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[Article]

# Simulated Effects of Recruitment Variability, Exploitation, and Reduced Habitat Area on the Muskellunge Population in Shoepack Lake, Voyageurs National Park, Minnesota

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*Abstract.*—The genetically unique population of muskellunge *Esox masquinongy* inhabiting Shoepack Lake in Voyageurs National Park, Minnesota, is potentially at risk for loss of genetic variability and long-term viability. Shoepack Lake has been subject to dramatic surface area changes from the construction of an outlet dam by beavers *Castor canadensis* and its subsequent failure. We simulated the long-term dynamics of this population in response to recruitment variation, increased exploitation, and reduced habitat area. We then estimated the effective population size of the simulated population and evaluated potential threats to long-term viability, based on which we recommend management actions to help preserve the long-term viability of the population. Simulations based on the population size and habitat area at the beginning of a companion study resulted in an effective population size that was generally above the threshold level for risk of loss of genetic variability, except when fishing mortality was increased. Simulations based on the reduced habitat area after the beaver dam failure and our assumption of a proportional reduction in population size resulted in an effective population size that was generally below the threshold level for risk of loss of genetic variability. Our results identified two potential threats to the long-term viability of the Shoepack Lake muskellunge population, reduction in habitat area and exploitation. Increased exploitation can be prevented through traditional fishery management approaches such as the adoption of no-kill, barbless hook, and limited entry regulations. Maintenance of the greatest possible habitat area and prevention of future habitat area reductions will require maintenance of the outlet dam built by beavers. Our study should enhance the long-term viability of the Shoepack Lake muskellunge population and illustrates a useful approach for other unique populations.

Maintaining the long-term viability of populations is not only an important goal of fishery management (Hallerman 2003) but is central to the stewardship of all resources that affect biodiversity (Meffe and Carroll 1997). Loss of biodiversity is considered by the U.S. Environmental Protection Agency as one of the four greatest risks to natural ecology and human well-being (USEPA 1990). Although extinction of entire species is often the focus of concern for biodiversity, loss of genetic diversity within species is far more prevalent and leads to declines in health, productivity, and the ability to adapt to environmental change and may ultimately lead to extinction (Myers 1997). Loss of biodiversity is also a serious concern within the fishery management community (Winter and Hughes 1997).

Shoepack Lake, in Voyageurs National Park (VNP), Minnesota, contains a unique population of muskellunge *Esox masquinongy* (Frohnauer et al. 2007, this issue) that is of special concern for several reasons. First, the Shoepack Lake muskellunge population (SLMP) is genetically unique (Hanson et al. 1983; Fields et al. 1997). Shoepack Lake has been isolated from other lakes containing muskellunge for over 10,000 years, allowing the SLMP to diverge genetically from other populations. This divergence contributes to the overall genetic diversity found within the species. Second, as the primary muskellunge fishery in VNP, the SLMP represents an outstanding recreational opportunity for park visitors. Sport fishing is an important component of recreational activity in national parks (Panek 1994) and the principal visitor activity

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in VNP (Kallemeyn et al. 2003), and, thus, management of fishery resources such as the SLMP is a high priority. Third, the SLMP has slower growth rates, lower body condition, higher densities, and higher angler catch per unit effort (CPUE ) than other muskellunge populations and a habitat area that fluctuates dramatically (Frohnauer et al. 2007). These characteristics have the potential to affect the long-term viability of the SLMP.

In assessing the long-term viability of the SLMP as a fishery resource and one that contributes to biodiversity, approaches from both fisheries science and conservation biology are necessary. Simulation modeling of future population responses to alternative scenarios, including different levels of exploitation, is widely used in fisheries science to evaluate management alternatives and to guide management decision-making (Johnson 1995). A simulation model is a simplified, yet quantitative representation of a fishery. Simulation models allow comparison of the relative effects of processes such as natural mortality, recruitment, exploitation, and many other potentially important factors on response variables such as population size or fishery yield. Johnson (1995) identified three important benefits of simulation modeling for fishery management. First, constructing a model requires assembly of all available information about the population or system to be modeled and conceptualization of the key components and interactions. Second, models facilitate learning about how the population or system functions by exploring responses to changes in one or more of the determining factors. Third, and perhaps most importantly, models allow managers to explore potential scenarios and alternative management actions. The quantitative outputs provide concrete results for comparison among scenarios and for evaluating the benefits and risks of management alternatives.

Identifying threats to a species and evaluation of the probability of its persistence over time are collectively known as population viability analysis (PVA; Akçakaya and Sjögren-Gulve 2000). Population viability analysis is an important tool for conserving biodiversity and also is useful for evaluating threats to populations within species, especially when populations represent clearly unique gene pools, such as in Pacific salmon (e.g., Emlen 1995; Allendorf et al. 1997). An important practical outcome of PVA is determining a population size that can withstand threats to long-term viability by examining potential impact factors (Lindenmayer et al. 1993; Reed et al. 1998). This population size is typically defined as the genetically effective population size ($N_e$), which is a more precise estimator of the size of the gene pool and, thus, a better indicator of potential loss of genetic variability. This is ultimately the best indicator of long-term population viability (Meffe and Carroll 1997; Allendorf and Ryman 2002; Hallerman 2003). Although no firm rules exist, a threshold minimum effective population size of 500 is often used as a rule-of-thumb indicator of the potential for the loss of genetic variability from random genetic drift, inbreeding depression, and bottlenecks and ultimately for the reduction in the long-term viability of the population (Hallerman 2003; Ryan et al. 2003; Taylor 2003). Effective population size below 50 is often interpreted as an indicator of immediate serious threat to genetic variability and potential extinction.

