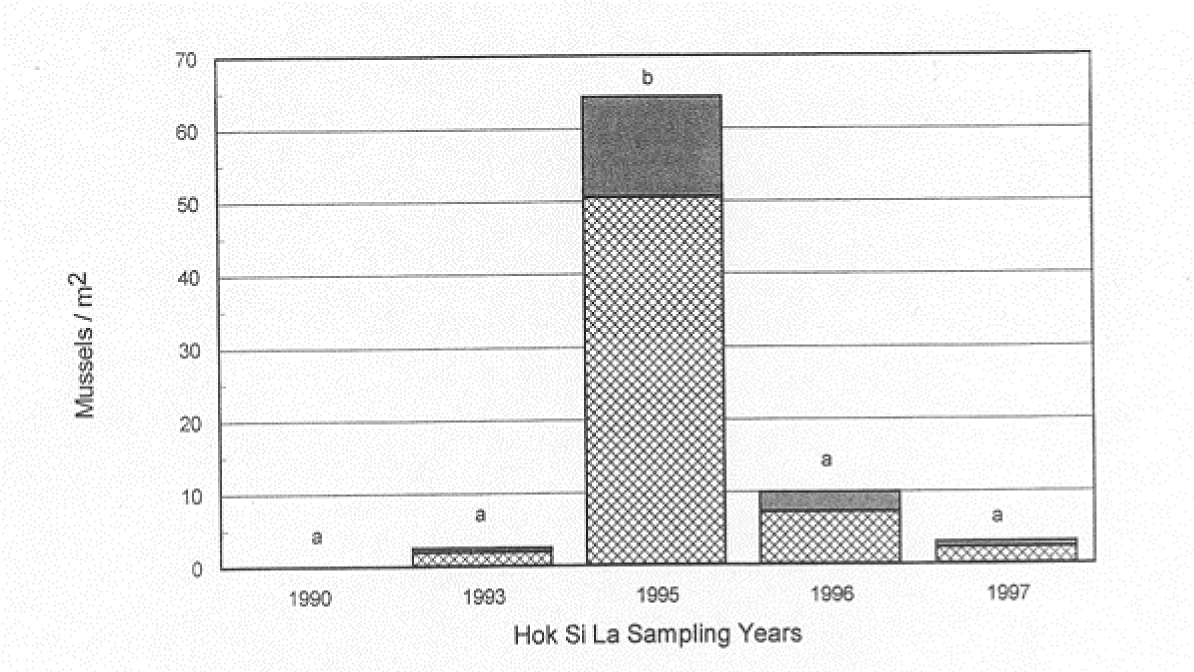

Figure 1.9. *D. polymorpha* densities + 1 standard error. Hok Si La, Minnesota. Means with a common letter are not significantly different ($p>0.05$) using an ANOVA and Tukey's multiple comparison test.

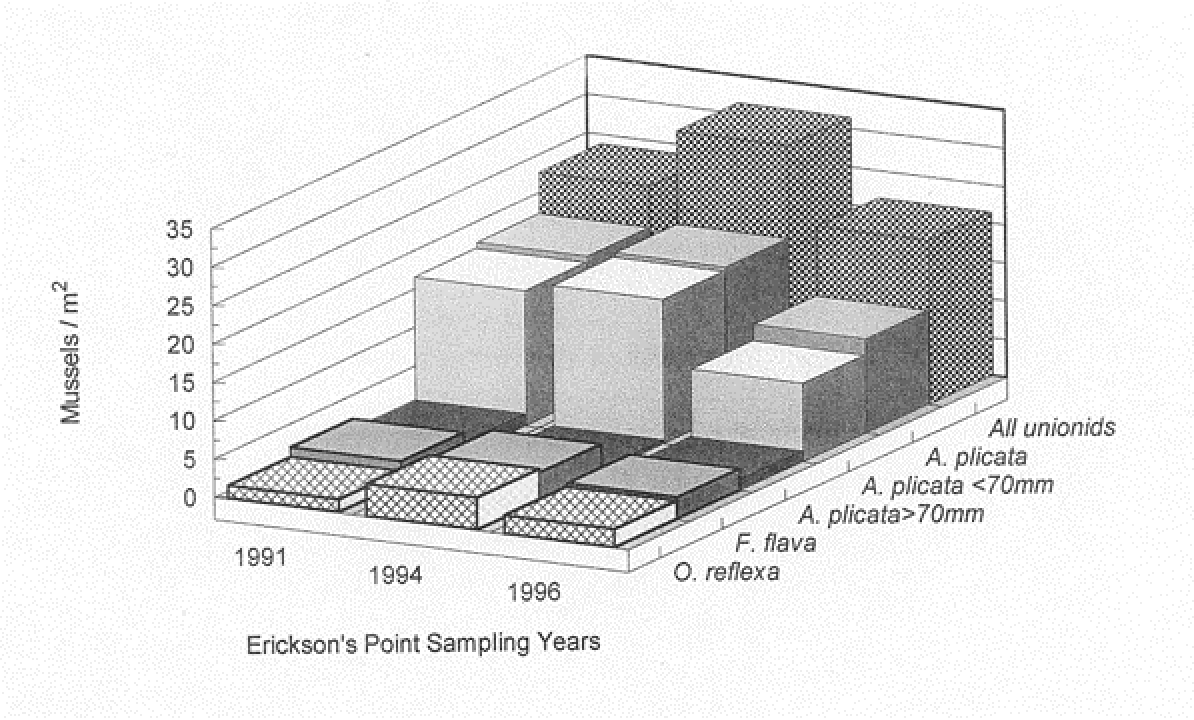

Figure 1.10. Mean unionid mussel densities measured at Erickson's Point, Wisconsin, 1991, 94, and 96.

legal-sized *A. plicata* did not change during this study ($F=1.432_{df=2}$, $p=0.242$) (Fig. 1.10, Table 1.2), densities of sub-legal sized *A. plicata* declined from 17.6/m^2 in 1991 to 10.3/m^2 in 1996 ($F=6.567_{df=2}$, $p=0.002$) (Fig. 1.10). Shell height histograms for this species illustrated that there is recent recruitment (Fig. 1.11).

There were no significant differences in densities of *F. flava* detected during this study ($F=0.292_{df=2}$, $p=0.748$). Densities measured were 2.9/m^2 in 1991 and remained close to this level through 1996 (Fig. 1.10).

The population of *O. reflexa* within this bed showed slight changes in density during this study ($F=3.507_{df=2}$, $p=0.035$). Densities were near 1.7/m^2 in 1991, increasing to 4.3/m^2 in 1994, and declining again to 2.4/m^2 in 1996 (Fig. 1.10, Table 1.2). Individuals of *D. polymorpha* were first collected in 1994 at Erickson's point, yet they have not significantly increased in density since that time ($F=3.076_{df=2}$, $p=0.052$) (Fig. 1.12).

Waterman's, Minnesota

A total of 17 mussel species was collected using quadrat samples and qualitative searches from 1991-97 (Table 1.1). The population density of all the mussel species collected from the bed showed significant declines. Overall density equaled 19.6 mussels/m^2 in 1991, dropping to a low of 8.8/m^2 in 1996 ($F= 7.681_{df=3}$, $p<0.0001$) (Fig. 1.13, Table 1.2).

This change in overall densities was attributed to population declines of the harvested mussel species, *A. plicata*, which dropped from 11.8/m^2 in 1991 to about 6.4/m^2 in 1997 ($F= 6.228_{df=3}$, $p=0.001$) (Fig. 1.13). Legal-sized *A. plicata*

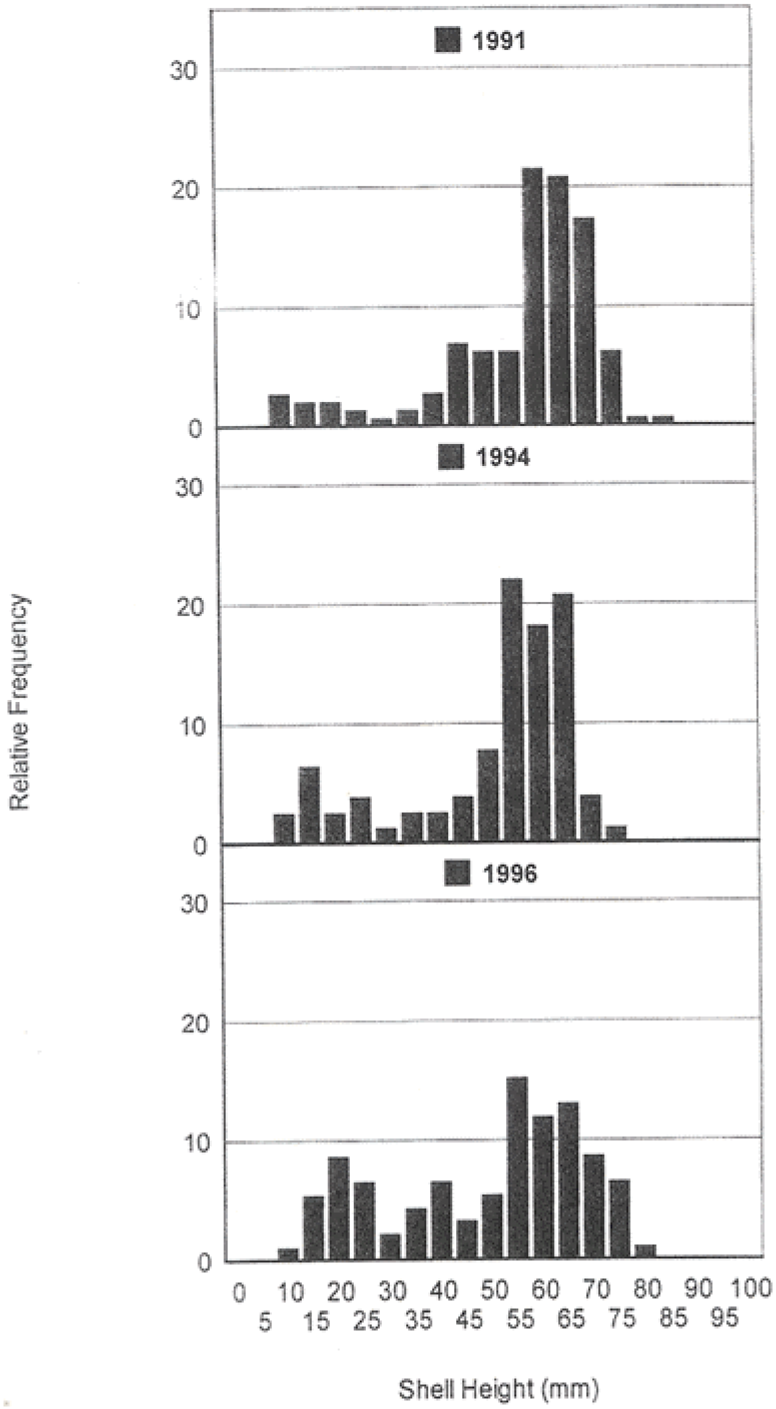

Figure 1.11. Erickson's Point *A. plicata* shell height distributions, 1991, 94, and 96.

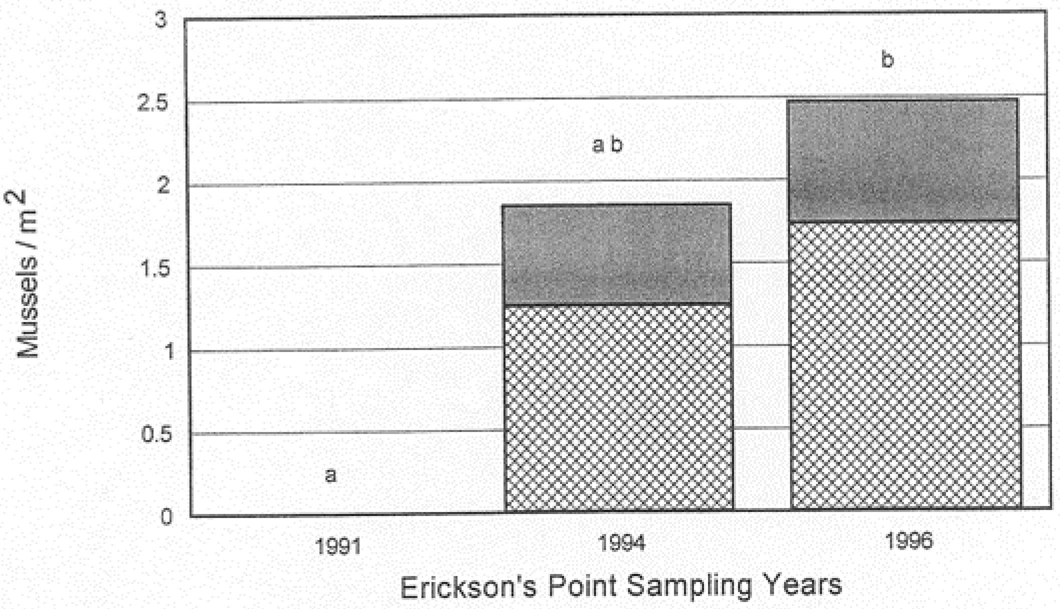

Figure 1.12. *D. polymorpha* densities + 1 standard error. Erickson's Point, Wisconsin. Means with a common letter are not significantly different ($p>0.05$) using an ANOVA and Tukey's multiple comparison test.

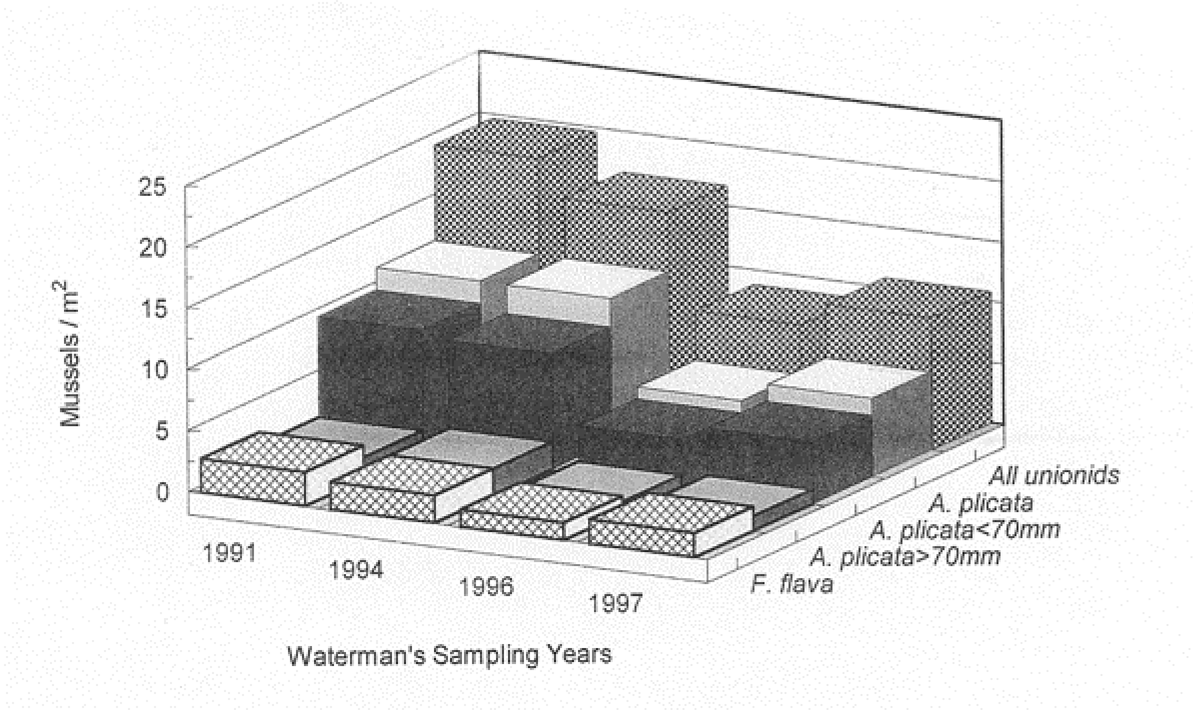

Figure 1.13. Mean unionid mussel densities measured at Waterman's, Minnesota, 1991, 94, and 96-97.

did not show signs of population declines ($F=1.282_{df=3}$, $p=0.285$), yet individuals of sub-legal size in the population did ($F= 5.575_{df=3}$, $p=0.001$) (Fig. 1.13, Table 1.2). Shell height distributions indicated that there did not appear to be any significant recruitment of juveniles into the population during the later years of this study (Fig. 1.14).

Unlike the commercially valuable *A. plicata*, the non-harvested mussel species, *F. flava*, did not show any significant declines in density from 1991-97 ($F=0.870_{df=3}$, $p=0.460$). The density of this mussel species remained at approximately 2-3 individuals/m^2 throughout this study (Fig. 1.13, Table 1.2). *D. polymorpha* was first found in low numbers in this mussel bed in 1991. Yet, there were no significant differences detected in population density from 1991-97 ($F=1.769_{df=3}$, $p=0.159$)(Fig. 1.15).

King's Coulee, Minnesota

The mussel community at this bed was comprised of species collected from quantitative quadrat samples and qualitative searches from 1995-97 (Table 1.1). Mussel density of all of these community members combined did not change significantly from 1995-97 and was equal to about 12 mussels/m^2 ($F=0.776_{df=2}$, $p=0.463$) (Fig. 1.16, Table 1.2).

Density of *A. plicata* did not change significantly throughout this study, equaling approximately 8/m^2 ($F=2.287_{df=2}$, $p=0.108$) (Fig. 1.16). Accordingly, both legal and sub-legal *A. plicata* densities did not change in any significant manner, ($F= 0.384_{df=2}$, $p=0.682$) and ($F=1.807_{df=2}$, $p=0.170$), respectively (Fig. 1.16,

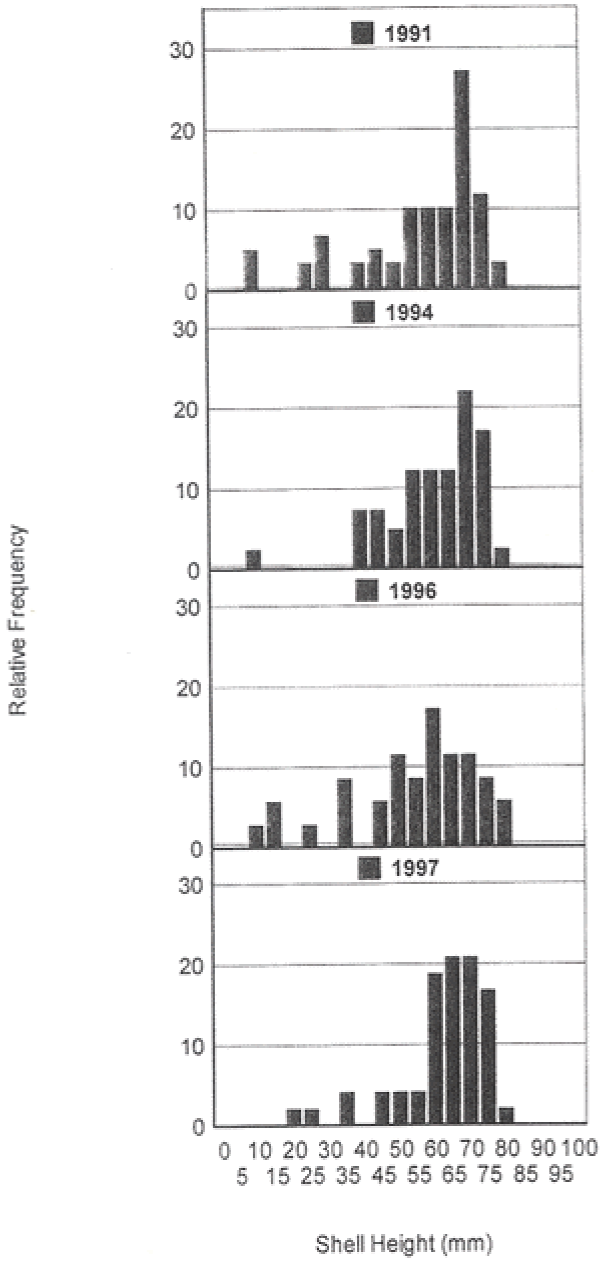

Figure 1.14. Waterman's *A. plicata* shell height distributions, 1991, 94, and 96-97.

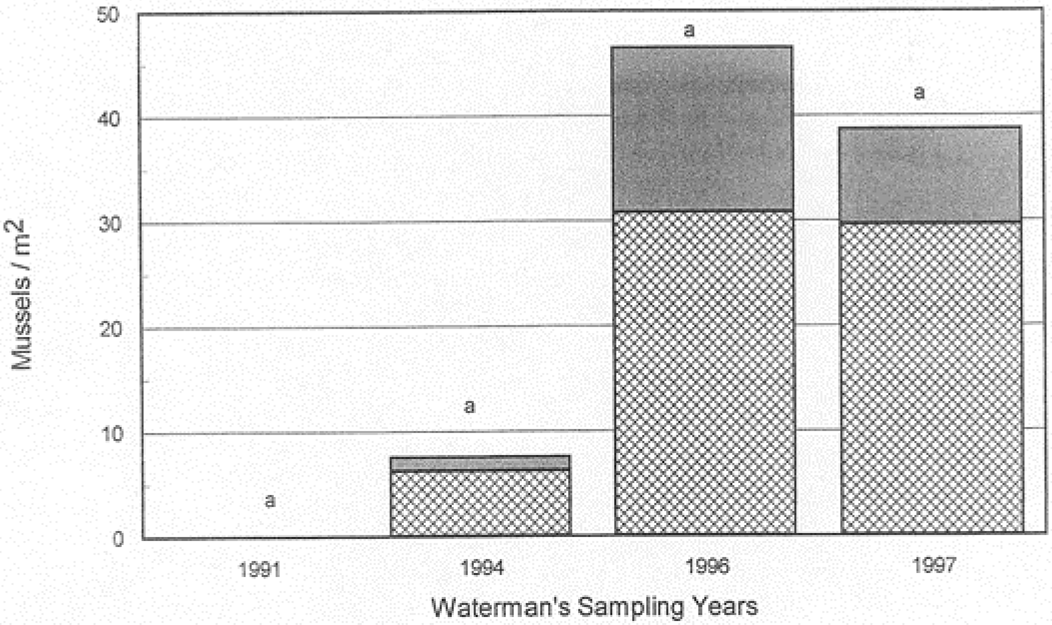

Figure 1.15. *D. polymorpha* densities + 1 standard error. Waterman's, Minnesota. Means with a common letter are not significantly different ($p > 0.05$) using an ANOVA and Tukey's multiple comparison test.

