

Simulation Models of Harvested and Zebra Mussel Colonized Threeridge Mussel Populations in the Upper Mississippi River

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ABSTRACT.—We simulated populations of threeridge mussels (*Amblema plicata*, Say, 1817) using empirically derived survival rates. Survival rates were derived from a mark-recapture study of mussels conducted in the Mississippi and Otter Tail rivers, Minnesota. The software package VORTEX was used to develop a base line population model which changed little or not at all 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 zebra mussel (*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. Adult survival is the life history stage most often impacted by both *D. polymorpha* colonizations and commercial harvesting. Population models simulating *D. polymorpha* mediated mortality revealed that population extinction was likely to occur within 50 y if survival rates remain at the levels recently measured. Models that simulated a commercial harvest of only 5% of the adult *A. plicata* population predicted that populations will decline by almost 50% in only 40 y. Our recommendation is that a concerted effort should be made to estimate the population size of potentially harvested populations of freshwater mussels. These estimates would allow for a more accurate estimate of what percentage of the adult mussels are actually being harvested. The population estimates would also allow for setting of quotas or limiting the number of permits for harvesters in the face of increased *D. polymorpha* infestations, thereby ensuring that harvested populations of mussels are not being over exploited. These modeling efforts will be useful for resource managers attempting to establish a sustainable harvest of commercially valuable mussel species which may be competing with a nonindigenous 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 (Lindenmayer *et al.*, 1995; Song, 1996). The primary reason for these analyses has been to assess the impact of environmental and human-induced disturbances 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

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et al., 1993), over-harvesting of commercially valuable species (Smith, 1919; Fuller, 1978; Anthony and Downing, 2001) and the invasion of nonindigenous 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 early studies were to locate mussel beds suitable for harvest (Wilson and Danglade, 1914) and to assess the impacts of harvesting on the resident mussel communities (Smith, 1919; Southall, 1925). These early studies revealed that, whereas 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 have on mussel populations, the state of Minnesota closed the mussel harvesting season on inland lakes and rivers in the early 1990s 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 about 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). In Mississippi River mussel populations, survival of *Amblema plicata* has been shown to decrease from about 98% to less than 65% when individuals were infested with over 100 *D. polymorpha* for several years (Hart *et al.*, 2001). To predict the fates of *A. plicata* populations under varying levels of commercial harvest and *D. polymorpha* infestations we simulated Lake Pepin *A. plicata* populations using the software package VORTEX (Lacy, 1993). We chose VORTEX because it 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).

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 *Amblema plicata*, as well as the decreasing survival attributed to *Dreissena polymorpha* colonizations. These modeling efforts were conducted to assist in the development of management strategies that will aid in ensuring the persistence of native mussel populations into the future.

METHODS

Baseline model assumptions and development.—Baseline population models were developed to simulate a stationary mussel population. *Amblema plicata* populations modeled in this exercise were considered, like most other mussels, to have a 50:50 sex ratio and be 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 y, 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 100,000 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 y 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 during 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 two offspring surviving to breeding age. The baseline survivorship schedule used in the stationary population growth model is shown in Table 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 1).

The baseline survival rates calculated for the juvenile mussels were used as inputs in the VORTEX model. Baseline stationary adult survival was calculated as the average survival measured at the REF and MOD sites within the Otter Tail River and Lake Pepin, Minnesota (Fig. 1) (Hart, 1999; Hart *et al.*, 2001), and was used as model inputs. Environmental variation (EV) in survival was calculated as demographic, or expected variation, *i.e.*, 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 REF, LOW and MOD sites for the baseline models.

Initial population sizes for the simulations were set at 30,000 mussels which is the maximum number 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. Although the number of individuals (30,000) used as the initial population size is undoubtedly 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 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 3000 and a ceiling level of 4500 individuals vs. 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

TABLE 1.—Life table illustrating stationary population structure used as baseline model inputs