A combination of approaches from fisheries science and conservation biology has several attractive benefits for evaluation of the long-term viability of fishery and biodiversity resources such as the SLMP. First, it increases awareness by fishery biologists of the need to conserve biodiversity, and increases awareness by conservation biologists of fishery management concerns. Second, it uses readily available and commonly used techniques from both disciplines, making it accessible to managers as well as specialized researchers. Finally, and perhaps most importantly, combining population modeling with estimation of the effective population size of simulated populations provides a broad, comprehensive evaluation of the variety of threats that exist and potential solutions to them that will maintain biodiversity and conserve the long-term viability of important fishery resources.

The goal of this study was to use the population and angler exploitation data generated in a companion study (Frohnauer et al. 2007) to simulate the effects of potential threats to the long-term viability of the SLMP. Our specific objectives were to (1) simulate the long-term population dynamics of the SLMP in response to recruitment variation, various levels of exploitation, and reduced habitat area; (2) estimate the effective population size of simulated populations; (3) evaluate potential threats to the long-term viability of the SLMP; and (4) recommend management actions to help preserve the long-term viability of the SLMP.

## Methods

*Population and exploitation data.*—Population and angler exploitation data were obtained from a companion study (Frohnauer et al. 2007). Intensive sampling and mark–recapture methods were used to quantify population abundance, population dynamics, survival, growth, age at maturity and fecundity. Angler surveys were used to quantify angler pressure, catch rates and exploitation. See Frohnauer et al. (2007) for detailed descriptions of population and angler exploitation methods.

*Population simulations.*—We used the Fishery Analysis and Simulation Tools (FAST) software package (Slipke and Maceina 2000) for population simulations. The FAST program uses the Jones modification of the Beverton–Holt equilibrium model to simulate a variety of scenarios and both population and fishery responses. Use of FAST for fisheries research and management simulations is increasing because of its broad scope of applications, menu-driven Windows interface, user-friendly graphical and spreadsheet output formats, and flexibility in structuring a vast array of simulations (e.g., Boxrucker 2002; Lovell and Maceina 2002; Quist et al. 2002; Slipke et al. 2002).

We used the dynamic pool model option (Slipke and Maceina 2000) in FAST to simulate annual adult population size for 100 years. The dynamic pool model option was used because it includes population size among its output variables. We considered fish age 5 and older to be adults based on the companion study (Frohnauer et al. 2007). The parameters used in the simulations are listed in Table 1. The parameters $L_\infty$, $K$, and $t_0$ were obtained from fitting the von Bertalanffy growth function (VBGF) to pooled female and male growth data in FAST. The parameters $a$ and $b$ were obtained from fitting the $\log_{10}$ transformed weight–length equation to pooled female and male weight–length data in FAST. The parameter $W_\infty$ was obtained by solving the weight–length equation for $L_\infty$. The parameter $\mathrm{Age}_{\mathrm{max}}$ was obtained from Casselman and Crossman (1986). The parameter Years was set at 130, but we discarded the results from the first 30 years because dynamic pool model algorithms require a number of years equal to the maximum age for simulated populations to include all age classes. The parameter $\mathrm{cm}_{\mathrm{current}}$, obtained from the companion study (Frohnauer et al. 2007), was equal to instantaneous natural mortality because current fishing mortality is essentially zero. The parameter $\mathrm{cm}_{\mathrm{2xcurrent}}$ was $\mathrm{cm}_{\mathrm{current}}$ multiplied by two, which was chosen to represent a potentially higher future natural mortality rate. This higher rate is comparable with other muskellunge populations (T. Simonson, Wisconsin Department of Natural Resources, personal communication). The parameter cf is an estimate of conditional fishing mortality. We used three values to examine the impacts of variable fishing mortality. The parameter $\mathrm{cf}_0$ was set at zero to establish a baseline or what this population would look like with no angling influence. We were interested in what effects maximum fishing pressure would have on the SLMP under current regulations. We did this by estimating the total number of muskellunge mortalities by using the highest calculated CPUE, highest possible angler-hours, and 100% harvest of legal-size fish. The parameter $\mathrm{cf}_{\mathrm{low}}$ was a hypothetical conditional fishing mortality rate representing the number of angling-related muskellunge deaths in relation to the population size before the destruction of a dam constructed by beavers *Castor canadensis*. The parameter $\mathrm{cf}_{\mathrm{high}}$ was a higher hypothetical conditional fishing mortality representing the same number of deaths due to angling in a population half the size of the current SLMP.