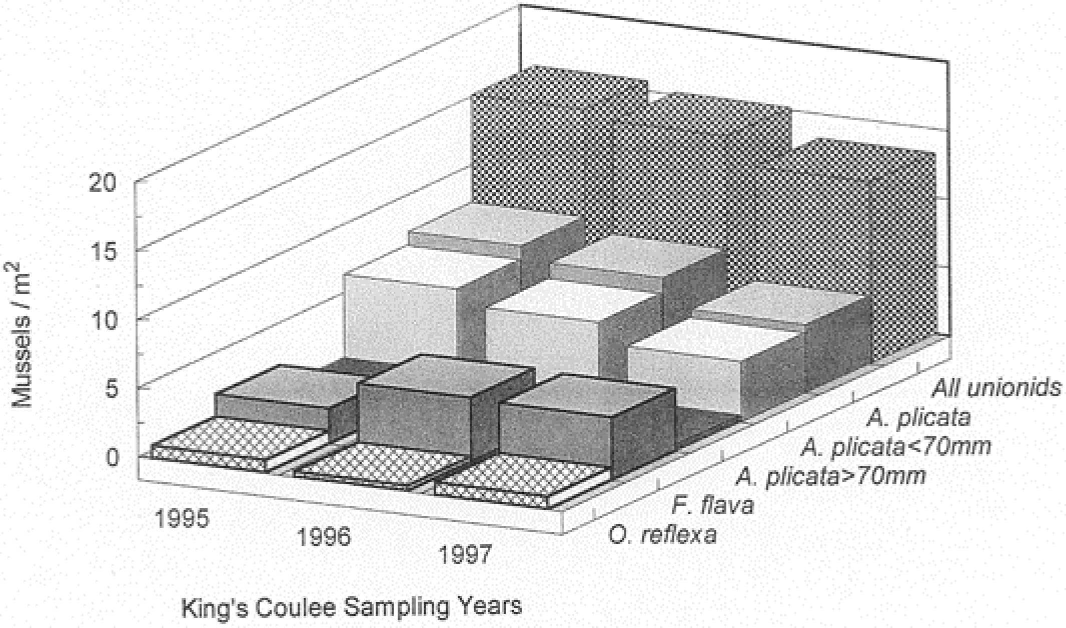

Figure 1.16. Mean unionid mussel densities measured at King's Coulee, Minnesota, 1995-97.

Table 1.2). Shell height distributions indicated that there were smaller sized individuals in the population, indicating some recent recruitment of juveniles into the population (Fig. 1.17).

Densities of *F. flava* did not show any significant changes during the time this bed was studied (F= 2.412 $_{df=2}$, p=0.096). Population density for this species remained at around 2.5-4 mussels/m^2 from 1995-97 (Fig. 1.16, Table 1.2).

Densities of *O. reflexa* were much the same as the other unionid species found in this mussel bed. Its densities had been rather stable, albeit low, at less than 1 mussel/m^2, with no significant differences being detected from 1995-97 (F=1.002 $_{df=2}$, p=0.371) (Fig. 1.16, Table 1.2).

The greatest change in the mussel community noted within this bed was the increase in density of *D. polymorpha*. Densities were >1,700 mussels/m^2 in 1995 and increased to over 4,100 mussels/m^2 in 1997 (F=6.314 $_{df=2}$, p=0.003) (Fig. 1.18).

Lacupolis, Wisconsin

Twenty-nine mussel species were collected from this bed during the study from 1993-97 (Table 1.1). Density of all the native mussel species found in the community was 70.6 mussels /m^2 in 1993, declining by 50%, to 34.7/m^2 in 1997 (F=16.646 $_{df=3}$, p<0.0001) (Fig. 1.19, Table 1.2). The most abundant members of the community whose declines attributed to the lowered density were the commercially valuable mussel species, *A. plicata* and *F. flava*.

Densities of *A. plicata* were equal to 18.5/m^2 in 1993 and dropped to a low

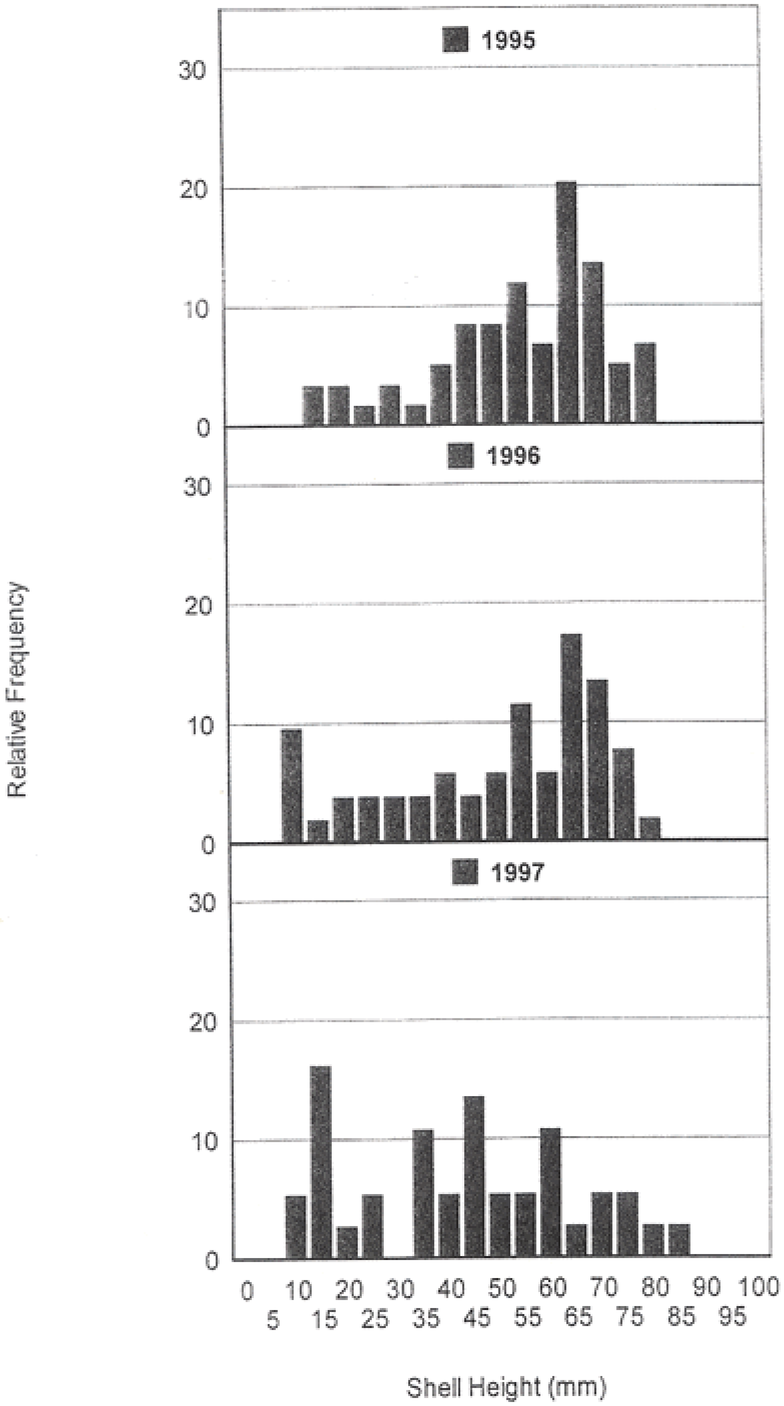

Figure 1.17. King's Coulee *A. plicata* shell height distributions, 1995-97.

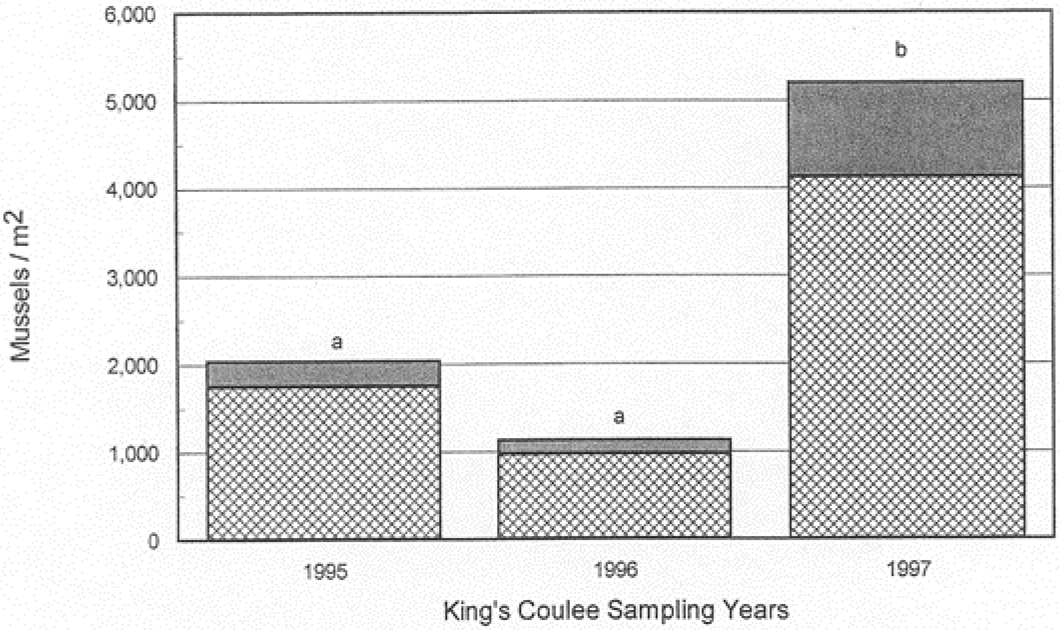

Figure 1.18. *D. polymorpha* densities + 1 standard error. King's Coulee, Minnesota. Means with a common letter are not significantly different ($p>0.05$) using an ANOVA and Tukey's multiple comparison test.

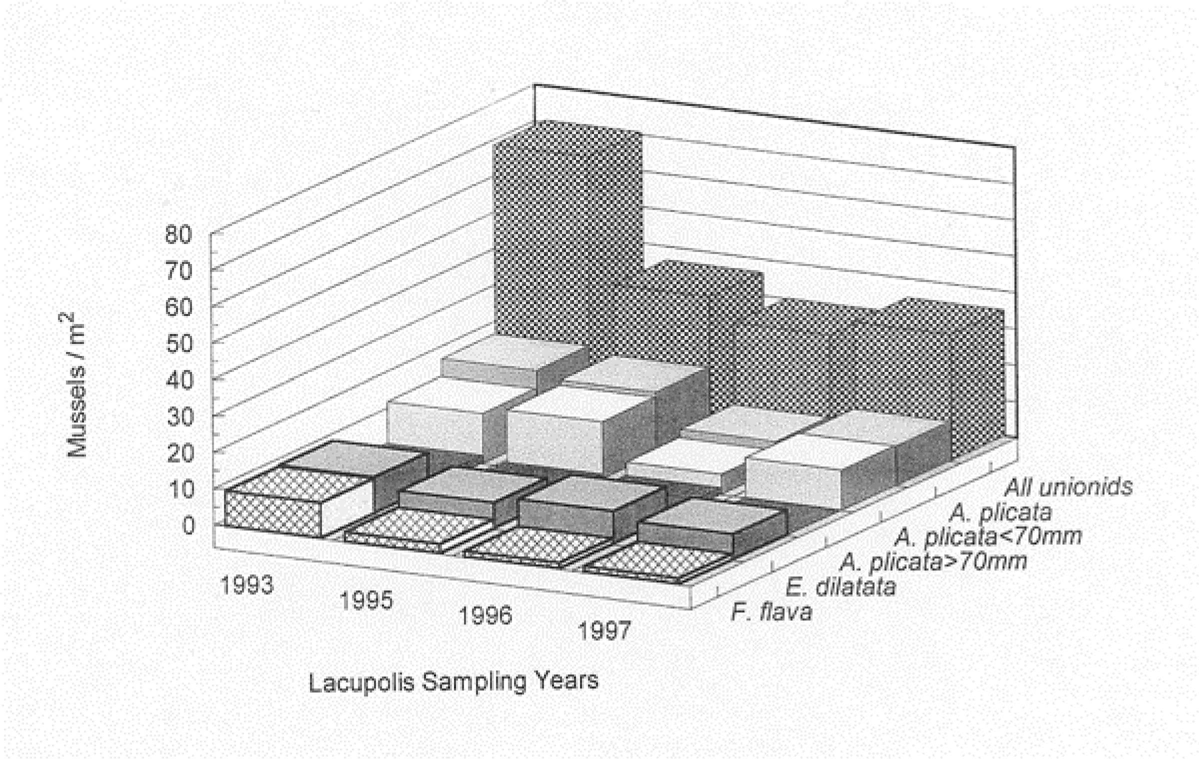

Figure 1.19. Mean unionid mussel densities measured at Lacupolis, Wisconsin, 1993, and 95-97.

of 7.7/m^2 in 1996 (F=4.512 $_{df=3}$, p=0.005) (Fig. 1.19, Table 1.2). Densities of both legal and sub-legal *A. plicata* were also significantly different during this study (F=2.873 $_{df=3}$, p=0.040 and F=4.379 $_{df=3}$, p=0.006, respectively) (Fig. 1.19, Table 1.2). Shell height histograms for this population indicated that there has not been much recruitment of juveniles into this bed. While there were some small individuals present, they did not appear to compose a large proportion of the population (Fig. 1.20).

Fusconaia flava, a species legally harvested from Wisconsin waters of the Mississippi River, showed significant declines from 1993-97 (F=22.897 $_{df=3}$, p<0.0001). Densities of this species were 9.7/m^2 in 1993, dropping to 1.6/m^2 in 1996-97 (Fig. 1.19, Table 1.2).

E. dilatata, a species noted as special concern in Minnesota, did not show any significant changes in population density from 1993-1997 (F=1.327 $_{df=2}$, p=0.270). Densities of this species stayed near 7-9 mussels/m^2 throughout the course of this study (Fig. 1.19).

A great concern for this community is that *D. polymorpha* was first collected from this mussel bed in 1993, and its densities have been increasing ever since (F=39.173 $_{df=3}$, p<0.0001). Densities increased from less than 4 *D. polymorpha*/m^2 in 1993 to over 1,400/m^2 in 1997 (Fig. 1.21).

***A. plicata* Age and Growth**

Strong linear relationships were found between the variables of shell height and shell length for *A. plicata* within all 7 quantitatively sampled sites.

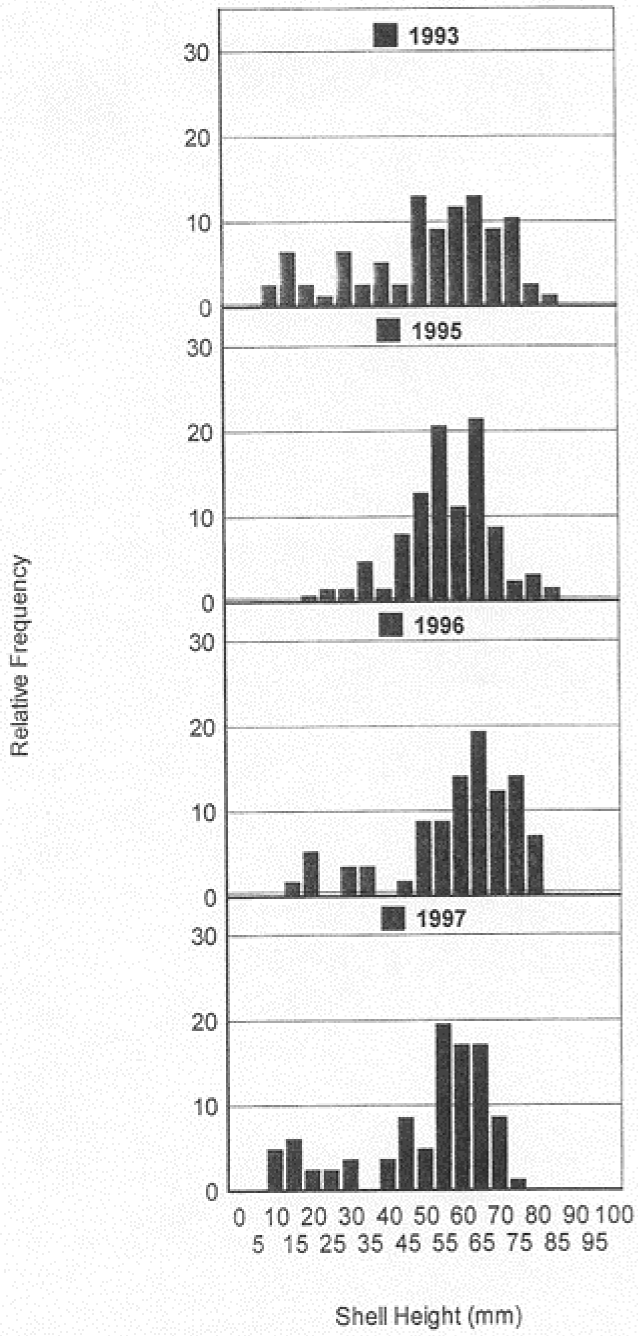

Figure 1.20. Lacupolis *A. plicata* shell height distributions, 1993, and 95-97.

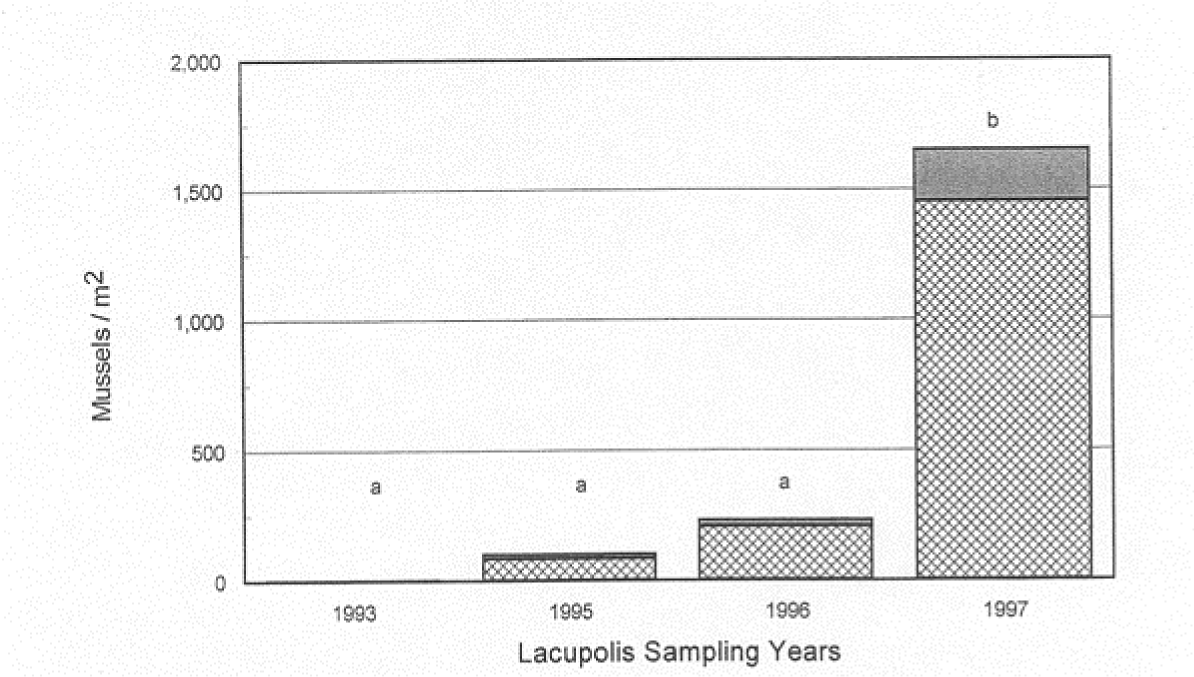

Figure 1.21. *D. polymorpha* densities + 1 standard error. Lacupolis, Wisconsin. Means with a common letter are not significantly different ($p>0.05$) using an ANOVA and Tukey's multiple comparison test.

The straight line regression equation, *shell height* = $a + b$(shell length), provided the best fit for all of the sites. The relationships between mussel age and shell mass, length, and height were best expressed by the power equation in the form of *shell mass, length, or height* = $a(\text{age}^{b})$.

This predictive equation provided good results in describing how growth of shell mass increases with age, yet the growth rate of shell dimensions seems to decline with increasing age. Regressions for individual sites are presented in a manner similar to the results of the density and demography portion of this paper.

Fredrich's Point, Minnesota

Shell length and height data were pooled for the sampling dates of 1995-97. Simple regressions of the shell length and height data revealed a high degree of correlation and predictive ability (Fig. 1.22, Table 1.3). Mussels collected from this site were aged only during 1995; therefore, we were only able to analyze age relationships for this year. Shell age had a strong predictive ability for determining shell mass, length, or height for data collected in 1995. Power equations provided the best fit for these data. Coefficients, constants, and relationships are presented in Table 1.3 and Figures 1.23-1.25.

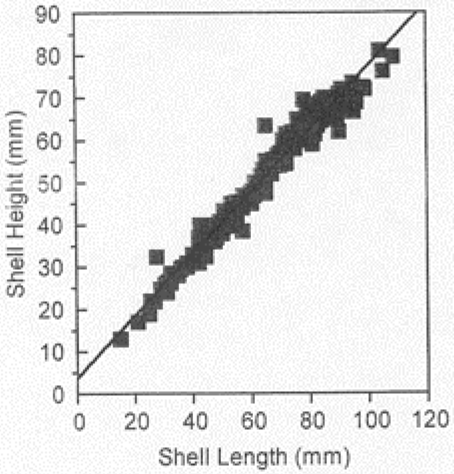

Figure 1.22. Fredrich's Point *A. plicata* shell length vs. height, 1995, 96, and 97.

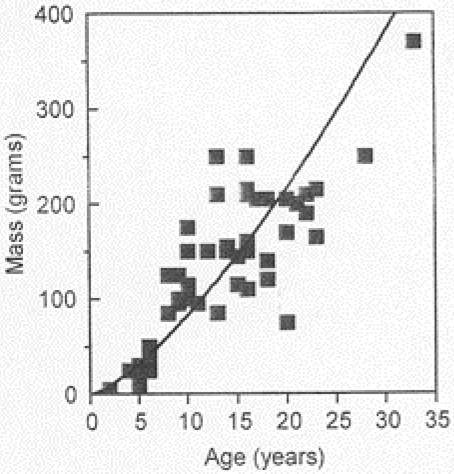

Figure 1.23. Fredrich's Point *A. plicata* age vs. shell mass, 1995.