Age (x)	l_x^1	S_x^2	m_x^3	$l_x m_x$
0	1.000000	0.100	0	0
1	0.100000	0.850	0	0
2	0.085000	0.870	0	0
3	0.073950	0.880	0	0
4	0.065076	0.900	0	0
5	0.058568	0.930	0	0
6	0.054469	0.950	0	0
7	0.051745	0.978	0	0
8	0.050607	0.978	0	0
9	0.049493	0.978	0	0
10	0.048405	0.979	1.25	0.060506
11	0.047388	0.979	1.25	0.059235
12	0.046393	0.979	1.25	0.057991
13	0.045419	0.979	1.25	0.056773
14	0.044465	0.979	1.25	0.055581
15	0.043531	0.979	1.25	0.054414
16	0.042617	0.979	1.25	0.053271
17	0.041722	0.979	1.25	0.052153
18	0.040846	0.979	1.25	0.051057
19	0.039988	0.979	1.25	0.049985
20	0.039148	0.979	1.25	0.048935
21	0.038326	0.979	1.25	0.047908
22	0.037521	0.979	1.25	0.046902
23	0.036733	0.979	1.25	0.045917
24	0.035962	0.979	1.25	0.044953
25	0.035207	0.979	1.25	0.044009
26	0.034467	0.979	1.25	0.043084
27	0.033744	0.979	1.25	0.042180
28	0.033035	0.979	1.25	0.041294
29	0.032341	0.979	1.25	0.040427
30				
			sum of $l_x m_x$	0.996574

¹ Number of organisms living at start of x

² Survival rate

³ Number of female offspring produced

30,000 initial individuals, we can assume that models with higher initial population sizes would behave in a like manner.

Using the baseline model inputs shown in Table 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 LOW site.

Tables 3 and 4 illustrate the changes in reproduction and juvenile survival schedules used in sensitivity analysis. Table 3 is the schedule of 5% first year survivorship and 8 offspring per breeding event, equal to a decline of 40% of the offspring reaching breeding age, while Table 4 illustrates the survivorship schedule relating to 15% first year survival and

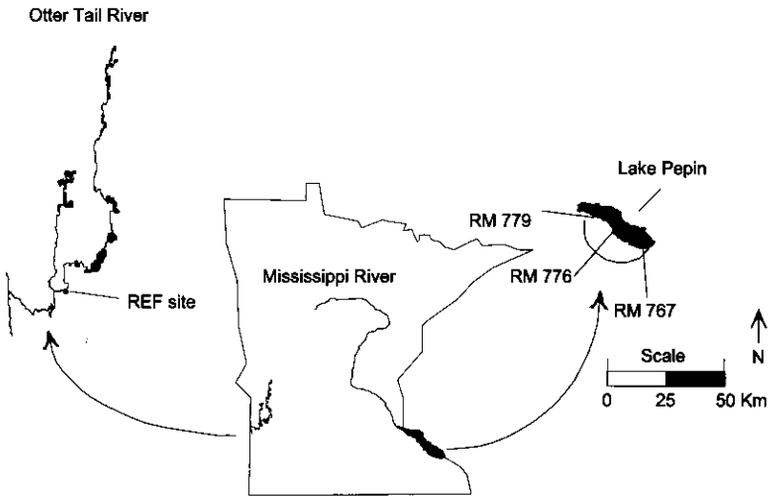


FIG. 1.—Mark/recapture sites that produced *Amblema plicata* survival rate data used in baseline and *Dreissena polymorpha* impact population models, Mississippi and the Otter Tail rivers, Minnesota

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 y, with populations being declared extinct if no individuals of either sex survived to the end of the 100-y 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 2 and 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 *Amblema 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 *Dreissena polymorpha* infestations were run using the stationary model as baseline inputs and altering adult and subadult survival. Simulations were conducted using empirically derived adult and subadult survival rates and EV of *Amblema plicata* measured at the HIH site (Hart, 1999). The rate of 75.6% for adult and subadult survival was used in the models and was attained by calculating the average of the mean annual survival across all sizes of mussels at the HIH 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.

TABLE 2.—Life table results for *Amblema plicata* under varying scenarios of reproduction and survival

Inputs	Stat. adult surv. and repro.		Stat. adult surv. low repro.		High adult surv. stat. repro.		Mod. adult surv. stat. repro.		Low adult surv. stat. repro.		High adult surv. high repro.		Mod. adult surv. high repro.		Low adult surv. high repro.	
	90	2.1	90	2.1	90	0.66	90	10	90	0.66	95	0.66	85	10	85	10
First year mortality (%)	90	85	90	95	90	90	90	90	90	95	95	85	85	95	85	95
Adult mortality (%)	2.1	2.1	0.66	2.1	30	0.66	10	10	30	0.66	0.66	10	10	10	30	30
Age begin breeding	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10	10
% of females that produce young	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25
Avg. # of young produced by successful females	10	12	10	8	10	10	10	10	10	12	8	12	12	8	12	8
Calculated values																
r	0.002	0.033	0.009	-0.044	-0.124	0.04	-0.036	-0.124	-0.036	-0.036	-0.002	-0.086	-0.086	-0.08	-0.189	-0.189
% population change ^a	0.2	3.4	0.9	-4.3	-11.7	4.1	-3.6	-11.7	-3.6	-3.6	-0.2	-8.3	-8.3	-7.7	-17.02	-17.02
% subadult	33	37	33	29	36	36	34	36	29	29	37	29	29	39	39	32
% adult	16	14	17	21	14	14	16	14	20	20	13	21	21	11	11	18

^a Change in population size from year 1 to next: $(R - 1)(100)$

TABLE 3.—Life table illustrating first year survival of 5.0% and 8 offspring per breeding event

Age (x)	l_x^1	S_x^2	m_x^3	$l_x m_x$
0	0.800000	0.050	0	0
1	0.040000	0.850	0	0
2	0.034000	0.870	0	0
3	0.029580	0.880	0	0
4	0.026030	0.900	0	0
5	0.023427	0.930	0	0
6	0.021787	0.950	0	0
7	0.020698	0.978	0	0
8	0.020243	0.978	0	0
9	0.019797	0.978	0	0
10	0.019362	0.979	1.00	0.019362
11	0.018955	0.979	1.00	0.018955
12	0.018557	0.979	1.00	0.018557
13	0.018167	0.979	1.00	0.018167
14	0.017786	0.979	1.00	0.017786
15	0.017412	0.979	1.00	0.017412
16	0.017047	0.979	1.00	0.017047
17	0.016689	0.979	1.00	0.016689
18	0.016338	0.979	1.00	0.016338
19	0.015995	0.979	1.00	0.015995
20	0.015659	0.979	1.00	0.015659
21	0.015330	0.979	1.00	0.015330
22	0.015009	0.979	1.00	0.015009
23	0.014693	0.979	1.00	0.014693
24	0.014385	0.979	1.00	0.014385
25	0.014083	0.979	1.00	0.014083
26	0.013787	0.979	1.00	0.013787
27	0.013497	0.979	1.00	0.013497
28	0.013214	0.979	1.00	0.013214
29	0.012937	0.979	1.00	0.012937
30				
			sum of $l_x m_x$	0.318904

¹ Number of organisms living at start of x

² Survival rate

³ Number of female offspring produced

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 2, 5–7). 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. 2). The deterministic life table model under the stationary reproduction and survival scenario resulted in an almost stationary population growth rate $r = 0.002$ (Table 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 decrease of adult survival equates to a population decline of about 12%

TABLE 4.—Life table illustrating 15% first year survival and 12 offspring per breeding event

Age (x)	l_x^1	S_x^2	m_x^3	$l_x m_x$
0	1.200000	0.150	0	0
1	0.180000	0.850	0	0
2	0.153000	0.870	0	0
3	0.13311	0.880	0	0
4	0.117137	0.900	0	0
5	0.105423	0.930	0	0
6	0.098044	0.950	0	0
7	0.093141	0.978	0	0
8	0.091092	0.978	0	0
9	0.089088	0.978	0	0
10	0.087128	0.979	1.50	0.130692
11	0.085299	0.979	1.50	0.127948
12	0.083507	0.979	1.50	0.125261
13	0.081754	0.979	1.50	0.122630
14	0.080037	0.979	1.50	0.120055
15	0.078356	0.979	1.50	0.117534
16	0.076711	0.979	1.50	0.115066
17	0.075100	0.979	1.50	0.112649
18	0.073523	0.979	1.50	0.110284
19	0.071979	0.979	1.50	0.107968
20	0.070467	0.979	1.50	0.105701
21	0.068987	0.979	1.50	0.103481
22	0.067538	0.979	1.50	0.101308
23	0.066120	0.979	1.50	0.099180
24	0.064732	0.979	1.50	0.097097
25	0.063372	0.979	1.50	0.095058
26	0.062041	0.979	1.50	0.093062
27	0.060739	0.979	1.50	0.091108
28	0.059463	0.979	1.50	0.089195
29	0.058214	0.979	1.50	0.087322
30				
			sum of $l_x m_x$	2.152599

¹ Number of organisms living at start of x

² Survival rate

³ Number of female offspring produced

per year (Table 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 2).