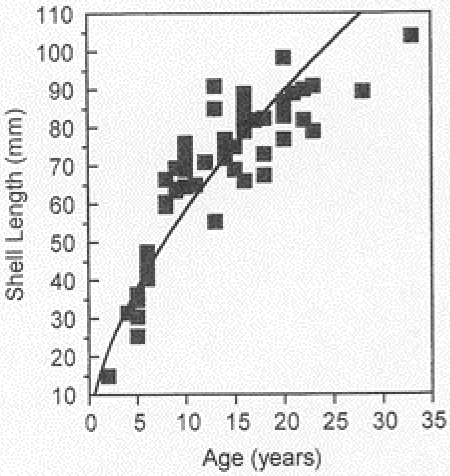

Figure 1.24. Fredrich's Point *A. plicata* age vs. shell length, 1995.

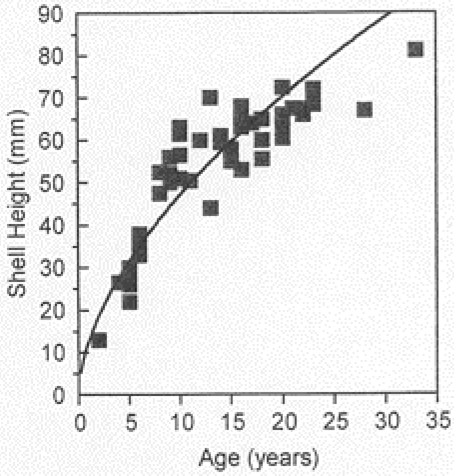

Figure 1.25. Fredrich's Point *A. plicata* age vs. shell height, 1995.

Table 1.3. Results of *A. plicata* shell length-height, age-shell mass, age-shell length, age-shell height, and shell height-mass. a, b = constants in the linear equation $Y = a + bx$ and the power equation $Y = ax^b$, n = number of individuals used in regression, and R^2 = coefficient of determination.

	Site and Shell Variables	**a**	**b**	**n**	**R^2**
Fredrich's Point	[1]shell length-height	3.76	0.737	231	0.972
	[2]age-mass	3.48	1.38	53	0.795
	[2]age-length	14.1	0.617	54	0.839
	[2]age-height	12.4	0.58	54	0.833
Methodist Point	[1]shell length-height	2.76	0.758	380	0.973
	[2]age-mass	1.41	1.81	115	0.936
	[2]age-length	14.2	0.657	115	0.938
	[2]age-height	11.7	0.643	115	0.939
Hok Si La	[1]shell length-height	6.26	0.696	285	0.942
	[2]age-length	15.7	0.613	201	0.828
	[2]age-height	13.8	0.566	201	0.804
Erickson's Point	[1]shell length-height	1.89	0.758	313	0.984
	[2]age-mass	0.660	2.15	143	0.945
	[2]age-length	10.5	0.796	143	0.936
	[2]age-height	8.5	0.780	143	0.935
	[2]height-mass	0.00206	2.72	143	0.989
Waterman's	[1]shell length-height	2.27	0.74	183	0.980
	[2]age-mass	0.701	2.02	59	0.955
	[2]age-length	12.4	0.701	59	0.963
	[2]age-height	9.88	0.685	59	0.959
	[2]height-mass	0.000865	2.93	59	0.986
King's Coulee	[1]shell length-height	2.21	0.753	148	0.978
Lacupolis	[1]shell length-height	3.85	0.728	342	0.955
	[2]age-length	10.5	0.735	77	0.948
	[2]age-height	9.35	0.690	77	0.951

[1] = straight line linear regression equation,
[2] = power equation.

Methodist Point, Minnesota

Shell length and height data were pooled for sampling years 1993, 1995, 1996, and 1997. Strong relationships existed between the *A. plicata* length and height data collected from this site (Fig. 1.26, Table 1.3). Power equations provided the best fit line for the age vs. shell mass and shell dimension regressions. The relationships between mussel age vs. mass, shell length, and shell height were strong and provided a high degree of predictive ability (Figs. 1.27-1.29, Table 1.3).

Hok Si La, Minnesota

A. plicata shell length and height data collected in 1990, 1993, and 1996-97 were pooled for the analysis of relationships between these variables. Shell length was a strong predictor of shell height (Fig. 1.30, Table 1.3). Power equations offered the best line fit for the prediction of shell length and height from mussel age data collected in 1990 and 1993 (Figs. 1.31-1.32, Table 1.3). *A. plicata* height or age was not measured in 1996 and 1997, precluding analysis.

Erickson's Point, Wisconsin

A straight line regression equation provided the best fit for the *A. plicata* shell length and height data collected during 1991, 1994, and 1996. Shell length was a strong predictor of shell height for these data (Fig. 1.33, Table 1.3), while power equations provided the best explanation for the relationships between the variables of age, shell mass, length, and height (Figs. 1.34-1.36, Table 1.3). Regressions were also performed on the variable of shell height vs. shell mass for

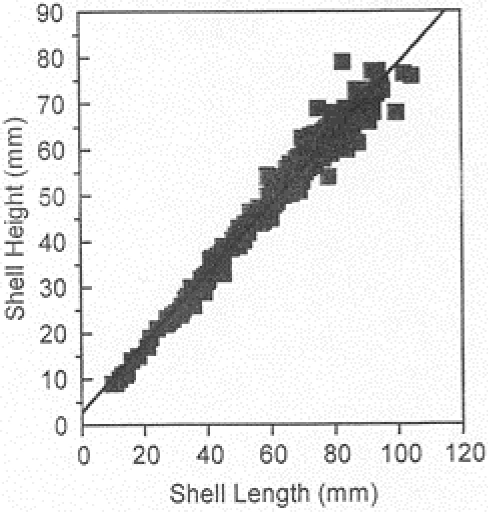

Figure 1.26. Methodist Point *A. plicata* shell length vs. height, 1993, 95, 96, and 97.

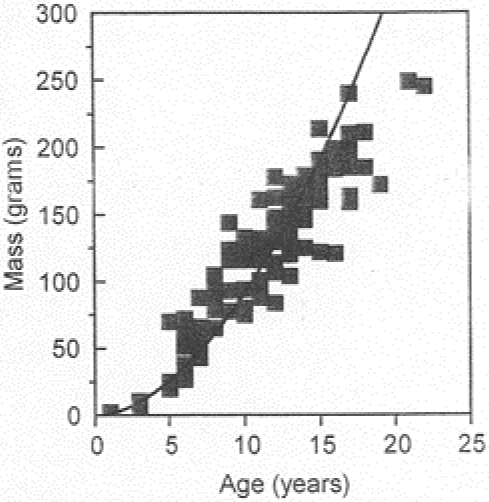

Figure 1.27. Methodist Point *A. plicata* age vs. shell mass, 1993.

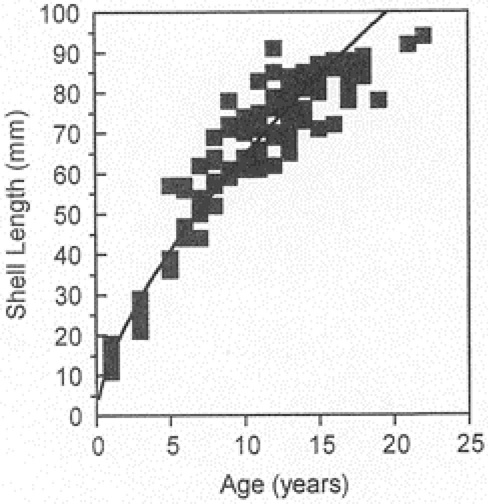

Figure 1.28. Methodist Point *A. plicata* age vs. shell length, 1993.

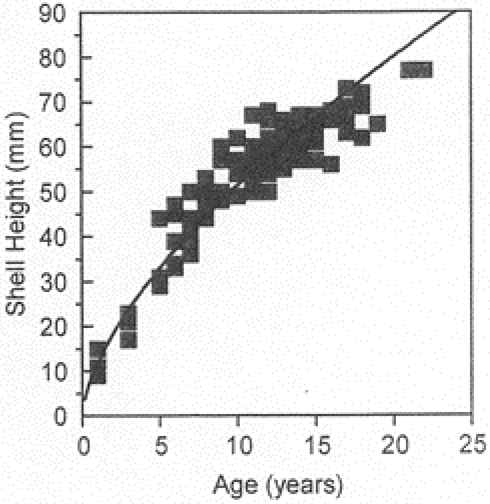

Figure 1.29. Methodist Point *A. plicata* age vs. shell height, 1993.

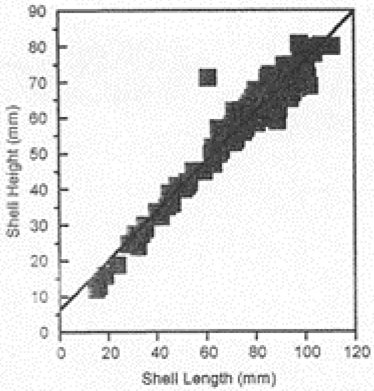

Figure 1.30. Hok Si La *A. plicata* shell length vs. height, 1990, 93, 96, and 97.

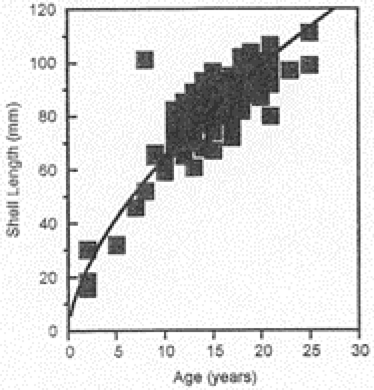

Figure 1.31. Hok Si La *A. plicata* age vs. shell length, 1990 and 93.

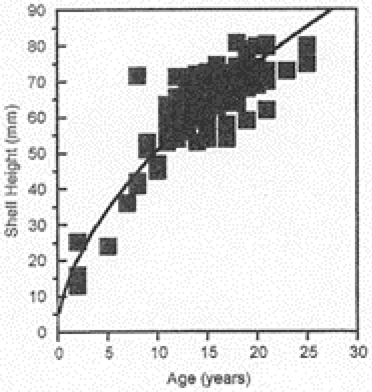

Figure 1.32. Hok Si La *A. plicata* age vs. shell height, 1990 and 93.

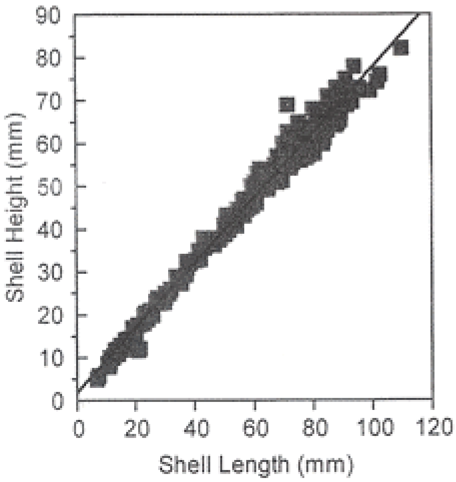

Figure 1.33. Erickson's Point *A. plicata* shell length vs. height, 1991, 94, and 96.

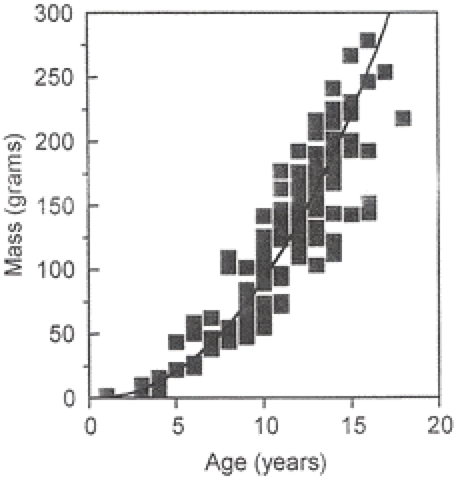

Figure 1.34. Erickson's Point *A. plicata* age vs. shell mass, 1991.

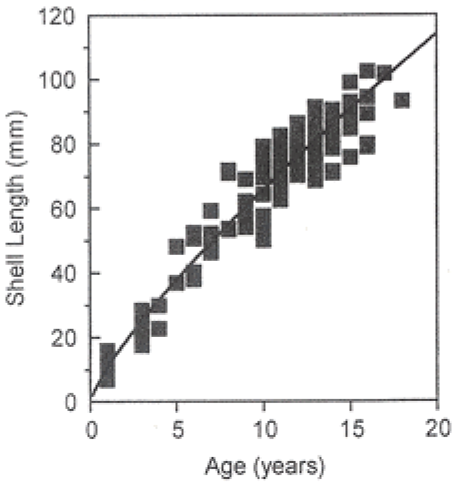

Figure 1.35. Erickson's Point *A. plicata* age vs. shell length, 1991.

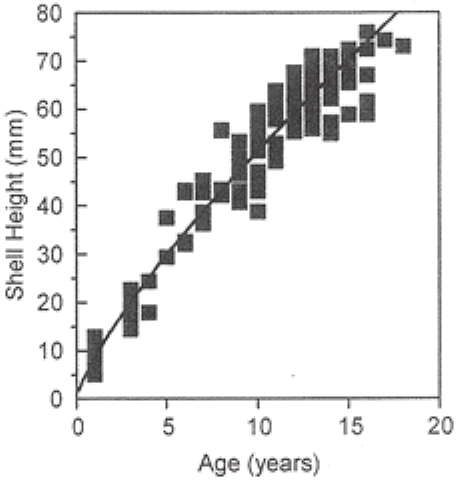

Figure 1.36. Erickson's Point *A. plicata* age vs. shell height, 1991.

data collected in 1991. A power equation provided the best fit for this relationship (Fig. 1.37, Table 1.3). Shell height was a strong predictor for shell mass, illustrating how shell mass increases with increasing shell size.

Waterman's, Minnesota

Measurements of *A. plicata* collected from this mussel bed indicated linear relationships between the variables of shell length and height. These relationships were much like the previous beds studied, in that shell length was a strong predictor of shell height (Fig. 1.38, Table 1.3). *A. plicata* age was also a good predictor of mussel mass, shell length, and height. Power equations fit all 3 of these data sets well, again illustrating how mussel mass increases exponentially with increasing age, while the growth of shell length and height declines with age (Figs. 1.39-1.41, Table 1.3). Regressions of shell height vs. shell mass were performed on data collected in 1991. A power equation provided the best fit for this relationship, with shell height being a strong predictor for shell mass (Fig. 1.42, Table 1.3).

King's Coulee, Minnesota

A. plicata shell length and height were measured in 1995-97, yet mussels were not aged during the study of this bed. Much like the other mussel beds studied, shell length of *A. plicata* was a strong predictor of shell height (Fig. 1.43, Table 1.3).

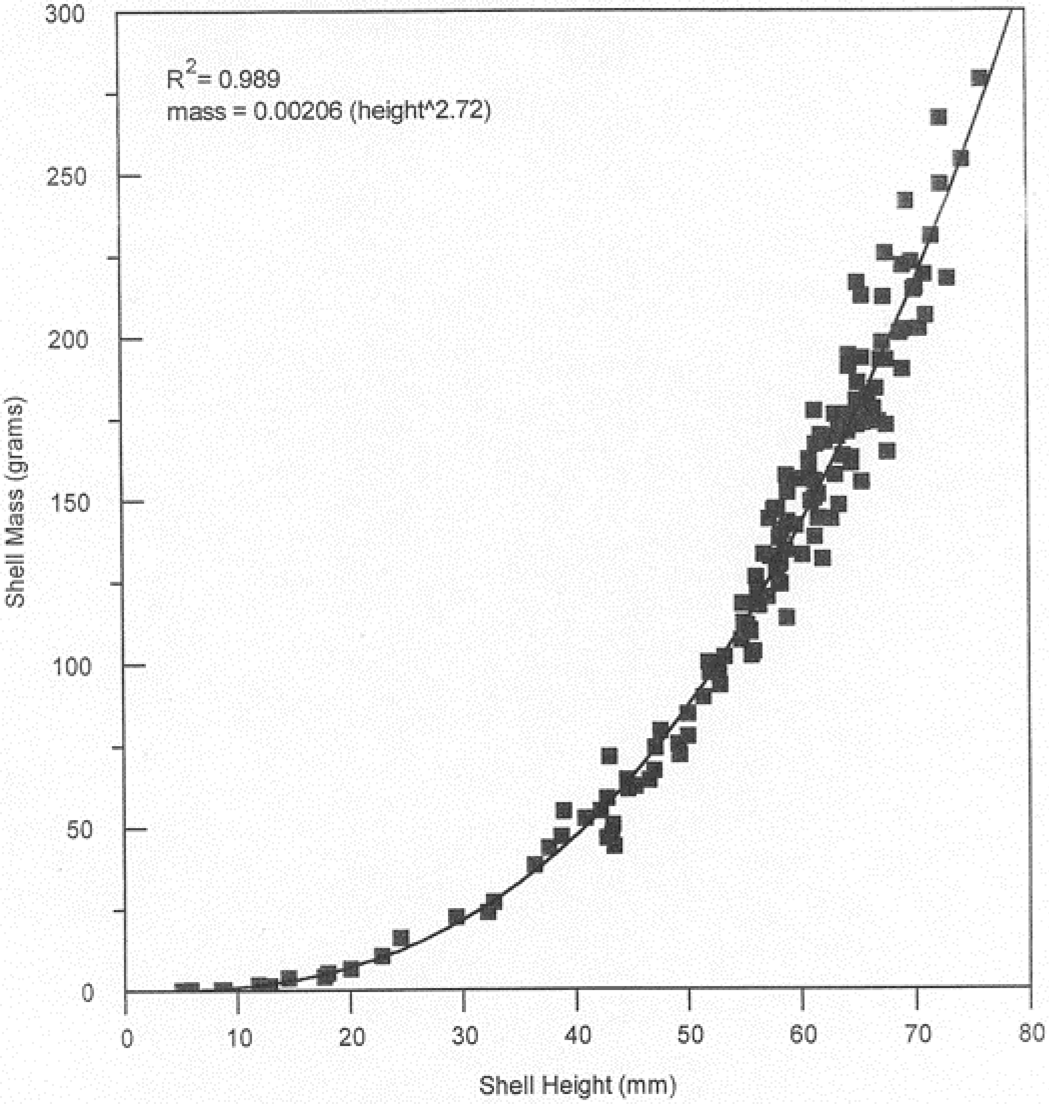

Figure 1.37. Erickson's Point *A. plicata* shell height vs. mass, 1991.

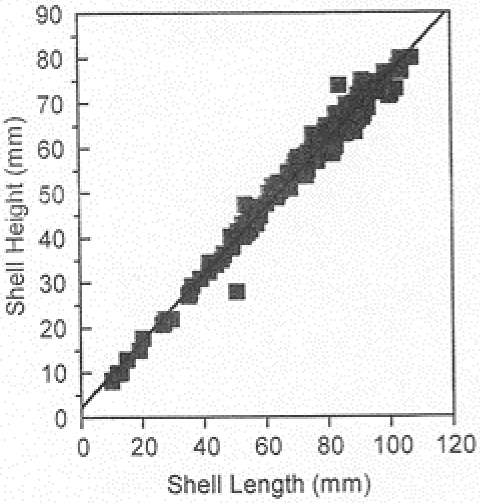

Figure 1.38. Waterman's *A. plicata* shell length vs. height, 1991, 94, 96, and 97.

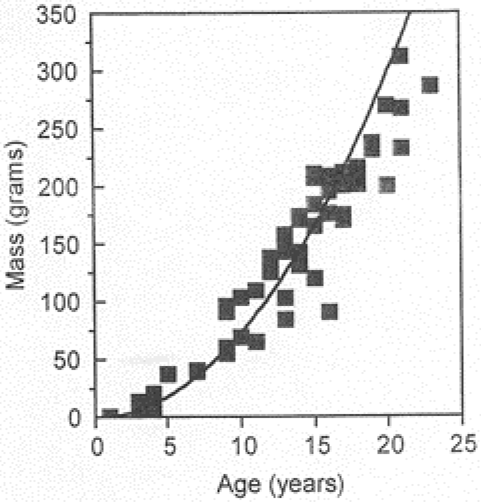

Figure 1.39. Waterman's *A. plicata* age vs. shell mass, 1991.

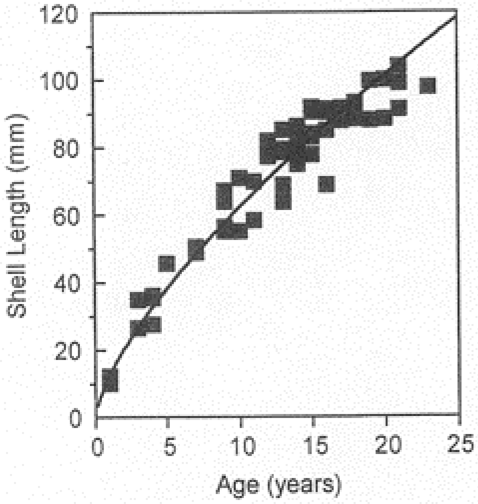

Figure 1.40. Waterman's *A. plicata* age vs. shell length, 1991.

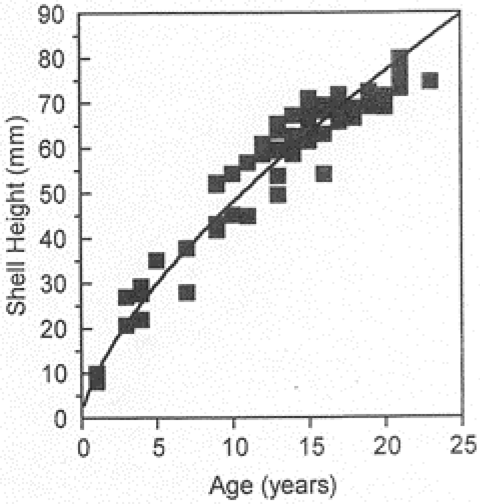

Figure 1.41. Waterman's *A. plicata* age vs. shell height, 1991.