Simulations that incorporated demographic and environmental stochasticity revealed results similar to those of the deterministic models (Tables 2, 5). The population of mussels with the stationary schedule grew slightly during the simulation and ended after 100 y with a population size of about 37,000 individuals (Table 5). Under the scenario of stationary adult survival and high reproduction, the population grew and the simulation ended with approximately 44,000 individuals surviving through the 100 y (Fig. 3a, Table 5). When reproduction was lowered to a mean of 8 offspring per breeding event and juvenile survival lowered while adult survival was held at the stationary level, the population size of mussels declined to a final size of about 650 individuals (Fig. 3a, Table 5).

TABLE 5.—Stochastic simulations of *Amblema plicata* populations under varying scenarios of reproduction and survival

Input	Stat. adult surv. and repro.		Stat. adult high surv. and repro.		Stat. adult low surv. and repro.		High adult surv. and repro.		High adult low surv. and repro.		Mod. adult surv. and repro.		Mod. adult high surv. and repro.		Mod. adult low surv. and repro.		Low adult surv. and repro.		Low adult high surv. and repro.		
	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	
Age of senescence	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	30	
Initial pop. size	30,000	30,000	30,000	30,000	30,000	30,000	30,000	30,000	30,000	30,000	30,000	30,000	30,000	30,000	30,000	30,000	30,000	30,000	30,000	30,000	
Upper limit	45,000	45,000	45,000	45,000	45,000	45,000	45,000	45,000	45,000	45,000	45,000	45,000	45,000	45,000	45,000	45,000	45,000	45,000	45,000	45,000	
Number of years simulated	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	
Number of iterations	500	500	500	500	500	500	500	500	500	500	500	500	500	500	500	500	500	500	500	500	
Mean r (st. error)	0.0046 (0.0003)	0.0352 (0.0007)	-0.0396 (0.0002)	0.0116 (0.0003)	-0.0347 (0.0003)	-0.1304 (0.0008)	0.0416 (0.0007)	-0.0311 (0.0002)	-0.0311 (0.0002)	-0.0311 (0.0002)	-0.0003 (0.0003)	-0.0841 (0.0003)	-0.0003 (0.0003)	-0.0003 (0.0003)	-0.0003 (0.0003)	-0.0883 (0.0006)	-0.1882 (0.0011)	-0.1882 (0.0011)	-0.1882 (0.0011)	-0.1882 (0.0011)	-0.1882 (0.0011)
Number of simulations going extinct	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Mean time to first extinction in years (st. error)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	71.10 (0.40)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	95.54 (0.42)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	90.34 (0.51)	49.6 (0.27)	49.6 (0.27)	49.6 (0.27)	49.6 (0.27)	
Prob. of extinction (st. error)	0.000 (0.0000)	0.000 (0.0000)	0.000 (0.0000)	0.000 (0.0000)	0.000 (0.0000)	1.000 (0.0000)	0.0 (0.0)	0.000 (0.0000)	0.000 (0.0000)	0.000 (0.0000)	0.000 (0.0000)	0.182 (0.0173)	0.000 (0.0000)	0.000 (0.0000)	0.000 (0.0000)	0.460 (0.0223)	1.000 (0.0000)	1.000 (0.0000)	1.000 (0.0000)	1.000 (0.0000)	1.000 (0.0000)
Mean pop. size for successful cases (st. error)	36,841 (328.56)	43,746 (177.69)	649.44 (15.09)	42,228 (132.10)	1175 (37.97)	0	44,259 (115.10)	1478 (30.14)	1478 (30.14)	1478 (30.14)	27,397 (421.66)	10 (0.33)	0.182 (0.0173)	0.000 (0.0000)	0.000 (0.0000)	0.460 (0.0223)	1.000 (0.0000)	1.000 (0.0000)	1.000 (0.0000)	1.000 (0.0000)	1.000 (0.0000)

TABLE 6.—Stochastic simulations of *Amblema plicata* populations under stationary reproduction schedules and varying harvesting scenarios

Inputs	5% of adults harvested	10% of adults harvested	15% of adults harvested	20% of adults harvested	25% of adults harvested
Mean r (SE)	-0.0198 (0.0003)	-0.0440 (0.0003)	-0.0689 (0.0003)	-0.0945 (0.0004)	-0.1153 (0.0005)
Number of simulations going extinct	0	0	4	307	493
Mean time to first extinction in years (SE)	0.0 (0.0)	0.0 (0.0)	94 (2.20)	92.09 (0.31)	80.18 (0.35)
Prob. of extinction (SE)	0.0 (0.0)	0.0 (0.0)	0.008 (0.004)	0.614 (0.022)	0.986 (0.005)
Mean pop. size for successful cases (SE)	4578 (95.33)	422.37 (10.43)	39.31 (1.21)	6.84 (0.37)	4.14 (0.91)

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 during the 100 y modeled (Fig. 3b, Table 5). When reproduction was held constant and adult survival lowered to 90%, the population of mussels declined dramatically and ended with only about 1200 individuals surviving (Fig. 3b, Table 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 y (Fig. 3b, Table 5). All of

TABLE 7.—Stochastic simulations of *Amblema plicata* populations under stationary reproduction schedules and varying survival rates attributed to *Dreissena polymorpha* infestations

Inputs	Increased mortality age 7	Increased mortality age 8	Increased mortality age 9	Increased mortality age 10
Percent survival age 7	75.6	97.8	97.8	97.8
Percent survival age 8	75.6	75.6	97.8	97.8
Percent survival age 9	75.6	75.6	75.6	97.8
Percent survival age ≥ 10	75.6	75.6	75.6	75.6
Mean r (SE)	-0.1693 (0.0012)	-0.1471 (0.0011)	-0.1280 (0.0009)	-0.1091 (0.0008)
Number of simulations going extinct	500	499	495	449
Mean time to first extinction in years (SE)	54.48 (0.41)	62.63 (0.41)	71.88 (0.48)	82.37 (0.47)
Prob. of extinction (SE)	1.0000 (0.0000)	0.9980 (0.0020)	0.9900 (0.0044)	0.8980 (0.0135)
Mean pop. size for successful cases (SE)	0.0	3.0 (0.00)	6.8 (2.82)	5.67 (0.56)