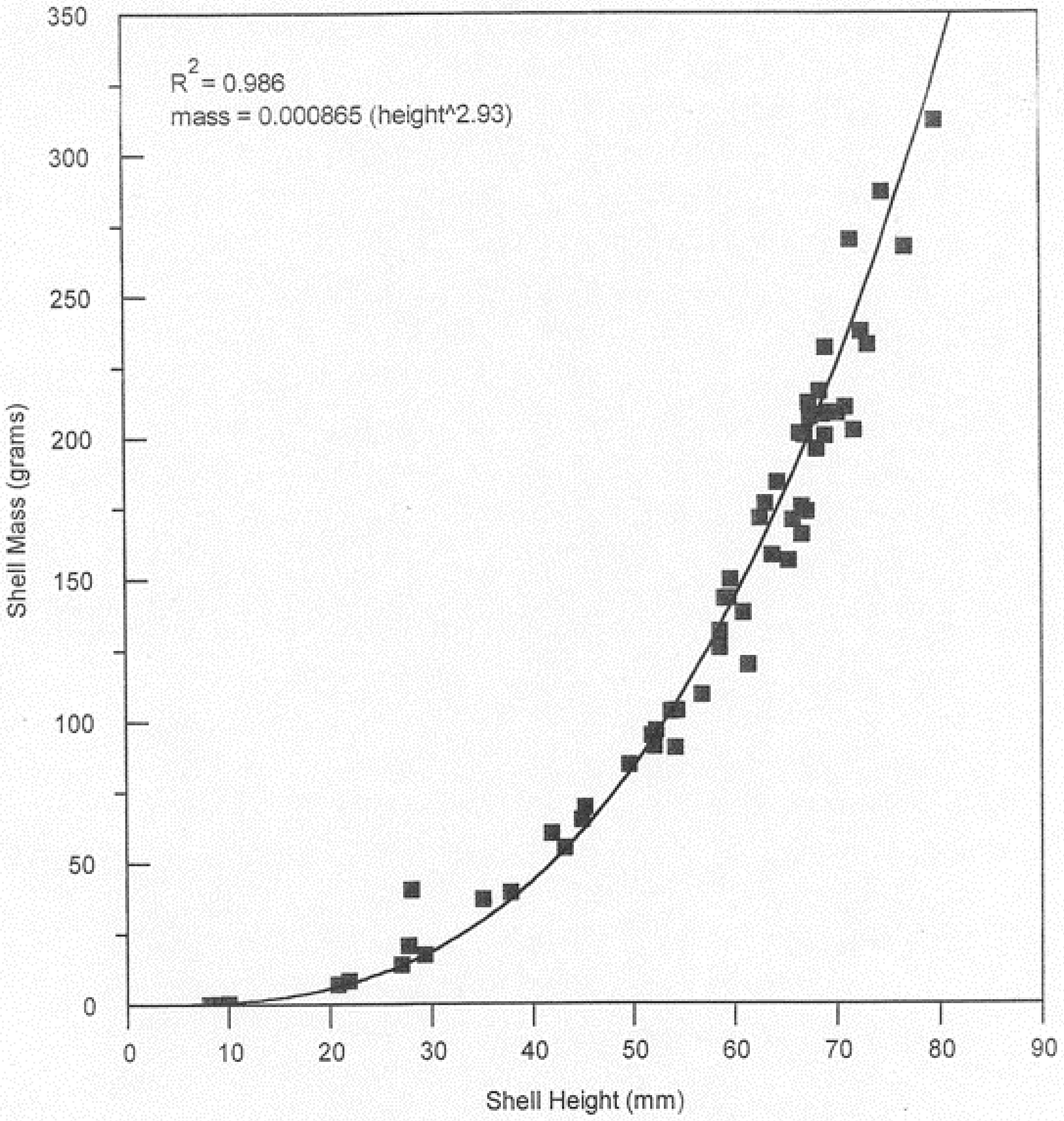

Figure 1.42. Waterman's *A. plicata* shell height vs. mass, 1991.

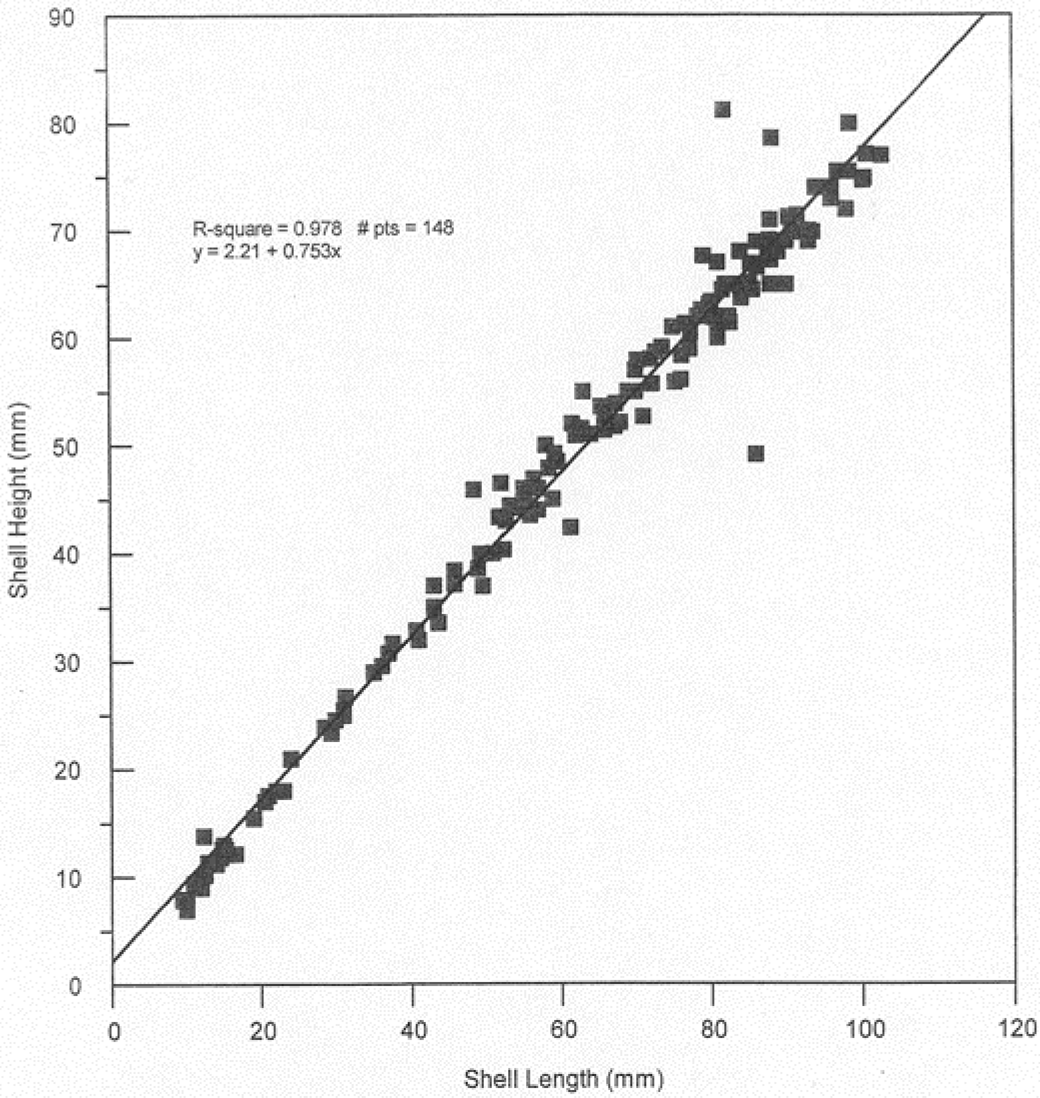

Figure 1.43. King's Coulee *A. plicata* shell length vs. height, 1995, 96, and 97.

Lacupolis, Wisconsin

A. plicata shell length was a strong predictor of shell height for the mussels measured in 1993 and 95-97 (Fig. 1.44, Table 1.3). Power equations provided the best fit for the prediction of mussel shell length and height from mussel age (Figs. 1.45-1.46, Table 1.3). These regression equations again revealed the strong correlation between how growth of an individual mussel's shell length and height declined with increasing age.

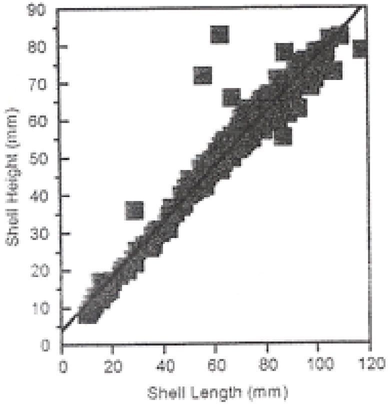

Figure 1.44. Lacupolis *A. plicata* shell length vs. height, 1993, 95, 96, and 97.

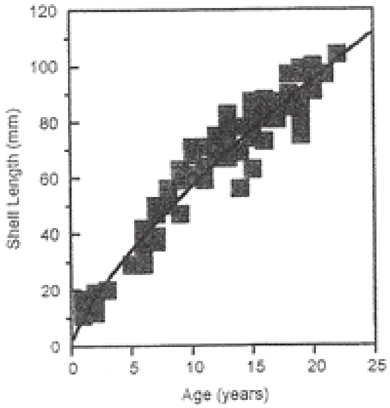

Figure 1.45. Lacupolis *A. plicata* age vs. shell length, 1993.

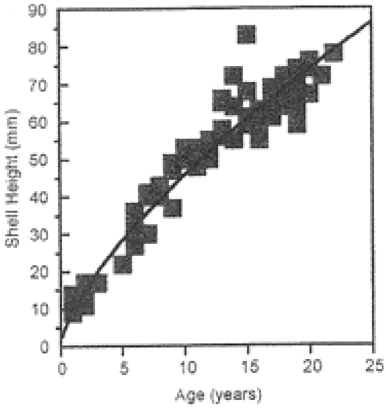

Figure 1.46. Lacupolis *A. plicata* age vs. shell height, 1993.

DISCUSSION

The commercially harvested mussel *A. plicata* showed significant declines at 5 of the 7 mussel beds sampled during this study. Declines came from both the legal and sub-legal individuals.

At several of these sites, density declines as great as 50% were detected. The most notable decline occurred at the Hok Si La mussel bed where densities of legal-sized *A. plicata* went from a high of 9/m^2 to about 3.5 mussels/m^2. Large numbers of commercial harvesters were noted working at this mussel bed in the late 1980s (Mike Davis, personal communication), and harvesters were often present during the summer months of this research (personal observation). The other noteworthy declines of *A. plicata* came from the Lacupolis bed, where densities were equal to over 18 mussels/m^2 in the early 1990s and declined to less than 9/m^2 during the late 1990s. This mussel bed is still actively harvested for not only *A. plicata*, but also *F. flava*. Densities of *F. flava* also declined at this bed, where densities were over 9/m^2 during the beginning of this research and dropped to around 2/m^2 in 1997.

While *F. flava* is legally harvested from Wisconsin border waters, it is not harvested in Minnesota. Population densities did not vary much at 4 of the 5 Minnesota beds studied. Other non-harvested mussel species, in both Minnesota and Wisconsin, showed either stationary or fluctuating population sizes during the time this study was conducted.

An assessment of the harvesting of mussels in the Mississippi River conducted by Welke and Miller (1990) revealed that over 360,000 pounds of live *A. plicata* were harvested from the Wisconsin portion of Lake Pepin in 1990. Welke and Miller (1990) speculated that this intense harvesting pressure could depress mussel stocks for several years. Records beginning in 1990 and documenting the harvest of *A. plicata* from the Minnesota beds of Lake Pepin reveal intense harvesting there as well. Harvest from Minnesota peaked in 1993, with approximately 125,000 pounds of mussels reportedly harvested (Fig. 1.47).

The regression equations developed in this study have shown a high degree of correlation between the shell variables that were measured. These equations can provide useful information for management decisions. For example, using regression equations developed in this study (Figs. 1.37 and 1.42), we calculated the number of legal-sized *A. plicata* per pound. Using Minnesota data (Fig. 1.42), the number of legal-sized *A. plicata* per pound is 2.03, while the number of individuals per pound using Wisconsin regression equations (Fig. 1.37) is 2.08. We calculated that about 254,000 live mussels were harvested from the Minnesota side of Lake Pepin in 1993 and an additional 750,000 mussels were taken from the Wisconsin side in 1990. Given these large numbers of individuals removed from the lake, as well as the findings of this study of declining population densities of *A. plicata* in Lake Pepin, Welke and Miller's (1990) concern that populations of this species may be reduced seems to be borne out. The stationary population sizes of non-harvested species and the diminishing harvested populations implicate commercial harvesting as a factor in

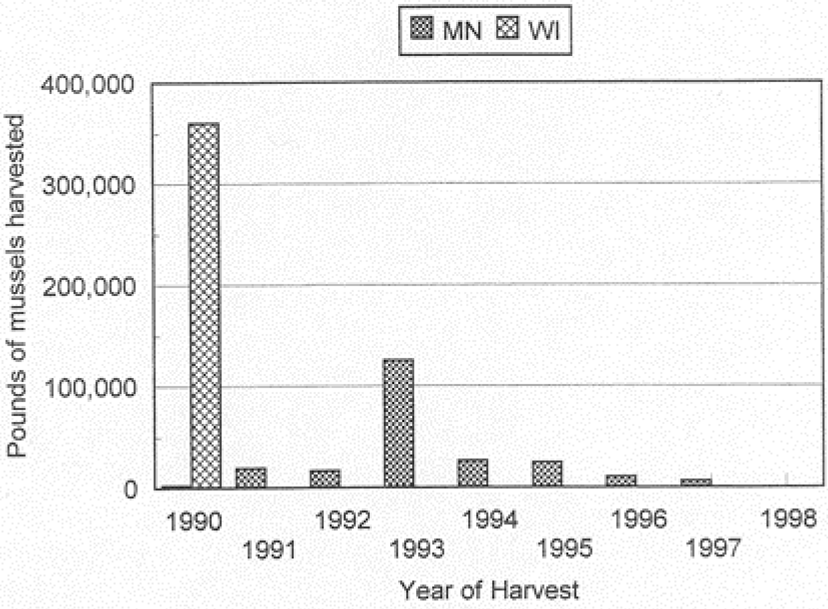

Figure 1.47. Reported pounds of *A. plicata* harvested from Lake Pepin, Minnesota (Minnesota DNR), and Wisconsin (Welke and Miller 1990).

these declines.

The ramifications of harvesting on other organisms have also been well documented. Declines in the commercially valuable black abalone (*Haliotis cracherodii*, Leach 1814) in coastal California regions were attributed to their over-harvest (Richards and Davis 1993). This species began to decline when increases in harvest occurred and replacement could not keep pace with its removal. Heath et al. (1988) reported that there had been a steady decline in the commercially harvested washboard mussel, *Megalonaias nervosa* (Rafinesque 1820), from some pools of the Upper Mississippi River. They implicated commercial harvesting as a factor because high levels of harvest had been occurring while low or no recruitment into the populations was evident.

Size distributions of the *A. plicata* populations sampled during this study indicate that there are very low levels of recruitment occurring. Since *A. plicata* are like other long-lived organisms, sporadic recruitment may be able to maintain the population (Congdon et al. 1994). Sporadic recruitment was not readily detectable in any appreciable numbers at any of the mussel beds studied, with the exception of the King’s Coulee bed, even though total substrate removal techniques were used to facilitate the collection of small individuals.

An additional factor that must be considered is the fate of not only *A. plicata* populations, but all of the mussel species residing in Lake Pepin and other regions of North America, in the face of the increasing prevalence of *D. polymorpha*. This exotic invader was first found in Lake Pepin in 1990 and has since become widespread and dominant in some areas of the lake.

D. polymorpha densities did decline at 1 of the mussel beds within the lake for unknown reasons. Possible reasons for this decline may be a loss of a veliger source to repopulate the bed or changes in the chemical composition of the water above the bed (Mellina and Rasmussen 1994). The first explanation seems most plausible, since densities of *D. polymorpha* were found to decrease with increasing distance upstream within the lake. Consequently a large veliger source has yet to be located above this particular mussel bed.

Currently *D. polymorpha* is most abundant in the lower one-third of the lake, and we found in excess of 20,000 individuals/m^2 in localized regions (personal observation). Densities of *D. polymorpha* at sampled mussel beds in this region of the lake are increasing rapidly, completely covering some portions of the lake bottom. While declines in population densities of unionid mussels in Lake Pepin cannot be directly attributed to infestations of *D. polymorpha* at this time (See Papers 2 and 3 of this dissertation.), they most assuredly will be impacted in the future, much like they have in other regions of North America (Gillis and Mackie 1994).

LITERATURE CITED

Congdon, J. D., A. E. Dunham, and R. C. van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): Implications for conservation and management of long-lived organisms. American Zoologist 34:397-408.

Cummings, K. S., and C. A. Mayer. 1992. Field guide to freshwater mussels of the Midwest. Illinois Natural History Survey Manual 5.

Cvancara, A. M. 1970. Mussels (Unionidae) of the Red River Valley in North Dakota and Minnesota, USA. Malacologia 10:57-92.

Ellis, M. M. 1931. A survey of conditions affecting fisheries in the Upper Mississippi River. United States Bureau of Fisheries 5:1-18.

Fuller, S. L. H. 1978. Freshwater mussels of the Upper Mississippi River: Observations at selected sites within the 9-foot cannel navigation project on behalf of the U. S. Army Corps of Engineers. Academy of Natural Science, Philadelphia, PA.

Gillis, P. L., and G. L. Mackie. 1994. Impact of the zebra mussel *Dreissena polymorpha*, on populations of Unionidae (Bivalvia) in Lake St. Clair. Canadian Journal of Zoology 72:1260-1271.

Heath, D. J., M. P. Engel, and J. A. Holzer. 1988. An assessment of the 1986 commercial harvest of freshwater mussels in the Mississippi River bordering Wisconsin. Summary Report, Wisconsin Department of Natural Resources. Madison, WI.

Isom, B. G., and C. Gooch. 1986. Rationale and sampling designs for freshwater mussels, Unionidae in streams, large rivers, impoundments, and lakes. In Rationale for Sampling and Interpretation of Ecological Data in the Assessment of Freshwater Ecosystems, ASTM STP 894. B. G. Isom ed. American Society for Testing and Materials, Philadelphia, PA.

Kovalak, W. P., S. D. Dennis, and J. M. Bates. 1986. Sampling effort required to find rare species of freshwater mussels. In Rationale for Sampling and Interpretation of Ecological Data in the Assessment of Freshwater Ecosystems, ASTM STP 894. B. G. Isom ed. American Society for Testing and Materials, Philadelphia, PA.

Mellina, E., and J. B. Rasmussen. 1994. Patterns in the distribution and abundance of zebra mussel (*Dreissena polymorpha*) in rivers and lakes in relation to substrate and physiochemical factors. Canadian Journal of Fisheries and Aquatic Sciences 51:1024-1036.

Miller, A. C., and B. S. Payne. 1995. Effects of increased commercial navigation traffic on freshwater mussels in the Upper Mississippi River: 1993 studies. Technical Report EL-95-11, U. S. Army Corps of Engineers Waterways Experiment Station, Vicksburg, MS.

Ricciardi, A., R. J. Neves, and J. B. Rasmussen. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. Journal of Animal Ecology 67:613-619.

Ricciardi, A., F. G. Whoriskey, and J. B. Rasmussen. 1995. Predicting the intensity and impact of *Dreissena* infestations on native unionid bivalves from *Dreissena* field density. Canadian Journal of Fisheries and Aquatic Sciences 52:1449-1461.

Richards, D. V., and G. E. Davis. 1993. Early warnings of modern population collapse in black abalone *Haliotis cracherodii*, Leach, 1814 at the California Channel Islands. Journal of Shellfish Research 12:189-194.

Smock, L. A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biology 10:375-383.

Southall, J. B. 1925. Mussel survey of Lake Pepin in 1924. With a discussion of the effects of the system of the alternate closure of sections of the lake to the taking of mussels. United States Bureau of Fisheries 57:1-3.

Thiel, P. A. 1981. A survey of unionid mussels in Upper Mississippi River (Pools 3 through 11). Technical Bulletin Number 124. Wisconsin Department of Natural Resources, Madison, WI.

Welke, K., and G. Miller. 1990. Commercial harvest of freshwater mussels in Wisconsin in 1990. Annual Report, Wisconsin Department of Natural Resources, Madison, WI.

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 E. Danglade. 1914. The mussel fauna of central and northern Minnesota. United States Bureau of Fisheries 803:1-26.

Zar, J. H. 1984. Biostatistical Analysis. Prentice Hall, Englewood Cliffs, NJ.

PAPER 2. EMPIRICAL SURVIVORSHIP RATES OF FRESHWATER MUSSELS IN THE PRESENCE OF ZEBRA MUSSEL *(Dreissena polymorpha)* INFESTATIONS, LAKE PEPIN, UPPER MISSISSIPPI RIVER, MINNESOTA AND WISCONSIN

ABSTRACT

A mussel mark-recapture study was initiated in Lake Pepin, Upper Mississippi River, Minnesota and Wisconsin, and the Otter Tail River, Minnesota. We measured survivorship of *Amblema plicata* (Say 1817) in areas with varying levels of *Dreissena polymorpha* infestations. Three native mussel beds in Lake Pepin were randomly selected, with the Methodist Point bed having low (0-10/m^2), the Hok Si La bed having moderate (25-100/m^2), and the King's Coulee bed having high (>250/m^2) densities of *D. polymorpha*. A reference site without *D. polymorpha* was selected in the Otter Tail River. We also measured survivorship of *Fusconaia flava* (Rafinesque 1820) and *Elliptio dilatata* (Rafinesque 1820) in Lake Pepin, and *F. flava* and *Lasmigona costata* (Rafinesque 1820) in the Otter Tail River. In 1996, 240 *A. plicata* in each bed were randomly selected, measured for maximum shell length and height, uniquely marked, and placed in low, open corrals. A total of 240 *E. dilatata* and 79 *F. flava* was measured and marked in Lake Pepin, while 113 L. costata and 240 *F. flava* were measured and marked in the Otter Tail River. In 1997 and 1998 marked mussels were recovered; identified; survivorship determined; and if alive, returned to the bed. Recovery rates of marked *A. plicata* at the Otter Tail, Methodist Point, Hok Si La, and King's Coulee mussel beds were 95.4%, 93.3%, 94.8%, and 74.2%, respectively. The mean number of *D. polymorpha* attached to marked *A. plicata* at the Otter Tail, Methodist Point, Hok Si La, and King's Coulee mussel beds during 1997 were 0.0, 1.4, 10.4, and 124.1 per *A. plicata*, respectively. Mean annual survivorship of

A. plicata was significantly greater at the Otter Tail (98%), Methodist Point (99%), and Hok Si La (98%) beds compared to the *D. polymorpha* infested King's Coulee mussel bed (76%) ($\chi^2_{df=3}$=93.93, p<0.0001). We attribute the difference in survivorship of *A. plicata* and *F. flava* to the infestation of *D. polymorpha*. Mean annual survivorship of the Otter Tail River *L. costata* and *F. flava* was greater than 99%. Survivorship of *E. dilatata* and *F. flava* from Lake Pepin was equal to 95% and 90%, respectively.