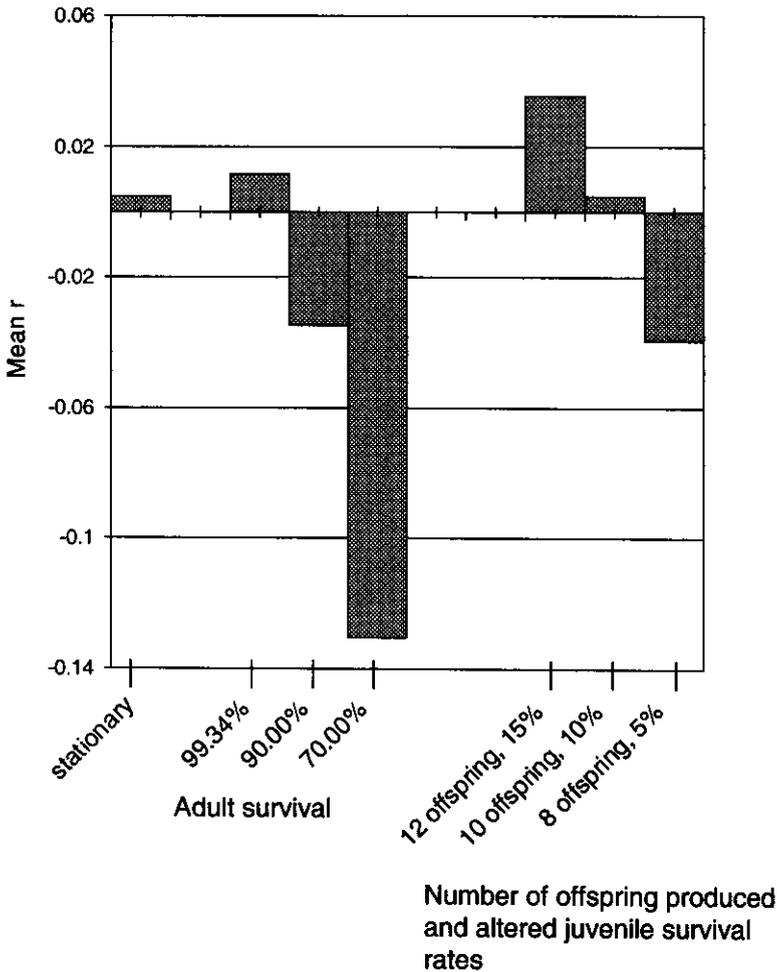


FIG. 2.—Sensitivity analysis illustrating differences in mean r due to alterations in demographic parameters

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 y, showing high potential for growth (Fig. 3c, Table 5). Models run with high adult survival and lowered reproduction declined through time and ended with a population size equal to about 1500 individuals (Fig. 3c, Table 5). The model run with moderate adult survival rates and high reproduction declined slightly from the initial population size (Fig. 3c, Table 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 y of 0.18 (Table 5). This population ended with only 10 individuals surviving throughout the simulation

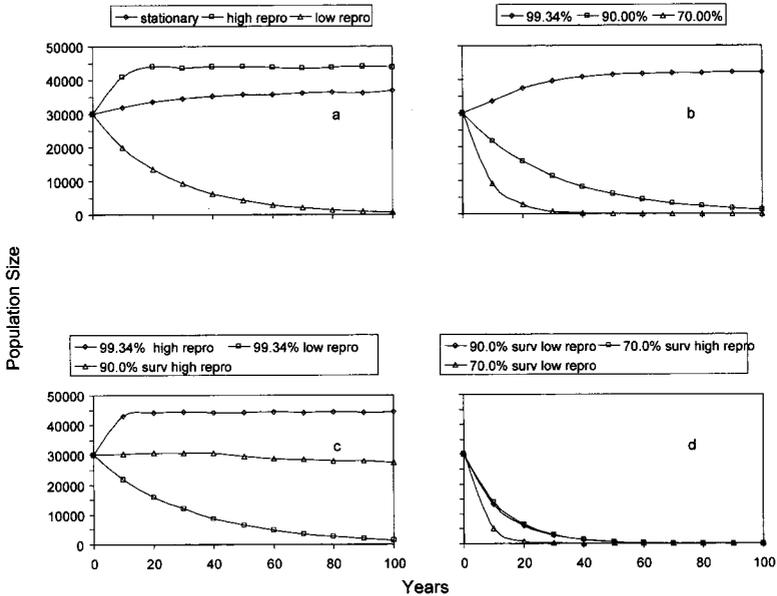


FIG. 3.—Projected population sizes simulating varying levels of reproduction and survival schedules. Panels: (a) population behavior simulating stationary survival and reproduction schedule while varying reproduction schedules; (b) population behavior simulating stationary reproduction and varying adult survival; (c) population behavior simulating varying adult survival and reproduction; (d) population behavior simulating additional varying adult survival and reproduction

(Fig. 3d). 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-y simulation (Fig. 3d). This population had a probability of extinction equal to 0.46 (Table 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 5). All of the simulations under this scenario became extinct, with the mean time to extinction being about 50 y resulting in a final population size of 0 (Fig. 3d). The model with the initial population size set at 3000 individuals under the worst case scenario behaved very similarly to the model with 30,000 initial individuals (Fig. 4). Therefore, these models would probably behave similarly if they had 300,000 initial individuals versus the 30,000 individuals that the model would allow.

*Models simulating harvest of *Amblyma plicata*.*—Population models that were developed to simulate commercial harvesting resulted in large declines in the population growth rate for all harvesting scenarios (Table 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 6). These results further illustrate that increasing the mortality of adult *Amblyma 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. 5a–e).