INTRODUCTION

There has been concern that the recent invasion of zebra mussels, *Dreissena polymorpha* (Pallas 1771), will have detrimental impacts on native faunal species (Fitzsimons et al. 1995, MacIsaac 1996, Ram and McMahon 1996). Concern has focused primarily on benthic organisms, most notably unionid mussels residing in the Great Lakes of the United States and Canada (Haag et al. 1993; Gillis and Mackie 1994; Schloesser et al. 1996, 1998). *D. polymorpha* impacts native bivalves by completely covering their shells, thereby increasing the probability of premature death due to starvation or suffocation (Ricciardi et al. 1995, Schloesser et al. 1996, Baker and Hornbach 1997). This threat has been realized in some areas of North America, as *D. polymorpha* populations have been reported to be as high as 700,000 mussels/m^2 in some regions of the Great Lakes, and are purportedly responsible for the decline or extirpation of local or regional unionid populations throughout the Great Lakes (Gillis and Mackie 1994; Schloesser and Nalepa 1994; Schloesser et al. 1996, 1998).

D. polymorpha populations were first reported in the Great Lakes in the mid-1980s and have since spread into the Mississippi River basin (Ludyanskiy et al. 1993, Tucker et al. 1993). *D. polymorpha* is now found throughout the Mississippi River from St. Paul, Minnesota, to near New Orleans, Louisiana (Ram and McMahon 1996). *D. polymorpha* was first reported in Lake Pepin, Upper Mississippi River, Minnesota and Wisconsin, in 1990 (M. Davis, personal observation) and is now found in some sections of the lake in excess of 20,000 mussels/m^2 (personal observation).

While there is a concern that increased mortality will occur in unionid populations, recent research has primarily been indirect in that mussel populations were monitored before and after infestations of *D. polymorpha*. When large changes in unionid densities have occurred in the presence of *D. polymorpha,* the population changes have been attributed to *D. polymorpha* (Haag et al. 1993, Gillis and Mackie 1994, Schloesser et al. 1998). While this information is useful for identifying a correlation between native mussel declines and increasing densities of *D. polymorpha* (Ricciardi et al. 1995, 1998), it could be argued that this relationship does not directly measure causation. Unfortunately, empirically derived results, which would directly link *D. polymorpha* infestations to an increase in mortality rates of unionid populations, are lacking.

As part of a long-term monitoring program of native mussels and *D. polymorpha* in Lake Pepin initiated in 1990, we conducted a mark and recapture study from 1995-98 on 3 populations of *Amblema plicata* (Say 1817) in Lake Pepin and 1 population in the Otter Tail River, Minnesota. We also marked *Elliptio dilatata* (Rafinesque 1820) and *Fusconaia flava* (Rafinesque 1820) in Lake Pepin, and *Lasmigona costata* (Rafinesque 1820) and *F. flava* in the Otter Tail River. The aim of this research was to measure baseline survivorship rates of these mussels in addition to survivorship under various levels of *D. polymorpha* infestations. The Otter Tail bed was included in this study to act as a reference because it is known to have a diverse mussel assemblage, free of *D. polymorpha* (Hart 1995). *A. plicata* were studied in this research primarily because 1) they are currently subjected to commercial harvest in Lake Pepin and other portions of the Mississippi River and 2) their populations are large enough to allow for statistical testing of the null hypothesis that there is no difference in survivorship of *A. plicata* under differing levels of *D. polymorpha* infestations. Since *A. plicata* is susceptible to *D. polymorpha* infestations (Baker and Hornbach 1997), estimates of survivorship rates of these populations are needed to assess the potential impacts of *D. polymorpha*. The results of this study will be useful for not only predicting changes in survivorship rates of *A. plicata* and *F. flava* under various levels of *D. polymorpha* infestations, but results will also provide baseline data regarding survivorship of *A. plicata*, *L. costata*, and *F. flava* in areas that are not currently colonized with *D. polymorpha*.

METHODS

Study Site Selection

This study was conducted in Lake Pepin, a natural lake in the Upper Mississippi River on the Minnesota-Wisconsin border (Fig. 2.1). A reference site was selected in the Otter Tail River, located in western Minnesota (Fig. 2.1). Lake Pepin extends from river mile (RM) 787 near Red Wing, MN, to RM 763.5 near Read's Landing, MN.

Seven mussel beds within Lake Pepin were stratified based on densities of *D. polymorpha* estimated from 30 (0.25 m^2) quadrat samples collected from each bed during the summer of 1995. (See Paper 1 of this dissertation.) Beds were stratified as having either low (0-10 *D. polymorpha*/m^2), moderate (25-100 *D. polymorpha*/m^2), or high (>250 D. polymorpha/m^2) densities of *D. polymorpha* in 1995, with one bed selected for study from each density strata. The low infestation site (LIS) was located at Methodist Point (RM 779), the moderate infestation site (MIS) at Hok Si La (RM776), and the high infestation site (HIS) at King's Coulee (RM767) (Fig. 2.1), each having densities of *D. polymorpha* equal to 0.4, 50.5, and 1750 *D. polymorpha*/m^2, respectively. The reference study site (CSS) in the Otter Tail River was randomly selected from a pool of 3 mussel beds known to have populations of *A. plicata* (Hart 1995). An additional site was selected near the outlet of Lake Pepin at Lacupolis (LCP) for the study of survivorship of *E. dilatata* and *F. flava* (Fig. 2.1).

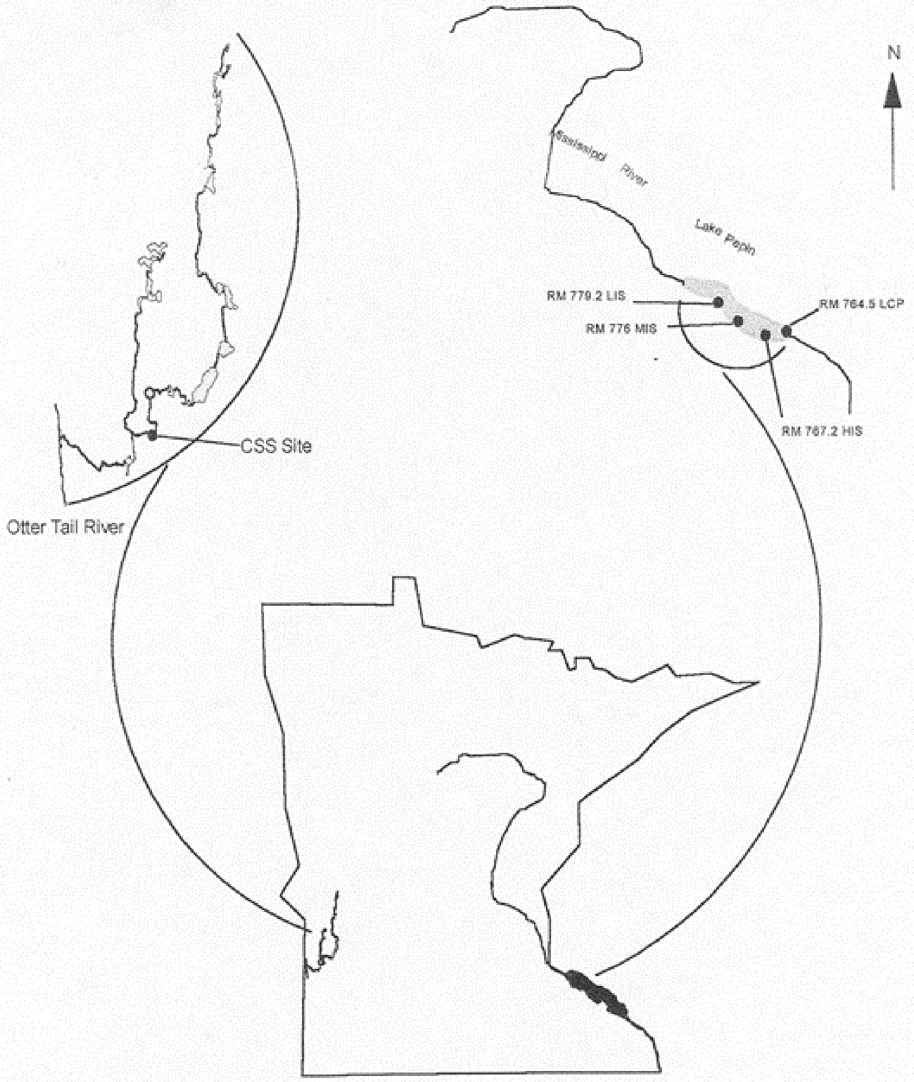

Figure 2.1. Mark/recapture sites, Lake Pepin, Minnesota and Wisconsin, and the Otter Tail River, Minnesota.

Mussel Marking and Recapture

During the summer of 1996 at each of these mussel beds, 240 *A. plicata* (Say 1817) per bed (960 total) were collected by divers using scuba. Divers at each bed collected every *A. plicata* they encountered by touch until 240 individuals were collected. At the LCP, site 240 *E. dilatata* and 79 *F. flava* were collected. In addition, 240 *F. flava* and 113 L*. costata* were collected from the CSS. During processing, collected mussels were held in mesh bags tied to the work boat, and lowered to the substrate-water interface. Mussels being processed in the boat were held in a 20-liter pail of water. Water in the pails was exchanged after every 10 mussels were processed to ensure oxygen levels were kept relatively constant.

Collected mussels were measured for shell length and height, and marked with a predetermined code etched into the right valve of the shell with the use of a battery-operated Dremel® tool. If *D. polymorpha* were attached to the marked native mussels, they were counted and left on the individual. An exception to these procedures was that of the 240 *E. dilatata* that were marked; we removed *D. polymorpha* from the shells of 48 individuals. This action was done to determine infestations rates of *D. polymorpha* upon *E. dilatata* and to determine the efficacy of *D. polymorpha* removal as it relates to survivorship of the unionid.

Marked mussels were placed in replicated, low, open corrals. The corrals at each of the 5 marking beds were constructed from 20, 10 cm high x 60 cm diameter, plastic cylinders attached to a wooden frame. These corrals were then anchored to the lake bed with concrete blocks. Twelve marked *A. plicata* were hand placed in each of the 20 cylinders. Marked *E. dilatata*, *L. costata*, and *F. flava* were treated in a manner similar to the *A. plicata*. Corrals were primarily designed to assist the diver in relocating marked mussels, while still allowing for movement of unionids within their individual cylinders. Corral locations were recorded with a global positioning system and augmented with field notes.

At each of the mussel beds in July or August 1997 and 1998, marked mussels were recovered by divers; returned to the boat; identified by their unique numbers; measured for shell length and height, survivorship determined; and if alive, returned to the corral. To test for differences in demographic size ratios of *A. plicata* between sites, mussels were assigned to one of three size groups based on shell length at the time of marking: small (≤ 72 mm), medium (72<x≤84 mm), or large (>84 mm).

Survivorship and sizes of marked *A. plicata*, both within and among study beds, were analyzed with contingency tables (Zar 1984). Survival rates were compared within and between sites using the statistical techniques presented in Sauer and Williams (1989). Mussels that were not recovered in both 1997 and 1998 were not included in mean annual survivorship analysis. To maintain an overall error rate of 0.05, p-values for each contingency test and comparison were adjusted with a sequential Bonnferoni correction (Rice 1990).

Log-linear models were used to test for interactions between the measured variables. Unlike standard ANOVAs which are primarily used to look for treatment effects, log-linear models are used to investigate the interaction of variables (Kennedy 1983, Zar 1984). Log-linear modeling begins with testing a fully saturated model containing all possible combinations of interactions. If no interactions are detected in the saturated model, modeling progresses to lower-order models (Sokal and Rohlf 1981). Using this approach, we subjectively looked for the model which resulted in a p-value greater than 0.05 (Stokes et al. 1995) and then accepted the next lowest model as the most parsimonious. We also tested for significant differences in the number of *D. polymorpha* present on marked *A. plicata* (colonization rates) within and among study beds with ANOVAs.

RESULTS

Survivorship of *A. plicata*

Recovery of marked *A. plicata* was high at all four of the mussel beds throughout the study. Recovery rates from 1996-98 at the CSS, LIS, MIS, and HIS beds were 95.4%, 93.3%, 94.8%, and 74.2% respectively.

Overall survivorship of *A. plicata* was high at the CSS bed as well as at the LIS and MIS mussel beds where *D. polymorpha* were found in low and moderate numbers. In contrast, survivorship was much lower at the HIS mussel bed with high *D. polymorpha* densities. Overall survivorship from 1996-98 was not significantly different between the CSS and LIS beds ($\chi^2_{df=1}$=2.22, p<0.14), and the CSS and MIS beds ($\chi^2_{df=1}$=1.80, p<0.18). Survivorship across all size classes was significantly different at CSS and HIS ($\chi^2_{df=1}$=110.49, p<0.0005), LIS and HIS ($\chi^2_{df=1}$=124.14, p<0.0005), LIS and MIS (χ^2=7.30,$_1$, p=0.021), and MIS and HIS beds ($\chi^2_{df=1}$=92.21, p<0.0005) (Fig. 2.2).

Also, when we excluded the mussels that were missing in 1997 from survival rate calculations, as their fate was unknown in 1997, and calculated mean annual survivorship, there were significant differences in survival rates among the CSS (98%), LIS (99%), and MIS (98%) beds compared to the HIS bed (76%) ($\chi^2_{df=3}$=91.93, p<0.00001) (Fig. 2.3).

Mean annual survivorship among size classes within beds was not significantly different at the LIS ($\chi^2_{df=2}$=3.20, p=0.20), MIS ($\chi^2_{df=2}$=2.82, p=0.24), and HIS beds ($\chi^2_{df=2}$=3.64, p=0.16) (Fig. 2.3). However, survivorship differed

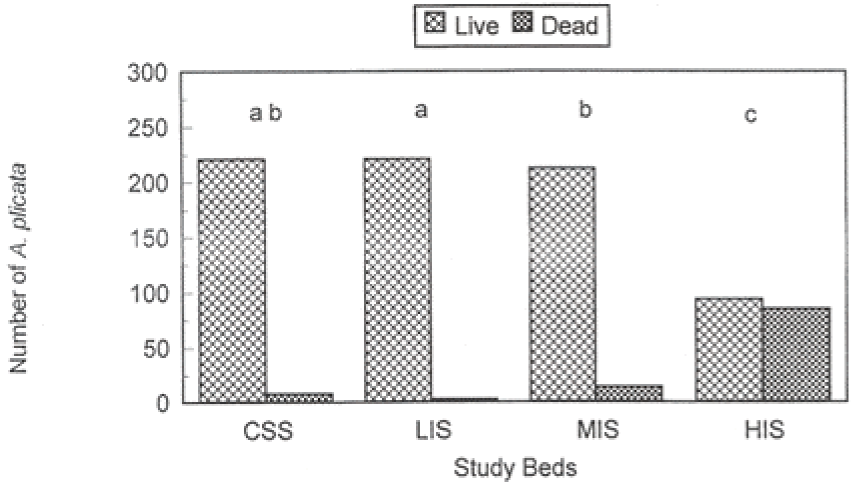

Figure 2.2. Overall survivorship of *A. plicata* across all size classes, 1996-98. Sites with a common letter are not significantly different, chi-square ($p>0.05$).

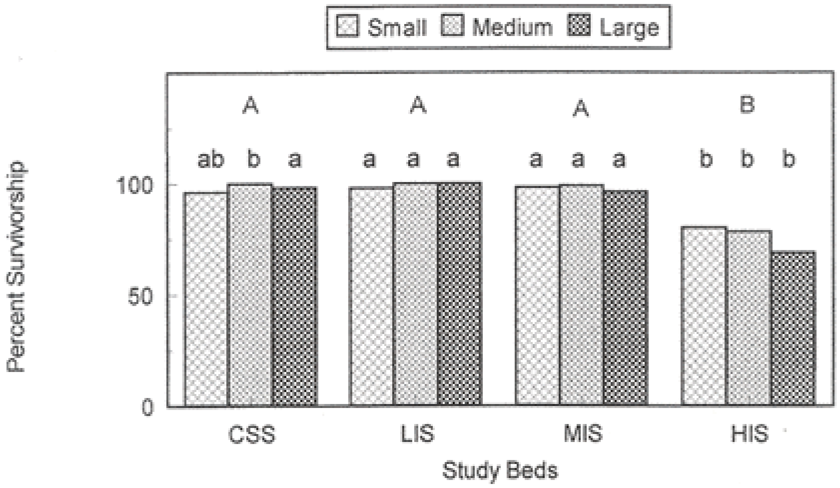

Figure 2.3. Mean annual survivorship of *A. plicata* within size classes. Data are from 1996-98. Rates with a common uppercase letter are not significantly different between beds ($p>0.05$), and rates with a common lowercase letter are not significantly different within beds ($p>0.05$).

among size classes at the CSS bed ($\chi^2_{df=2}$=7.20, p=0.03), with larger-sized mussels showing greater mortality compared to medium-sized individuals ($\chi^2_{df=1}$=5.19, p=0.02) (Fig. 2.3). The difference in survivorship among size classes in the Otter Tail bed is statistically significant, but perhaps not biologically significant, as we recovered only 8 dead mussels, with 221 of the 240 marked being found alive at the end of the study (Fig. 2.2). In contrast, 85 of the 240 marked mussels were found dead at the HIS bed (Fig. 2.2).

We used contingency tables to test for differences in size distributions of the marked mussels to determine if they differed between sites. This analysis was done to test if size, hence age, influences survival. Size distributions of marked mussels were not significantly different at the LIS and HIS beds ($\chi^2_{df=2}$ =1.38, p=0.50) (Fig. 2.4). Yet, size distributions were significantly different at the LIS and MIS beds ($\chi^2_{df=2}$ =32.65, p<0.0004) and MIS and HIS beds ($\chi^2_{df=2}$=18.62, p<0.0004), while the CSS size distributions were significantly different from all other beds (p<0.0005) (Fig. 2.4).

Log-linear modeling revealed that the main effects in the saturated model were significant, but indicated no significant 3 or 4-way interactions. The model containing year x survival, site x survival, and site x size interactions was the most parsimonious model for these data (Table 2.1). This model indicated that survivorship is highly dependent upon site (a category of *D. polymorpha* density), mussel size, and year to a lesser degree.

The differential survival among the mussel beds prompted us to investigate

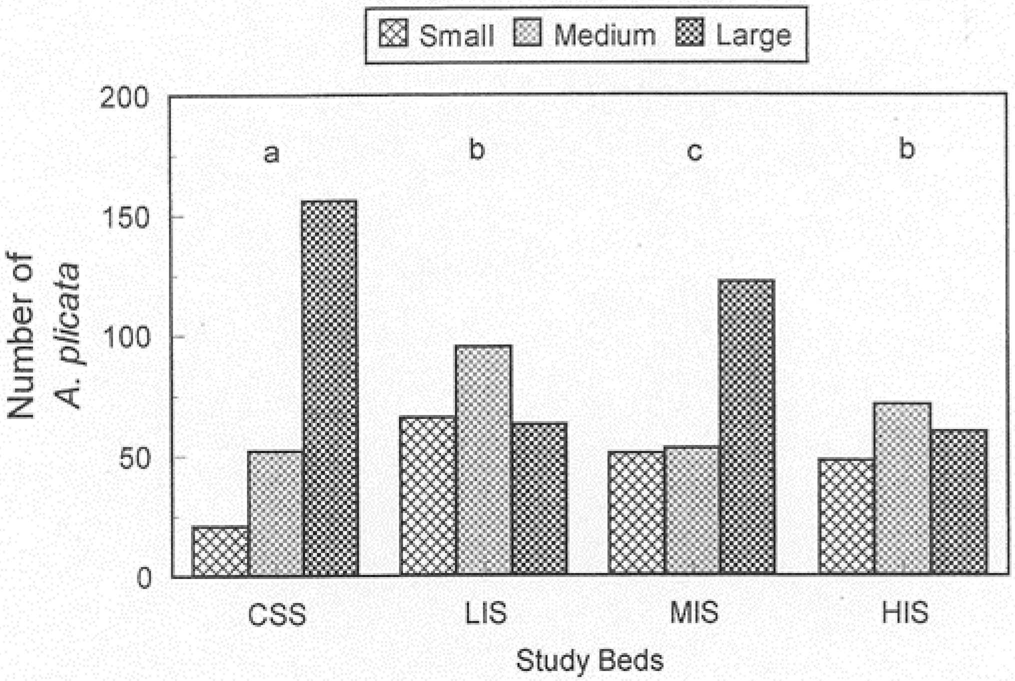

Figure 2.4. Size distributions of marked *A. plicata.* Sites with a common letter are not significantly different (p>0.05).

Table 2.1. Log-linear test of *A. plicata* survivorship in relation to site and size.

Source	Degrees of Freedom	Chi-Square	Probability
Year	1	4.70	0.0302
Survival	1	202.24	0.0001
Year x Survival	1	11.46	0.0007
Site	3	21.86	0.0001
Survival x Site	3	85.80	0.0001
Size	2	92.21	0.0001
Site x Size	6	141.89	0.0001
Likelihood Ratio	21	38.51	0.0112

the degree of *D. polymorpha* infestation rates within beds. The Otter Tail River has not been invaded by *D. polymorpha,* so it was not included in this analysis. From 1996-98, the mean number of *D. polymorpha* attached to marked *A. plicata* was significantly different between the three beds within Lake Pepin ($F=190.36_{df = 8,1943}$, $p<0.05$). Tukey's post hoc multiple comparison tests revealed significant differences in infestation rates between the LIS and HIS, and MIS and HIS beds ($p<0.05$), yet there were no significant differences within these beds over the course of this study ($p>0.05$) (Fig. 2.5).

Survivorship of *E. dilatata*

Recovery of marked *E. dilatata* was high over the course of this study (>80% from 1996-97). Mean annual survivorship was similar for both groups of marked mussels that had either *D. polymorpha* removed or retained during the initial marking process. Survival rates of *E. dilatata* that had *D. polymorpha* removed (97%) vs those which retained *D. polymorpha* (92%) were not significantly different ($\chi^2_{df = 1}=3.54$, $p=0.06$) (Fig. 2.6).