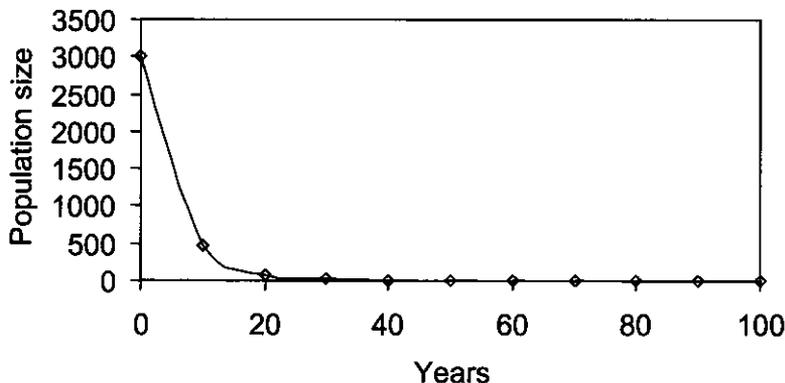


FIG. 4.—Projected population sizes under low adult survival and low reproduction schedules. The initial population size was set at 3000 individuals

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

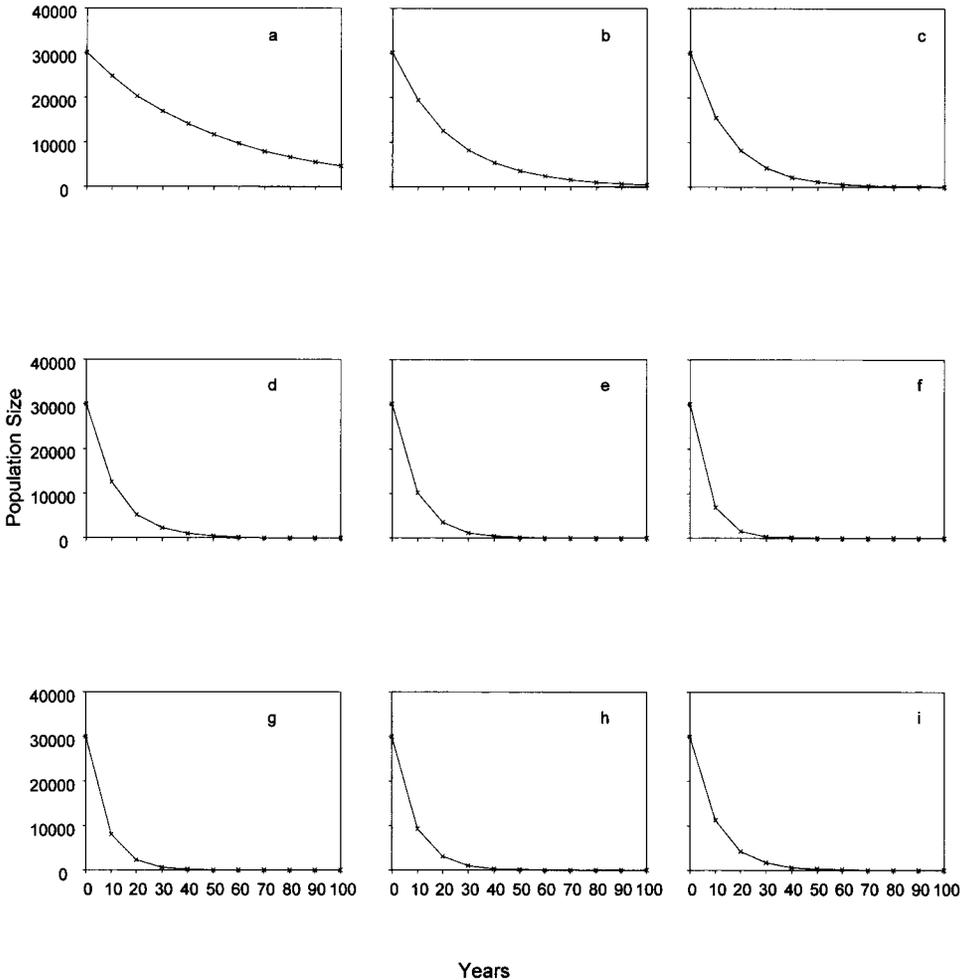
The greatest decline in population growth came when the empirically derived survival rate of 75.6% was assigned to mussels at age 7 through senescence (Fig. 5f, Table 7). Life table analysis carried out in the VORTEX program calculated population growth to be declining by 14% annually. The worst case 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. 5g–i, Table 7). These results illustrate a poor outlook for population survival of *Amblyma plicata* under any of these four scenarios.