D. polymorpha re-infested those individuals of *E. dilatata* that were cleaned in 1996. Colonizations of cleaned *E. dilatata* were significantly different from those *E. dilatata* that had not been cleaned of *D. polymorpha*. While there were significant differences between years in the number of *D. polymorpha* colonized on the *E. dilatata* within treatments, i.e. cleaned vs. uncleaned, ($F=56.137_{df=5}$, $P<0.00001$), the number of *D. polymorpha* between treatment groups was not significantly different among years (Fig. 2.7). The number of *D. polymorpha* on

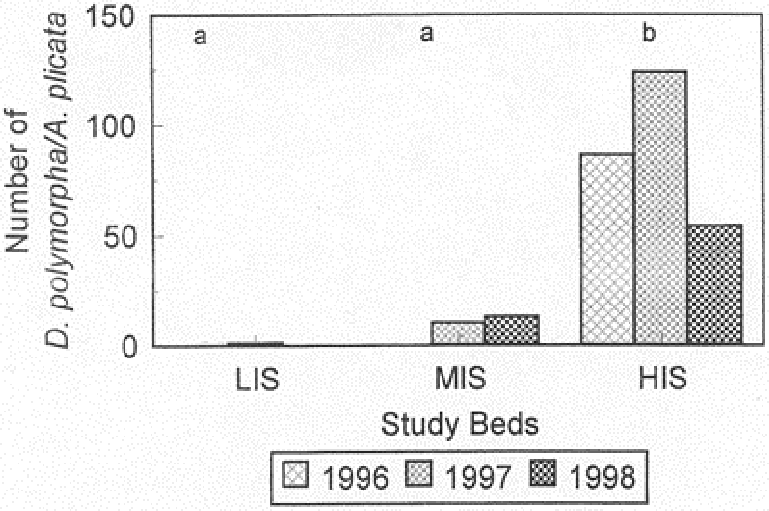

Figure 2.5. Mean number of *D. polymorpha* attached to *A. plicata* at the study sites from 1996-98. Means with a common letter are not significantly different, ANOVA with Tukey's multiple comparison test, (p>0.05).

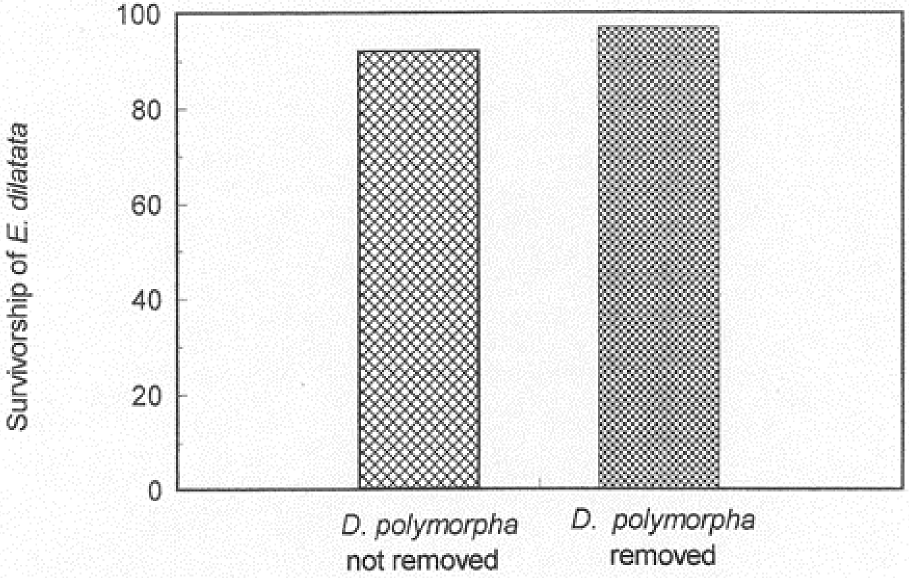

Figure 2.6. Mean annual survivorship of *E. dilatata*, 1996-98, LCP site, individuals with *D. polymorpha* vs. individuals with *D. polymorpha* removed in 1996, no significant difference $X^2_{df=1} = 3.55$, p= 0.06.

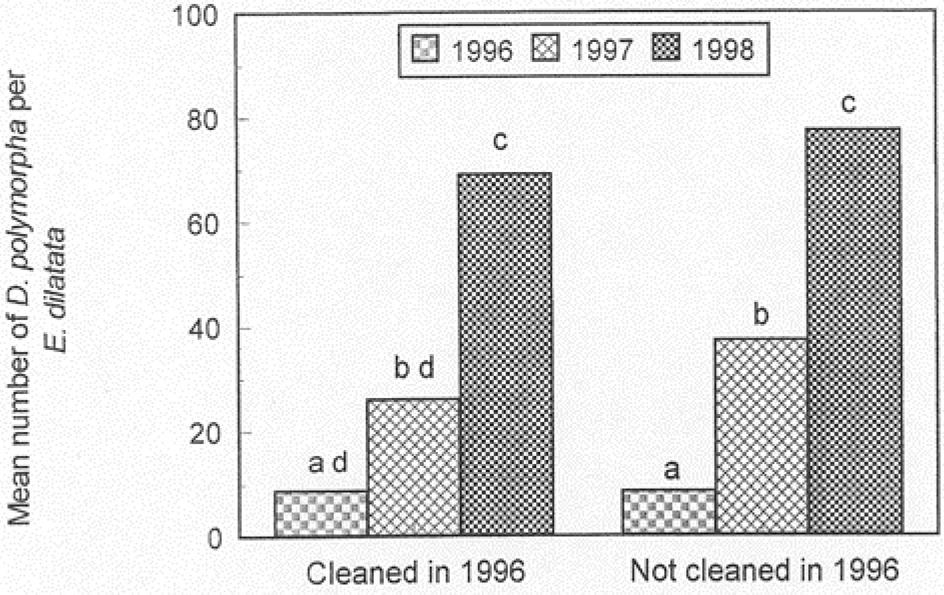

Figure 2.7. Mean number of *D. polymorpha* infested upon *E. dilatata* at the LCP site, 1996-98. Individuals cleaned of *D. polymorpha* in 1996 are compared to individuals not cleaned of *D. polymorpha*. Means with a common letter are not significantly different (p>0.05), ANOVA, Tukey's multiple comparison test.

those individuals in 1998 that were both cleaned and left uncleaned in 1996 was equal to about 70.

Survivorship of *F. flava*

Survival rates of marked *F. flava* in the Otter Tail River and Lake Pepin were significantly different, 99.29% and 90.25%, respectively ($\chi^2_{df = 1}$ =6.03, p=0.01) (Fig. 2.8). Colonizations of *D. polymorpha* upon marked *F. flava* in the Lake Pepin site were less than 10 *D. polymorpha*/*F. flava* in 1996, increasing to over 70/*F. flava* in 1998 (Fig. 2.9). This colonization of *F. flava* was not a factor in survivorship for the *F. flava* mussels in the Otter Tail River because there are no *D. polymorpha* present.

Survivorship of *L. costata*

Recovery of marked *L. costata* was equal to over 90% from 1996-98. Survivorship of this mussel species was extremely high and was equal to over 99% over the course of this study (Fig. 2.10). This survival rate is similar to the rates measured for the other species of mussels studied in the Otter Tail River.

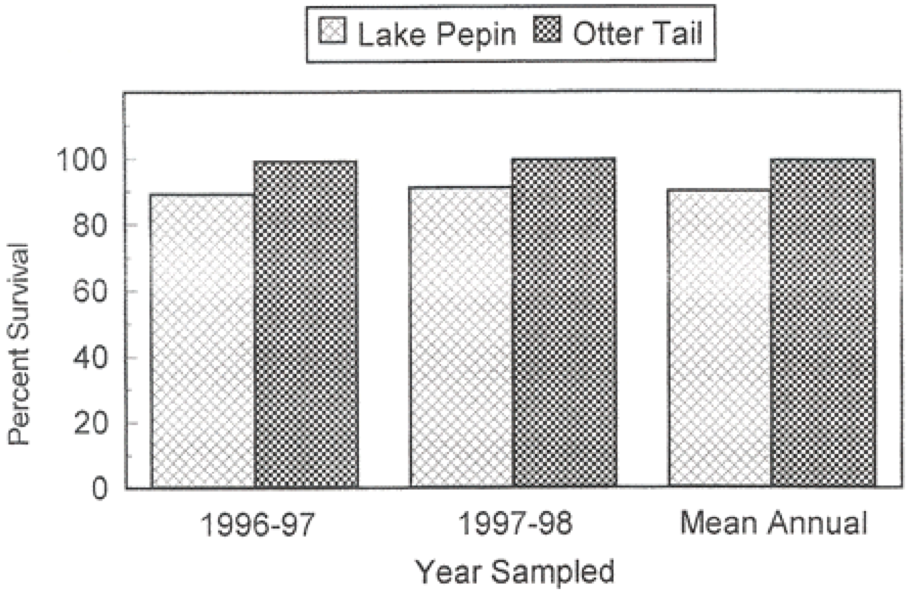

Figure 2.8. Annual survivorship of *F. flava*, LCP and the CSS sites.

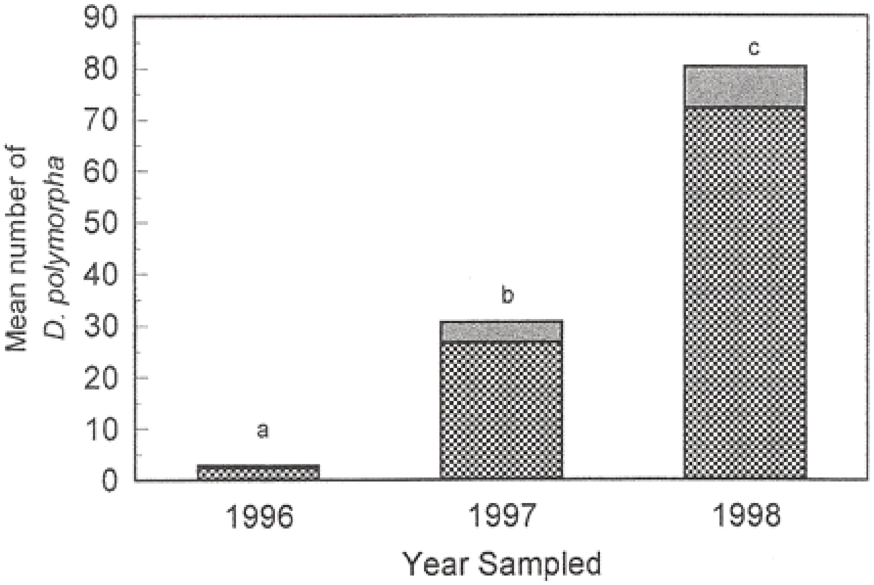

Figure 2.9. Mean number of *D. polymorpha* infested upon marked *F. flava*, LCP site, 1996-98. Means with a common letter are not significantly different (p>0.05), ANOVA and Tukey's multiple comparison test.

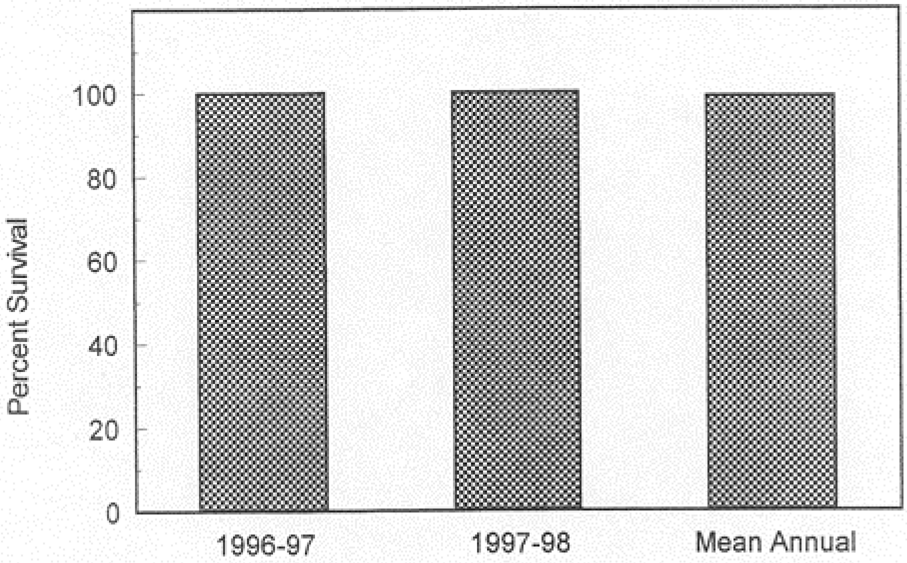

Figure 2.10. Annual survivorship of *L. costata*, CSS site, 1996-98.

DISCUSSION

We attribute the difference in survivorship of *A. plicata* between the HIS and all other beds to the high levels of *D. polymorpha* infestations found at the HIS bed. Mean annual survivorship within size classes of *A. plicata* was much lower in the HIS bed then in the relatively infestation free LIS bed, while size class distributions were statistically similar. Additionally, no significant difference in mean annual survivorship was detected between the LIS (99%), MIS (98%), and CSS (98%) beds, even though they differed slightly in size distributions. Furthermore, the LIS and HIS beds had statistically the same size distributions, yet differed greatly in survivorship. Therefore, we believe the differential survival measured in this study cannot be attributed to size differences in marked mussels. The survivorship of *A. plicata* measured at the LIS, MIS, and CSS beds was much greater than rates reported for other mussel species. Survival of *L. costata* and *F. flava* at the CSS beds was also extremely high. Survival of *D. polymorpha*- colonized *F. flava* was much lower compared to the non-infested population at the CSS bed. The lowered survival of *F. flava* indicates that *D. polymorpha* adversely impacted this relatively thick-shelled mussel species. While we do not have another site with which to compare survival of *E dilatata*, it does seem apparent that their survival is being lowered by *D. polymorpha* infestations as well. Individuals cleaned of *D. polymorpha* were colonized to levels equal to their uncleaned counterparts by the time this study concluded. These results suggest that cleaning unionids of *D. polymorpha*, unless done on an annual basis, does not increase the long-term probability of their survival.

We concur with Ricciardi et al. (1995) that there is a lack of directly measured survivorship data in the literature. Cope and Waller (1995) provided an extensive review of native mussel mortality associated with relocation efforts. However, the majority of these studies have several confounding variables, making comparisons with our survival estimates difficult. In an experiment to assess handling impacts on relocated mussels, Waller et al. (1995) measured survivorship of *A. plicata* over a 4-5 month time period. While their experiments were shorter in duration than ours, they reported survival rates similar to what we observed at the relatively uninfested LIS bed (survivorship > 90%, this study). Dunn (1993) reported survivorship rates of *A. plicata* ranging from 29-55% over the course of 4 years of monitoring relocated mussels. Although these survival rates appear low, Dunn (1993) states that the "mortality" may be due to migration of the marked mussels away from her site. Thus, Dunn's (1993) results may actually be recovery rates, and exclusion of unrecovered mussels may have produced survival rates similar to those observed in this study. In our analysis we used only live and dead recoveries, and did not include mussels whose fates were unknown.

Negus (1966) reported mean annual survivorship of 78% for 5-8 year old *Anodonta anatina* in the Thames River, but used a life-table approach versus direct measurements. Menkens and Boyce (1993) stated the use of life tables may be wrought with pitfalls, including unattainable assumptions, and should be used only with independent, supporting data. Therefore, since Negus (1966) used a very different approach than we did to determine survivorship and *Anodonta anatina* is reported to be a relatively short-lived species, her results are probably not comparable to what we measured for *A. plicata*.

While the aforementioned researchers measured survivorship in areas that were not currently infested with *D. polymorpha*, our study allowed for the direct comparison of survivorship rates in areas of the same water body that had both low and high levels of *D. polymorpha,* as well as in a river that has not yet been invaded with *D. polymorpha*.

The HIS population of *A. plicata* in Lake Pepin exhibited lower survivorship when compared to the other populations within the lake and at the reference bed in the Otter Tail River. The year x survival and site x survival interactions indicate that survivorship is dependent upon the year survivorship was measured, and, perhaps more importantly, the location and hence the number of *D. polymorpha* that have colonized the unionids. The site x size interaction revealed in the log-linear model was also significant in the contingency table analysis. The size distributions of marked mussels at the CSS and MIS beds were different from both the HIS and LIS beds, yet the *A. plicata* at the CSS and MIS beds exhibited survivorship similar to the LIS bed. Therefore, we believe the size of the mussels in these populations was not a large contributor to overall survival in this study. The interaction terms of year x survival and site x survival is most evident within the HIS bed since the other populations of marked mussels exhibited such low mortality. The higher mortality rate of mussels at the HIS bed indicates survival of *A. plicata* is greatly influenced by *D. polymorpha* colonization.

The significant site x survival interaction reinforces our finding that survivorship of unionid mussels was highly dependent upon the number of *D. polymorpha* attached to the native mussels. Ricciardi et al. (1995) predicted severe mortality

(>90%) when densities of *D. polymorpha* reach about 6000 mussels/m^2 and 100 *D. polymorpha*/unionid. We did not measure mortality this high, yet, it seems likely that, in the next few years with increasing densities of *D. polymorpha* and, hence, greater infestations of unionids in Lake Pepin, lowered unionid survival will become evident.

We report the declines in survivorship of *F. flava* and *A. plicata*, two species noted as relatively hardy when infested with *D. polymorpha* (Haag et al. 1993, Baker and Hornbach 1997). Therefore, it is even more cause for concern for the other less resilient mussels that also inhabit the habitats of *F. flava* and *A. plicata* (Haag et al. 1993, Gillis and Mackie 1994, Nalepa 1994). Some of these thin shelled species have been shown to be impacted more severely than *A. plicata* (Haag et al. 1993, Baker and Hornbach 1997). Considering Haag et al.'s (1993) and Baker and Hornbach's (1997) results, it appears the rather high mortality we measured for *D. polymorpha* infested *A. plicata* and *F. flava* would be even greater for other species under conditions similar to what we measured.

The large difference in survivorship of the HIS and LCP mussels, compared to the uninfested mussel populations, is alarming. The decline in populations of other long-lived organisms due to reduced adult survival has been well documented. Congdon et al. (1994) modeled survivorship of snapping turtles (*Chelydra serpentina*), a long-lived aquatic organism much like *A. plicata*, and showed population stability was most sensitive to changes in adult and juvenile survivorship. Their models predicted that a 10% increase in adult mortality would result in the adult population being reduced by one-half over a 20-year time period. The significant declines in adult survival that we measured will most likely have a negative effect on mussel populations in the future, much like it has been documented in other animals with similar life history traits. Therefore, we believe that freshwater mussel populations will experience continued declines in Lake Pepin if *D. polymorpha* infestations continue at their current rate.

LITERATURE CITED

Baker, S. M., and D. J. Hornbach. 1997. Acute physiological effects of zebra mussel (*Dreissena polymorpha*) infestations on two unionid mussels, *Actinonaias ligamentina* and *Amblema plicata*. Canadian Journal of Fisheries and Aquatic Sciences 54:512-519.

Congdon, J. D., A. E. Dunham, and R. C. van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): Implications for conservation and management of long-lived organisms. American Zoologist 34:397-408.

Cope, W. G., and D. L. Waller. 1995. Evaluation of freshwater mussel relocation as a conservation and management strategy. Regulated Rivers: Research and Management 11:147-155.

Dunn, H. L. 1993. Survival of Unionids four years after relocation. In Conservation and Management of Freshwater Mussels, Proceedings of a UMRCC Symposium. K. S. Cummings, A. C. Buchanan, and L. M. Koch eds. Upper Mississippi River Conservation Committee. Rock Island, IL.

Fitzsimons, J. D., J. H. Leach, S. J. Nepszy, and V. W. Cairns. 1995. Impacts of zebra mussel on walleye (*Stizostedion vitreum*) reproduction in western Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 52:578-586.

Gillis, P. L., and G. L. Mackie. 1994. Impact of the zebra mussel, *Dreissena polymorpha,* on populations of Unionidae (Bivalvia) in Lake St. Clair. Canadian Journal of Zoology 72:260-1271.

Haag, R. W., D. J. Berg, D. W. Garton, and J. L. Farris. 1993. Reduced fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in Western Lake Erie. Canadian Journal of fisheries and Aquatic Sciences 50:13-19.

Hart, R. A. 1995. Mussel (Bivalvia: Unionidae) habitat suitability criteria for the Otter Tail River, MN. Master's thesis, North Dakota State University, Fargo, ND.

Kennedy, J. J. 1983. Analyzing Qualitative Data Introductory Log-Linear Analysis for Behavioral Research. Praeger, New York, NY.

Ludyanskiy, M. L., D. McDonald, and D. MacNeill. 1993. Impact of the zebra mussel, a bivalve invader. Bioscience 43:533-544.

MacIsaac, H. J. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland water of North America. American Zoologist 36:287-299.

Menkens, Jr., G. E., and M. S. Boyce. 1993. Comments on the use of time-specific and cohort life tables. Ecology 74:2164-2168.

Nalepa, T. F. 1994. Decline of native bivalves (Unionidae: Bivalvia) in Lake St. Clair after infestation by the zebra mussels *Dreissena polymorpha*. Canadian Journal of Fisheries and Aquatic Sciences 51:2227-2233.

Negus, C. L. 1966. A quantitative study of growth and production of unionid mussels in the River Thames at Reading. Journal of Animal Ecology 35:513-532.

Ram, R. L., and R. F. McMahon. 1996. Introduction: The biology, ecology, and physiology of zebra mussels. American Zoologist 36:239-243.

Ricciardi, A., R. J. Neves, and J. B. Rasmussen. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. Journal of Animal Ecology 67:613-619.

Ricciardi, A., F. G. Whoriskey, and J. B. Rasmussen. 1995. Predicting the intensity and impact of *Dreissena* infestations on native unionid bivalves from Dreissena field density. Canadian Journal of Fisheries and Aquatic Sciences 52:1449-1461.

Rice, W. R. 1990. A consensus combined p-value test and the family-wide significance of component tests. Biometrics 46:303-308.

Sauer, J. R., and B. K. Williams. 1989. Generalized procedures for testing hypothesis about survival or recovery rates. Journal of Wildlife Management 53:137-142.

Schloesser, D. W., W. P. Kovalak, G. D. Longton, K. L. Ohnesorg, and R. D. Smithee. 1998. Impact of zebra and quagga mussels (*Dreissena* spp.) On freshwater unionids (Bivalvia: Unionidae) in the Detroit River of the Great Lakes. American Midland Naturalist 140:299-313.

Schloesser, D. W., and T. F. Nalepa. 1994. Dramatic decline of unionid bivalves in offshore waters of Western Lake Erie after infestation the zebra mussel, Dreissena polymorpha. Canadian Journal of Fisheries and Aquatic Sciences 51:2234-2242.

Schloesser, D. W., T. F. Nalepa, and G. L. Mackie. 1996. Zebra mussel infestation of unionid bivalves (Unionidae) in North America. American Zoologist 36:300-310.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Company, San Francisco, CA.