DISCUSSION

The most startling findings of this study were that populations of *Amblyma plicata* are in imminent danger of localized extinctions if commercial harvesting removes more than 5% of the population or if *Dreissena polymorpha* infestations continue at the current rate. The results of this modeling effort concur with the findings reported by Hart *et al.* (2002), *i.e.*, *A. plicata* populations are declining in Lake Pepin. Sensitivity analysis for the *A. plicata* populations simulated in this study illustrate that this long-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 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). 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 *Amblyma plicata* population being harvested annually, the population began to decline almost immediately (Fig. 5a). The half-life of the population



FIGS. 5a–i.—Projected population sizes simulating varying levels of commercial harvest, reproduction and survival schedules. Panels: (a) population behavior simulating 5% harvest; (b) population behavior simulating 10% harvest; (c) population behavior simulating 15% harvest; (d) population behavior simulating 20% harvest; (e) population behavior simulating 25% harvest; (f) population behavior simulating a stationary reproduction schedule with survival rates of 75.6% beginning at age 7; (g) population behavior simulating a stationary reproduction schedule with survival rates of 75.6% beginning at age 8; (h) population behavior simulating a stationary reproduction schedule with survival rates of 75.6% beginning at age 9; (i) population behavior simulating a stationary reproduction schedule with survival rates of 75.6% beginning at age 10

under a 5% harvest scenario is only about 40 y, while it is less than 10 y 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 be, particularly from smaller sized rivers. During the 1993 commercial harvest season in Lake Pepin, MN, well over 125,000 pounds of *A. plicata* mussels were reported harvested (Hart *et al.*, 2002). This harvest equates to roughly 250,000 mussels being collected from the Minnesota side of Lake Pepin.

The annual removal of 5–10% of the population does not appear to be 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 y, 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.

This phenomenon has been found in populations of other long-lived animals. 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 y. They found a carefully managed sport harvest may be sustainable, yet commercial harvesting would undoubtedly cause drastic population declines. Population stability of wandering albatrosses, *Diomedea exulans*, and wood turtles, *Clemmys insculpta*, are also dependent on adult survival (Croxall *et al.*, 1990; Harding, 1991). Croxall *et al.* (1990) reported that a 2% decrease in adult survival 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 *Amblema plicata* in that they are slow growing, long-lived molluscs. During their study Richard and Davis (1993) 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 commercially harvested Oregonian province (Richards and Davis, 1993).

Hart *et al.* (2002) noted that there have been significant declines in both overall densities and large individuals of *Amblema plicata* at several sampled mussel beds in Lake Pepin, yet nonharvested 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, illustrating that small increases in adult, i.e., harvest sized, mortality of *A. plicata* will surely result in steady population declines.

We also found that an increase in adult mortality due to *Dreissena polymorpha* infestations increased the probability of extinction for these modeled populations. The empirically measured survival rates of adult and subadult 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 survival study reported by Hart *et al.* (2001) and the results of this modeling effort.

While we did not alter the reproductive schedule for the *Dreissena polymorpha* models, the sensitivity analysis results reported above illustrate that alteration in reproductive output may 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. In this study we modeled populations with lowered survival rates equal to about 75% (Hart, 1999), which is much more conservative than recent 65% survival estimates for these populations (Hart *et al.*, 2001). Therefore, we regard the results pertaining to increased mortality of *Amblema plicata* due to *D. polymorpha* infestations to be quite conservative in terms of probability of population extinctions.

While the population dynamics, population densities, etc., of many animal species are not well known, rarely are these organisms subjected to commercial harvest. Therefore, it is our recommendation that a concerted effort should be made to first estimate the population size of harvested populations of freshwater mussels. These estimates would allow for a more accurate estimate of what percentage of the adult mussels are actually being harvested from the lake. These population estimates could be used to set harvest quotas or limit the number of permits for harvesters in the face of increased *Dreissena polymorpha* infestations, thereby ensuring that populations of harvested mussels are not being over exploited.

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