Stokes, M. E., C. S. Davis, and G. G. Koch. 1995. Categorical Data Analysis Using the SAS System. SAS Institute, Inc., Cary, NC.

Tucker, J. K., C. H. Theiling, K. D. Blodgett, and P. A. Thiel. 1993. Initial occurrences of zebra mussels (*Dreissena polymorpha*) on freshwater mussels (family Unionidae) in the upper Mississippi River system. Journal of Freshwater Ecology 8:245-251.

Waller, D. L., J. J. Rach, W. G. Cope, and G. A. Miller. 1995. Effects of handling and aerial exposure on the survival of unionid mussels. Journal of Freshwater Ecology 10:199-207.

Zar, J. H. 1984. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, NJ.

PAPER 3. POPULATION VIABILITY ANALYSIS OF *Amblema plicata* (Say 1817) MUSSEL POPULATIONS SUBJECTED TO HARVESTING AND *Dreissena polymorpha* (Pallas 1771) INFESTATIONS IN LAKE PEPIN, UPPER MISSISSIPPI RIVER, MINNESOTA

ABSTRACT

We simulated populations of *Amblema plicata* (Say 1817) using empirically derived survival rates. The software package VORTEX was used to develop a base line population model which exhibited little or no change through time. Models based on the initial base line data were constructed to simulate behaviors of *A. plicata* populations under various levels of mortality attributed to *Dreissena polymorpha* (Pallas 1771) colonizations. Models were also developed that simulated varying levels of commercial harvesting of *A. plicata*. Sensitivity analysis revealed that *A. plicata* populations are most sensitive to alterations in adult survival. It is adult survival that is the life history stage that is most often impacted by both *D. polymorpha* colonizations and commercial harvesting. Population models simulating *D. polymorpha* induced mortality revealed that population extinction was likely to occur within about 50 years if survivorship is held at the levels that have recently been measured. Models that simulated a commercial harvest of only 5% of the adult *A. plicata* population predict that populations will decline by almost 50% in only 40 years. These modeling efforts will be useful for resource managers striving to establish a sustainable harvest of a commercially valuable species which is currently competing with a non-indigenous species.

INTRODUCTION

Population viability analyses (PVA), the study of the processes and causes of population extinction (Soulé 1987, Shaffer 1990), have been performed for numerous plant and animal species throughout the world (e.g., Lindenmayer et al. 1995, Song 1996). The primary reasons for these analyses has been to assess the impact that environmental and human-induced disturbances may have on the affected populations (Lindenmayer et al. 1995), therefore facilitating the assignment of a probability of extinction for the population under study.

Like most other animal groups, freshwater mussel populations have been exposed to a variety of environmental and human mediated disturbances. The most detrimental impacts upon mussels have been attributed to habitat destruction (Stansbery 1970, Williams et al. 1993), over-harvesting of commercially valuable species (Smith 1919, Fuller 1978), and the invasion of non-indigenous species (Haag et al. 1993, Gillis and Mackie 1994, Schloesser and Nalepa 1994).

Freshwater mussels have been harvested and studied throughout the major North American river drainages since the late 1800s (Smith 1898, Wilson and Danglade 1914). The primary objectives of these studies were to locate mussel beds suitable for harvest (Wilson and Danglade 1914) and to assess the impacts the harvesting was having on the resident mussel communities (Smith 1919, Southall 1925). These early studies revealed that while a strictly controlled harvest may not deplete mussel stocks, over-harvesting does have devastating effects on native mussels (Smith 1919, Southall 1925).

Because of concern of the impacts harvesting may have on mussel populations, the state of Minnesota closed the mussel harvesting season on inland lakes and rivers, and increased size restrictions for the harvesting of *Amblema plicata* (Say 1817) mussels from the border waters of the Mississippi River. These measures were taken to provide an additional level of protection for the mussel communities.

There is also concern pertaining to the impacts that the recently arrived non-indigenous species *Dreissena polymorpha* (Pallas 1771) may have on the long-term persistence of native mussel populations (Williams et al. 1993). Survival of *A. plicata* has been shown to decrease from about 98% to 75% when individuals were infested with over 100 *D. polymorpha* for several years. (See Paper 2 in this dissertation).

We simulated Lake Pepin *A. plicata* populations with the use of the software package VORTEX (Lacy 1993), to predict their fates under varying levels of commercial harvesting and *D. polymorpha* infestations. The models we developed examined the effects of alteration in demographic and environment variation, which were simulated to mimic increases in baseline mortality rates. Alterations of mortality rates were designed to simulate varying levels of commercial harvest of adult *A. plicata*, as well as the decreasing survivorship attributed to *D. polymorpha* infestations. These modeling efforts were conducted to assist in the development of management strategies that will aid in ensuring the persistence of these mussel populations into the future.

We chose VORTEX because this software incorporates an individual-based stochastic model which uses a Monte Carlo approach to simulate demographic and environmental stochastic occurrences that may affect the target populations (Lacy 1993). VORTEX also conducts a standard deterministic life table analysis using the Leslie matrix method (Leslie 1945, Lacy and Clark 1993).

METHODS

Baseline Model Assumptions and Development

Baseline population models were developed to simulate a stationary mussel population. *A. plicata* populations modeled in this exercise were considered to be like most other mussels thus, having a 50:50 sex ratio and being polygynous. An additional assumption of these models was that all breeding-age males participated in breeding activities, with the age of breeding and senescence assigned to the ages of 10 and 30 years, respectively, for both males and females.

We included a density-dependent function for reproduction which modeled the probability that successful mussel reproduction would decline when population sizes declined (Lacy et al. 1995; see Kjos et al. 1998 for a description of the density-dependent function). This assumption is realistic considering that unionid mussels reproduce by the males broadcasting their sperm cells into the water column, with the females having to draw the sperm into their gill chambers through their in-current siphons (McMahon 1991). Therefore, it is intuitive that when there are fewer individuals present in the population, the probability that a female would draw in water containing sperm cells would decrease.

Because it is known that female unionid mussels can produce well over 100,00 glochidia (McMahon 1991), we developed a juvenile survivorship schedule that did not incorporate glochidia, but instead used an estimate of the mean number of offspring that successfully settle on suitable substrate after their parasitic life stage has metamorphosed. This method allowed for the number of offspring incorporated into the model to be at a level that would not exceed computer memory, yet would still be realistic (McMahon 1991, Kjos et al. 1998). In calculating the estimate for the number of offspring, we used techniques following those presented in Kjos et al. (1998). For the baseline model, we estimated the mean number of offspring landing onto suitable substrate, herein called age 0, produced by a successfully breeding female to be 10.

This average number of offspring was then used in the following calculations. We first calculated juvenile survivorship, age 0-<10 years of age, by developing a survivorship schedule that would result in the initial 10 offspring produced by an average female being reduced to a total of 2 individuals surviving to breeding age over the course of the breeding female's life span. This schedule was developed by calculating the number of offspring required to survive to breeding age per successful female per breeding event (OR) as OR = 2/(LE/(PB*LE)), where LE = the life expectancy after breeding age and PB = the percentage of females that successfully breed in a given year.

Knowing the required number of offspring that must survive to breeding age per breeding event, we used a life table modeling approach to back calculate the mean number of offspring produced by a female with appropriate age specific juvenile mortality rates. This model results in a juvenile survivorship schedule that effectively replaces a female and her mate with 2 offspring surviving to breeding age. The baseline survivorship schedule that was used in the stationary population growth model is shown in Table 3.1. Because we are only modeling the females with the life table, the sum of the $l_x m_x$ column should equal 1 for a stationary population (Krebs 1994). The sum of the $l_x m_x$ column for our stationary model is equal to

0.99657, which validates the assumption of the baseline model being stationary with regards to population growth (Table 3.1).

The baseline survivorship rates calculated for the juvenile mussels were used as inputs in the VORTEX model. Baseline stationary adult survivorship was calculated as the average survivorship measured at the CSS and MIS sites within the Otter Tail River, and Lake Pepin, Minnesota (Fig. 3.1), and was used as model inputs. Environmental variation (EV) in survivorship was calculated as demographic, or expected variation, ie., the binomial variance (p(1-p)/n-1)), minus the observed inter-year variation (Lacy 1993, Lacy et al. 1995). We used the average EV of the CSS, LIS, and MIS sites for the baseline models. (See Paper 2 of this dissertation for site descriptions.)

Initial population sizes for the simulations were set at 30,000 mussels which is the maximum amount allowed in VORTEX models (Lacy et al. 1995), while carrying capacity, or the population ceiling, was set at an additional 50% of the initial population size. While the number of individuals (30,000) used as the initial population size is undoubtably less than the number of mussels inhabiting the mussel beds of Lake Pepin, a higher number of mussels used in the simulations would not have had any appreciable difference in the results of the models because processes involving this many individuals become increasingly

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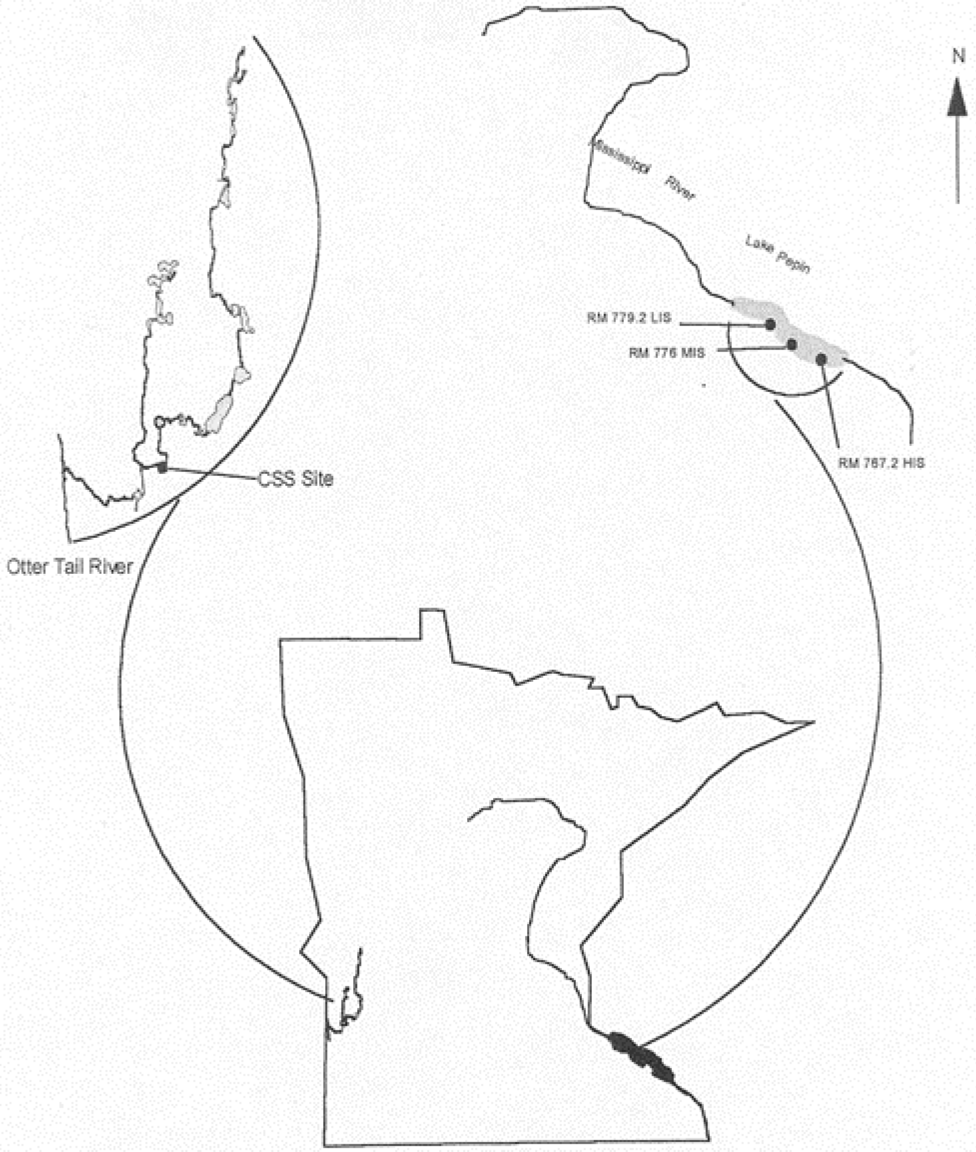

Figure 3.1. Mark/recapture sites that produced *A. plicata* survivorship data subsequently used in baseline and *D. polymorpha* impact population models, Lake Pepin and Otter Tail River, MN.

more deterministic in nature and the central limit theory becomes apparent. We did, however, run a model scenario to validate this assumption. We set the initial population size equal to 3,000 and a ceiling level of 4,500 individuals versus 30,000 and 45,000 individuals, and ran the model under the worst case scenario of adult survival and reproduction. If this model with fewer initial individuals behaved similar to the one with 30,000 initial individuals, we can assume that models with higher initial population sizes would also behave in a like manner.

Using the baseline model inputs shown in Table 3.2, we conducted sensitivity analysis to determine which parameters affected the population growth rate the most dramatically (Bart 1995). We held survival rates at the stationary level and altered reproductive output and juvenile mortality by incremental amounts. Reproduction and juvenile mortality were also held at the stationary level while adult survival was altered. For the high adult survival model, we used the rate measured for adults at the LIS site.

Tables 3.3 and 3.4 illustrate the changes in reproduction and juvenile survival schedules used in sensitivity analysis. Table 3.3 is the schedule of 5% first year survival and 8 offspring per breeding event, equal to a decline of 40% of the offspring reaching breeding age, while Table 3.4 illustrates the survivorship schedule relating to 15% first year survival and 12 offspring per breeding event, which is an increase of 180% of the offspring reaching breeding age compared to the stationary model.

The stationary and subsequent models were simulated 500 times for 100

<MISSING TABLE 3.2>

<MISSING TABLE 3.3>

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years, with populations being declared extinct if no individuals of either sex survived to the end of the 100-year simulation. If a particular modeling scenario caused the computer to abort, due to too many individuals surviving from year to year, it was run with fewer iterations as noted in Tables 3.2 and 3.5.

Models Simulating Harvest of *Amblema plicata*

We simulated mussel harvesting by increasing adult mortality over the baseline models by increments of 5%. Using this method we were able to express harvesting of mussels in terms of the percentage of individuals removed from the population on a yearly basis. This technique seemed the most appropriate because we did not have any reliable data on the initial population size of *A. plicata* in Lake Pepin which could be related to the harvest records that were available. Therefore, when managers are making decisions on setting harvest limits, they will be able to determine the actual number of mussels that can be safely removed from the population. The setting of harvest limits will only be possible, however, if accurate population estimates are derived in the future.

Models Incorporating *Dreissena polymorpha* Impacts

Models predicting the fates of the mussel populations under *D. polymorpha* infestations were run using the stationary model as baseline inputs and altering adult and sub-adult survival. Simulations were conducted using empirically derived adult and sub-adult survivorship rates and EV of *A. plicata* measured at the HIS. (See Paper 2 this dissertation.) The rate of 75.6% for adult and sub-adult survivorship was used in the models and was attained by calculating the

<MISSING TABLE 3.5>

average of the mean annual survivorship across all sizes of mussels at the HIS site. We modeled 4 different scenarios with each either incorporating survival rates equal to 75.6% beginning at age 7, 8, 9, or adult (age 10), through senescence. For the *D. polymorpha* impact models, we did not vary reproductive output since empirically measured data for this parameter were not available.

RESULTS

Baseline Model and Sensitivity Analysis

The mussel population scenarios outlined previously were modeled with the output reported in terms of the population growth rate, probability of population extinction, and the population size remaining at the end of the simulations (Tables 3.2 and 3.5-3.7). The results of these modeling efforts provide a range of plausible population behaviors under various scenarios.

Sensitivity analysis illustrated that these populations of mussels are most sensitive to perturbations affecting changes in adult survival rates (Fig. 3.2). The deterministic life table model under the stationary reproduction and survivorship scenario resulted in an almost stationary population growth rate r = 0.002 (Table 3.2). Decreasing adult survival by approximately 28% from the stationary rate of 97.9% to 70%, resulted in a change in r from 0.002 to -0.124. This alteration of adult survival equates to a population decline of about 12% per year (Table 3.2). A corresponding decline in reproduction and juvenile survival of 40% resulted in a decline in r from 0.002 to -0.044 which approximates a population decline of 4% per year (Table 3.2).

Simulations that incorporated demographic and environmental stochasticity revealed results similar to those of the deterministic models (Tables 3.2 and 3.5). The population of mussels with the stationary schedule grew slightly over the course of the simulation and ended after 100 years with a population size of about 37,000 individuals (Table 3.5). Under the scenario of stationary adult survival

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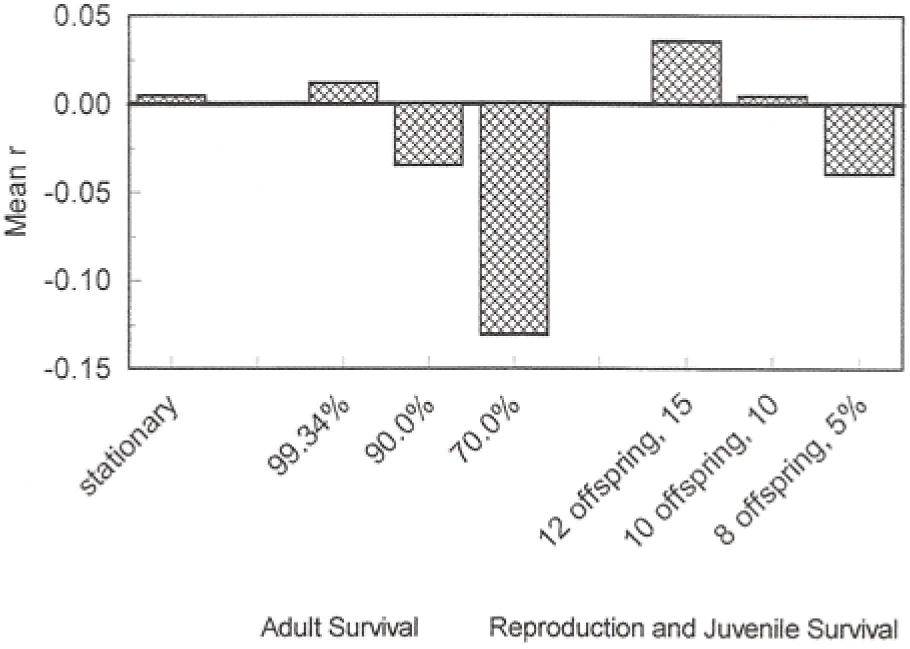

Figure 3.2. Sensitivity analysis illustrating differences in mean r due to alterations in demographic parameters.

and high reproduction, the population grew in size, and the simulation ended with approximately 44,000 individuals surviving through the 100 years (Fig. 3.3, Table 3.5). When reproduction was lowered to a mean of 8 offspring per breeding event and juvenile survival lowered while adult survivorship was held at the stationary level, the population size of mussels declined to a final size of about 650 individuals (Fig. 3.3, Table 3.5).

When populations of mussels were simulated with a stationary reproduction schedule and mean annual adult survival increased to 99.34%, the result was a population increasing in size over the course of the 100 years modeled (Fig. 3.4, Table 3.5). When reproduction was held constant and adult survival lowered to 90%, the population of mussels declined dramatically and ended with only about 1,200 individuals surviving (Fig. 3.4, Table 3.5). Under the low adult survival (70%) and stationary reproduction, the initial population size of 30,000 dwindled to extinction, with the mean time to first extinction being about 71 years (Fig. 3.4, Table 3.5). All of the 500 iterations of this simulation went extinct, further illustrating that alterations to base line adult survival rates have a greater impact on population growth and stability than do similar, or even greater, changes in reproductive output.

We altered both adult survival and reproduction in the following models. Under both high survival and reproduction, the population increased to the ceiling in about 20 years, showing high potential for growth (Fig. 3.5, Table 3.5). Models run with high adult survival and lowered reproduction showed declines through time and ended with a population size equal to about 1,500 individuals (Fig. 3.5, Table 3.5). The model run with moderate adult survivorship and high reproduction declined slightly from the initial population size (Fig. 3.5, Table 3.5).

When survival of adult mussels was decreased to the moderate level and reproduction was lowered as well, the population had a probability of extinction over the 100 years of 0.18 (Table 3.5). This population ended with only 10 individuals surviving throughout the simulation (Fig. 3.6). When a model was run with adult survival of 70%, reproduction equal to 12 offspring per breeding event, and juvenile survival rates increased, the resulting population declined to about 20 individuals at the end of the 100-year simulation (Fig. 3.6). This population had a probability of extinction equal to 0.46 (Table 3.5), again reinforcing that alterations to adult survival are most sensitive to perturbations. Under the worst case scenario of adult survival equal to 70% and females only producing on average 8 offspring per breeding event, the probability of extinction was equal to 1.0 (Table 3.5). All of the simulations under this scenario became extinct, with the mean time to extinction being about 50 years, thus resulting in a final population size of 0 (Fig. 3.6). The model with the initial population size set at 3,000 individuals under the worst case scenario behaved very similar to the model with 30,000 initial individuals (Fig. 3.7). Therefore, these models would probably behave similarly if they had 300,000 initial individuals versus the 30,000 individuals that the model would allow.

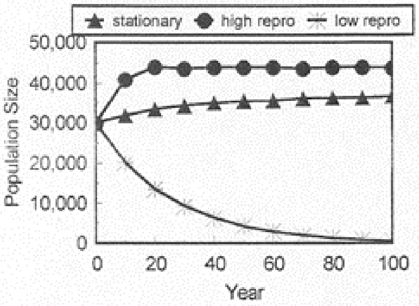

Figure 3.3. Projected population sizes under stationary survival and reproduction schedule, and varying reproduction schedules.

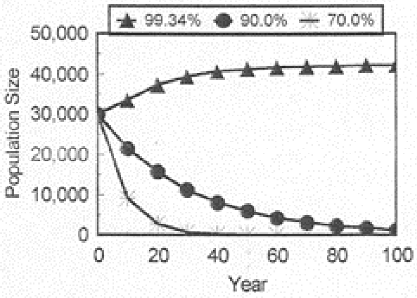

Figure 3.4. Projected population sizes under stationary reproduction and varying adult survival.

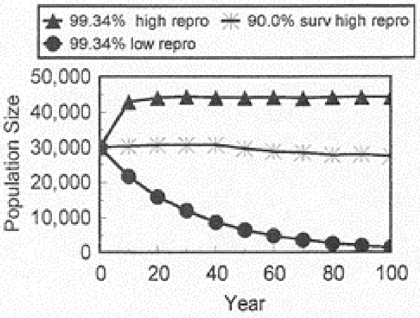

Figure 3.5. Projected population sizes under varying adult survival and reproductive schedules.

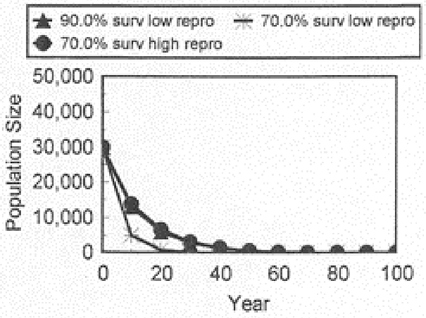

Figure 3.6. Projected population sizes under varying adult survival and reproductive schedules.

Models Simulating Harvest of *Amblema plicata*

Population models that were developed to simulate commercial harvesting resulted in large declines in the population growth rate for all harvesting scenarios (Table 3.6). The model simulating the smallest harvest level, 5% of the adults in the population, resulted in a mean r equal to -0.0198. Subsequent models representing harvests of 10%, 15%, 20%, and 25% of the adults present in the population resulted in population growth rates of r= -0.0440, -0.0689, -0.0945, and -0.1153, respectively (Table 3.6). These results further illustrate that increasing the mortality of adult *A. plicata*, either by removal from the population or by death, drastically decreases the population growth and increases the probability of extinction in the future (Figs. 3.8-3.12).

Models Incorporating *Dreissena polymorpha* Impacts

Mussel populations modeled with stationary survival and increased age-specific mortality rates attributed to *D. polymorpha* infestations behaved similar to the worst case scenario that was modeled during sensitivity analysis. Increasing mortality to the levels measured at the HIS site to the modeled individuals caused the projected population sizes to decline rapidly and the probability of extinction to increase greatly.

The greatest decline in population growth came when the empirically derived survival rate of 75.6% was assigned to mussels at age 7 through senescence (Fig. 3.13, Table 3.7). Life table analysis carried out in the VORTEX program calculated population growth to be declining by 14% annually. The worst

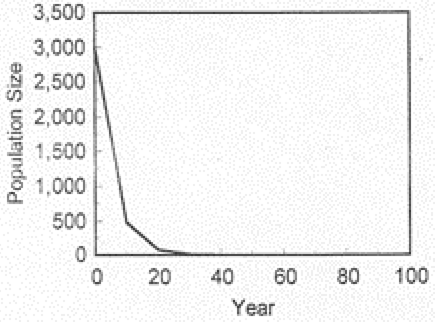

Figure 3.7. Projected population sizes under low adult survival and low reproduction, initial population size set at 3,000.

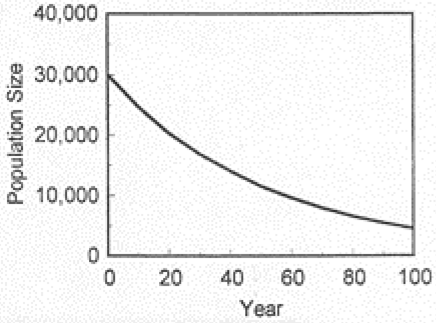

Figure 3.8. Projected population sizes under a 5% harvest scenario.

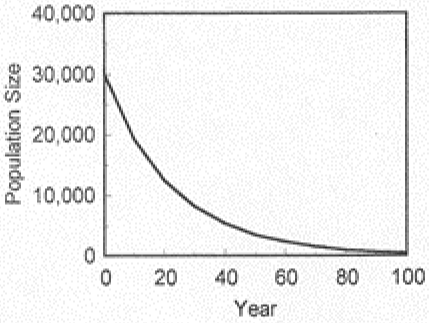

Figure 3.9. Projected population sizes under a 10% harvest scenario.

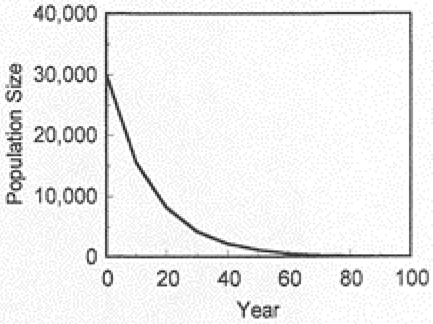

Figure 3.10. Projected population sizes under a 15% harvest scenario.

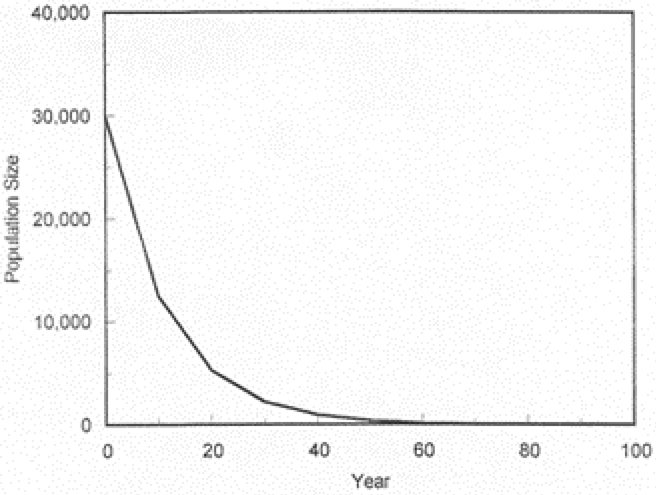

Figure 3.11. Projected population sizes under a 20% harvest scenario.

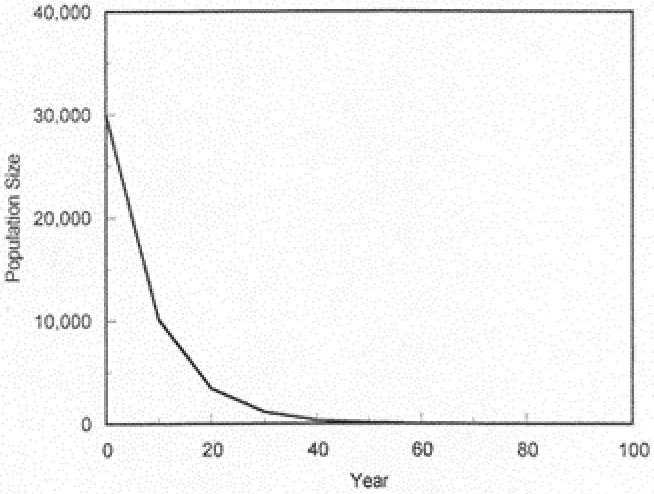

Figure 3.12. Projected population sizes under a 25% harvest scenario.

case scenario modeled under the sensitivity analysis section resulted in an annual population decline of about 17%. A similar trend in population behaviors can be seen in those models where the survival rate of 75.6% was applied to individuals beginning at age 8, 9, or 10 through adulthood (Figs. 3.14-3.16, Table 3.7). These results illustrate a poor outlook for population survival of *A. plicata* under any of these four scenarios.

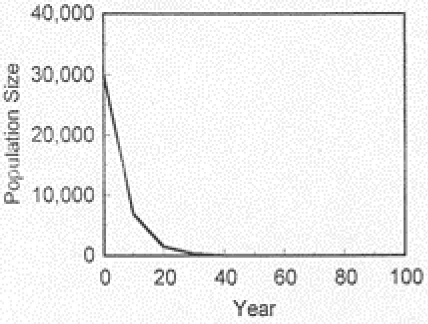

Figure 3.13. Projected population sizes under stationary reproduction with survival rates of 75.6% beginning at age 7.

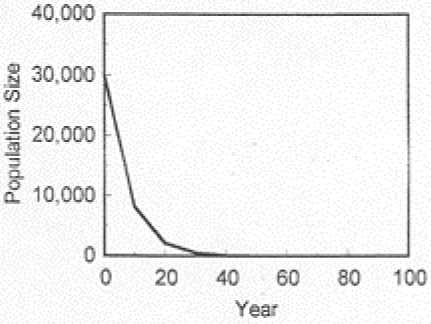

Figure 3.14. Projected population sizes under stationary reproduction with survival rates of 75.6% beginning at age 8.

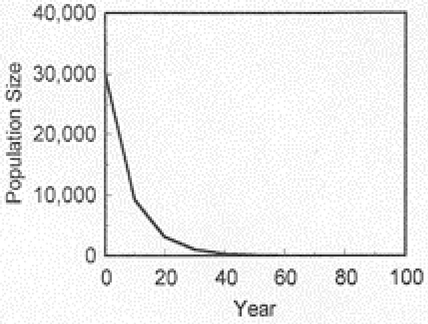

Figure 3.15. Projected population sizes under stationary reproduction with survival rates of 75.6% beginning at age 9.

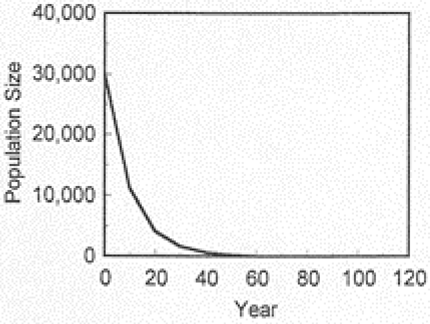

Figure 3.16. Projected population sizes under stationary reproduction with survival rates of 75.6% beginning at age 10.

DISCUSSION

The most startling findings of this study were that populations *of A. plicata* are in imminent danger of localized extinctions if commercial harvesting removes more than 5% of the population or if *D. polymorpha* infestations continue at the current rate. The results of this modeling effort concur with the findings reported in Paper 1 of this dissertation, i.e., *A. plicata* populations are declining in Lake Pepin. Sensitivity analysis for the *A. plicata* populations simulated in this study illustrate that this longed-lived mussel species is highly sensitive to decreases in adult survival. It is this demographic parameter that is most directly affected by commercial harvesting and most readily measured as an impact due to *D. polymorpha* infestations.

Mussel harvesters are restricted from taking the smaller-sized individuals and therefore strive to collect the largest and, hence, usually the oldest, individuals because they are more valuable (Bowen et al. 1994). Therefore, it is this practice of taking the larger adults that can jeopardize the population stability of long-lived mussel species in the future.

When we simulated 5% of the *A. plicata* population being harvested annually, the population began to decline almost immediately (Fig. 3.8). The half-life of the population under a 5% harvest scenario is only about 40 years, while it is less than 10 years when 25% of the adults are harvested annually. While we do believe harvesting 25% of the legal-sized adults may be unrealistic, removal of 5-10% may not. During the 1993 commercial harvest season in Lake Pepin, MN, well over 125,000 pounds of *A. plicata* mussels were reported harvested. (See Paper 1 in this dissertation.) This harvest equates to roughly 250,000 mussels being collected from the Minnesota side of Lake Pepin. (See Paper 2 in this dissertation.)

The annual removal of 5-10% of the population does not appear to a lot of animals, especially compared to other harvesting scenarios. Yet, it has been shown that small, chronic increases in adult mortality rates, e.g., harvesting, results in population declines. Sixty-seven percent of the commercial mussel harvesters who had been collecting for over 10 years, surveyed on the Wheeler Reservoir of the Tennessee River, reported declines in the number of mussels they harvested (Bowen et al. 1994). Of those harvesters surveyed, 84% attributed the decline in mussel numbers to over-harvesting.

Congdon et al. (1994), in their study of snapping turtles (*Chelydra serpentina*), reported that a 10% increase in adult mortality would reduce the number of adults in the population by one-half in only 20 years. They found a carefully managed sport harvest of this and other long-lived organisms may be sustainable, yet commercial harvesting would undoubtably cause drastic population declines. Population stability of wandering albatrosses, *Diomedea exulans*, and wood turtles, *Clemmys insculpta*, have also been found to be dependent on adult survival (Croxall et al. 1990, Harding 1991). Croxall et al. (1990) reported that a 2% decrease in adult survivorship of *D. exulans* resulted in significant population declines.

Richards and Davis (1993) implicated commercial harvest as a contributing factor in the massive declines of black abalone *(Haliotis cracherodii)* at the Oregonian province site in their study. Black abalone are much like *A. plicata* in that they are slow growing and long-lived. During their study they found large numbers of abalone dying in adjacent areas to the Oregonian site. When these adjacent sites were closed to commercial harvesting, the large harvest-sized individuals began to disappear from the Oregonian province (Richards and Davis 1993).

Paper 1 of this dissertation noted that there have been significant declines in both overall densities and large individuals of *A. plicata* at several sampled mussel beds in Lake Pepin, yet non-harvested mussel species have shown stable densities. These results implicate commercial harvesting as a factor in these declines. The results of the modeling efforts support this hypothesis as well. It has been shown in this dissertation that small increases in adult, i.e., harvest sized, mortality of *A. plicata* will surely result in steady population declines.

It was also found that an increase in adult mortality due to *D. polymorpha* infestations increased the probability of extinction for these modeled populations. The empirically measured survival rates of adult and sub-adult mussels used in these models appears to be too low to ensure the impacted mussel populations survival. Thus, this measured low survival resulted in high extinction probabilities for these populations of mussels. The predicted rapid decline of the mussel populations heavily infested with *D. polymorpha* in Lake Pepin has apparently already occurred in similarly infested areas of the Laurentian Great Lakes. Ricciardi et al. (1995) predicted that severe mussel mortality should occur when infestations of *D.*

polymorpha equaled 100 dreissenids/unionid. Ricciardi et al. (1998) predicted that the regional extinction rate of mussels in the Mississippi River Basin is accelerating. Their prediction has been validated by the survivorship study reported in Paper 2 of this dissertation and the results of this modeling effort.

While we did not alter the reproductive schedule for the *D. Polymorpha* models, the sensitivity analysis results reported above illustrate that alteration in reproductive output probably does not have a significant impact on population behavior. However, alterations in reproduction, e.g., lowered output, would likely lead to a decrease in population growth. Therefore, we regard the results pertaining to increased mortality of *A. plicata* due to *D. polymorpha* infestations to be somewhat conservative in terms of probability of population extinctions.

It is our recommendation that a concerted effort should be made to estimate the population size of *A. plicata* residing in Lake Pepin. This estimate would allow for a more accurate estimate of what percentage of the adult mussels are actually being harvested from the lake. The population estimates would also allow for the setting of quotas, or limiting the number of permits for harvesters in the face of increased *D. polymorpha* infestations, thereby ensuring the population of *A. plicata* is not being exploited.

LITERATURE CITED

Bart, J. 1995. Acceptance criteria for using individual-based models to make management decisions. Ecological Applications 5:411-420.

Bowen, Z. H., S. P. Malvestuto, W. D. Davies, and J. H. Crance. 1994. Evaluation of the mussel fishery in Wheeler Reservoir, Tennessee River. Journal of Freshwater Ecology 9:313-319.

Congdon, J. D., A. E. Dunham, and R. C. van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): Implications for conservation and management of long-lived organisms. American Zoologist 34:397-408.

Croxall, J. P., P. Rothery, S. P. C. Pickering, and P. A. Prince. 1990. Reproductive performance, recruitment and survival of wandering albatrosses *Diomedia exulans* at Bird Island, South Georgia. Journal of Animal Ecology 59:775-796.

Fuller, S. L. H. 1978. Freshwater mussels (Mollusca: Bivalvia: Unionidae) of the Upper Mississippi River: Observations at selected sites within the 9-foot navigation channel project on behalf of the U.S. Army Corps. of Engineers. Academy of Natural Science, Philadelphia, PA.

Gillis, P. L., and G. L. Mackie. 1994. Impact of the zebra mussel, *Dreissena polymorpha*, on populations of Unionidae (Bivalvia) in Lake St. Clair. Canadian Journal of Zoology 72:1260-1271.

Haag, W. R., D. J. Berg, D. W. Garton, and J. L. Farris. 1993. Reduced survival and fitness in native bivalves in response to fouling by the introduced zebra mussel (*Dreissena polymorpha*) in western Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 50:13-19.

Harding, J. H. 1991. Comments on herpetological collecting: The need for considering life history data in management and regulatory planning. Bulletin of Chicago Herpetological Society 26:157-159.

Kjos, C., O. Byers, P. Miller, J. Borovansky, and U.S. Seal (eds.) 1998. Population and habitat viability assessment workshop for the winged mapleleaf mussel (*Quadrula fragosa*): final report. CBSG, Apple Valley, MN.

Krebs, C. J. 1994. Ecology: The Experimental Analysis of Distribution and Abundance, fourth edition. HarperCollins College Publishing. New York, NY.

Lacy, R. C. 1993. VORTEX: A computer simulation model for population viability analysis. Wildlife Resources 20:45-65.

Lacy, R. C., and T. W. Clark. 1993. Simulation modeling of American marten (*Martes americana*) populations: Vulnerability to extinction. Great Basin Naturalist 53:282-292.

Lacy, R. C., K. A. Hughes, and P. S. Miller. 1995. VORTEX: A stochastic simulation of the extinction process. Version 7 users manual. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183-212.

Lindenmayer, D. B., M. A. Burgman, H. R. Akcakaya, R. C. Lacy, and H. P. Possingham. 1995. A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modeling the viability of wildlife metapopulations. Ecological Modeling 82:161-174.

McMahon, R. F. 1991. Mollusca: Bivalvia. In Ecology and Classification of North American Freshwater Invertebrates. J. H. Thorpe and A. C. Covich, eds. Academic Press, San Diego, CA.

Ricciardi, A., R. J. Neves, and J. B. Rasmussen. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. Journal of Animal Ecology 67:613-619.

Ricciardi, A., F. G. Whoriskey, and J. B. Rasmussen. 1995. Predicting the intensity and impact of *Dreissena* infestation on native unionid bivalves from *Dreissena* field density. Canadian Journal of Fisheries and Aquatic Sciences 52:1449-1461.

Richards, D. V., and G. E. Davis. 1993. Early warnings of modern population collapse in black abalone *Haliotis cracherodii*, Leach, 1814 at the California Channel Islands. Journal of Shellfish Research 12:189-194.

Schloesser, D. W., and T. F. Nalepa. 1994. Dramatic decline of unionid bivalves in offshore waters of western Lake Erie after infestation by the zebra mussel *Dreissena polymorpha*. Canadian Journal of Fisheries and Aquatic Sciences 51:2234-2242.

Shaffer, M. L. 1990. Population viability analysis. Conservation Biology 4:39-40.

Smith, H. M. 1898. The mussel fishery and pearl-button industry of the Mississippi River. Bulletin of the United States Fish Commission 18:289-314.

Smith, H. M. 1919. Freshwater mussels, a valuable national resource without sufficient protection. United States Bureau of Fisheries 43:1-5.

Song, Y. L. 1996. Population viability analysis for two isolated populations of Haianan eld's deer. Conservation Biology 10:1467-1472.

Soulé, M., editor. 1987. Viable Populations for Conservation. Cambridge University Press, New York, NY.

Southall, J. B. 1925. Mussel survey of Lake Pepin in 1924. With a discussion of the effects of the system of the alternate closure of sections of the lake to the taking of mussels. United States Bureau of Fisheries 57:1-3.

Stansbery, D. H. 1970. Eastern freshwater mollusks (1): the Mississippi and St. Lawrence River systems. Malacologia 10:9-22.

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 E. Danglade. 1914. The mussel fauna of central and northern Minnesota. United States Bureau of Fisheries 803:1-26.

GENERAL CONCLUSIONS

This dissertation presented three inter-related research projects, with the intention that the results of each paper would build upon the other. In 1990 researchers believed the level of commercial harvesting of mussels under the current system could potentially lead to declines in their population densities (M. Davis, personal communication). Also during this time, the threat of the introduction of the non-indigenous species *D. polymorpha* into Lake Pepin was realized when their presence within the lake was confirmed (M. Davis, personal communication). Therefore, a quantitative sampling regime for freshwater mussels was developed and implemented. By 1995 it became apparent harvesters had been removing large amounts of mussels from the lake (Welke and Miller 1990), and *D. polymorpha* densities were increasing throughout the Mississippi River (Tucker et al. 1993).

It was realized that more information would be required to link commercial harvesting and *D. polymorpha* colonizations to the apparent unionid mussel declines. For this reason, a mark/recapture study of selected species of unionid mussels was initiated. This marking research, which ran from 1995-98, revealed large differences in the survival rates of mussels that were colonized with *D. polymorpha* when compared to those that were not. The native mussel species, *A. plicata* and *F. flava*, which were marked in areas with high infestations of *D. polymorpha* showed approximately 25 and 10% increases in mortality, respectively, when compared to marked, uninfested populations. While other studies have noted a correlation between declines in unionid mussel densities and increases in *D. polymorpha* infestations (Gillis and Mackie 1994), we showed a direct link between *D. polymorpha* infested unionids and survival.

By measuring in situ survivorship, we were able to integrate these rates into computer simulations. These simulations predicted potential outcomes for the modeled populations. The PVA we conducted predicts that large declines in native mussel densities will soon become apparent if *D. polymorpha* colonization continues at the current rate.

About 75 years ago, researchers argued that mussel densities would decline due to harvesting if they were collected at levels greater than the population can replace (Southall 1925). Both our computer simulations and quantitative sampling results support Southall's (1925) predictions that commercial over-harvesting of mussel populations can lead to their declines.

The simulations predicted significant declines when levels as low as 5% of the adults were harvested from the population. Unfortunately, we do not know the current level of harvest from Lake Pepin relative to the population size of the mussels. However, the integration of the results of this research revealed that long-term declines in mussel populations, measured with quantitative sampling, were predicted with computer simulations.

This research also discerned the mean annual survivorship of several understudied species of unionid mussels. We believe the integration of these research projects provides new and important contributions to the study of freshwater mussel life-history and population dynamics.

LITERATURE CITED

Gillis, P. L., and G. L. Mackie. 1994. Impact of the zebra mussel, *Dreissena polymorpha*, on populations of Unionidae (Bivalvia) in Lake St. Clair. Canadian Journal of Zoology 72:1260-1271.

Southall, J. B. 1925. Mussel survey of Lake Pepin in 1924. With a discussion of the effects of the system of the alternate closure of sections of the lake to the taking of mussels. United States Bureau of Fisheries 57:1-3.

Tucker, J. K., C. H. Theiling, K. D. Blodgett, and P. A. Thiel. 1993. Initial occurrences of zebra mussels (*Dreissena polymorpha*) on freshwater mussels (Family: Unionidae) in the upper Mississippi River system. Journal of Freshwater Ecology 8:245-251.

Welke, K., and G. Miller. 1990. Commercial harvest of freshwater mussels in Wisconsin in 1990. Annual Report, Wisconsin Department of Natural Resources, Madison, WI.