Recruitment in the SLMP and in most muskellunge populations is unknown. Therefore, we used the fixed recruitment option and sequentially varied recruitment values in pilot simulations to determine the mean recruitment value required to generate the current estimated adult population size. The same procedure was used to determine the recruitment value required to generate a hypothetically lower adult population size of the same density as at the beginning of the companion

TABLE 1.—Parameters used in dynamic pool model simulations of the muskellunge population in Shoepack Lake, Minnesota. See text for additional information and sources of parameters.

| Parameter | Description | Value |
|---|---|---|
| $L_\infty$ | Maximum length (mm) | 726 |
| $K$ | Growth coefficient | 0.251 |
| $t_0$ | Time when length = 0 (years) | −0.523 |
| $W_\infty$ | Maximum weight (g) | 2,222.2 |
| $\mathrm{Age}_{\mathrm{max}}$ | Maximum age (years) | 30 |
| $a$ | Intercept of regression of weight versus length | −5.345 |
| $b$ | Slope of regression of weight versus length | 3.038 |
| Years | Number of years specified in simulations | 130 |
| $\mathrm{cm}_{\mathrm{current}}$ | Current conditional natural mortality rate | 0.05 |
| $\mathrm{cm}_{2\times\mathrm{current}}$ | Two times current conditional natural mortality rate | 0.10 |
| $\mathrm{cf}_0$ | No conditional fishing mortality | 0 |
| $\mathrm{cf}_{\mathrm{low}}$ | Hypothetical low conditional fishing mortality rate | 0.025 |
| $\mathrm{cf}_{\mathrm{high}}$ | Hypothetical high conditional fishing mortality rate | 0.05 |
| Recruitment SD | Natural variability in recruitment | 25 or 45 |

study (Frohnauer et al. 2007), but inhabiting the smaller habitat area present in Shoepack Lake after the beaver dam failure. For final simulations we used the random (normally distributed) recruitment option, using the values identified in pilot simulations as mean values and arbitrarily chosen low (SD = 25) and high (SD = 45) levels of yearly variation to illustrate how differing levels of recruitment variation could affect population dynamics.

The procedures detailed above resulted in final simulations representing 12 different combinations of natural mortality rate, fishing mortality rate, and recruitment variability. Each of the 12 combinations was simulated for the current average adult population size and for a hypothetical lower adult population size that could be expected to result from long-term reduction in habitat area. These twenty-four 100-year population simulations represent a realistic range of scenarios given what is known about muskellunge biology in general, population status, population dynamics, angler exploitation, and documented susceptibility to habitat area reduction of the SLMP.

*Estimating effective population size.*—We used the approach developed by Hill (1972), Nunney (1993), and Nunney and Elam (1994) to estimate effective population size from population size. This method is classified by Nunney and Elam (1994) as an ecological method, which they argue is preferred over genetic methods for evaluation of alternative conservation strategies. The method results in an estimated ratio of effective population size to population size, which can then be used as a multiplier to convert population size estimates to effective population size estimates. We multiplied our simulated annual populations by this ratio to obtain simulated annual effective population sizes.

The equation for the ratio of effective population size to population size is

$$N_e/N = 4r(1-r)T/[rA_f(1+I_{Af}) + (1-r)A_m(1+I_{Am}) + (1-r)I_{bm} + rI_{bf}], \tag{1}$$

where $N_e$ is effective population size, $N$ is population size, $r$ is sex ratio, $T$ is generation time, $A_f$ is average female adult life span, $A_m$ is average male adult life span, $I_{Af}$ is the standardized variance of female adult life span, $I_{Am}$ is the standardized variance of male adult life span, $I_{bf}$ is the standardized variance of female reproductive success, and $I_{bm}$ is the standardized variance of male reproductive success. The sex ratio was assumed to be 1:1 because we had no evidence of a skewed sex ratio in our sampling data (Frohnauer 2004). Generation time was calculated as

$$T = M_i - 1 + A_i, \tag{2}$$

where $M_i$ is mean age of maturity and $A_i$ is the mean life span of adult fish. Mean life span was calculated as

$$A_i = (A_f + A_m)/2. \tag{3}$$

Using length data from Frohnauer (2004) and sex-specific VBGFs (Frohnauer et al. 2007) rearranged to solve for age, we estimated the value of $A_f$ to be 11 and the value of $A_m$ to be 9.6. Using values of 6 for $M_i$ obtained from Frohnauer et al. (2007), and 10.3 for $A_i$ calculated with equation (3), we estimated the value of $T$ to be 15.3. Standardized variances of adult life spans were calculated as the variance divided by the mean squared, resulting in values of 0.786 for $I_{Af}$ and 0.189 for $I_{Am}$.

We obtained two sets of estimates for the standardized variance of reproductive success, one based on the observed mortality rate (Frohnauer et al. 2007) and another based on two times the observed mortality rate, which is comparable to that for other muskellunge populations (T. Simonson, Wisconsin Department of Natural Resources, personal communication). Standardized variance of female reproductive success (Nunney and Elam 1994) was calculated as

$$I_{bf} = (1-\alpha_f)/\alpha_f, \tag{4}$$

where $\alpha_f$ is the Poisson-distributed proportion of successful females (Nunney and Elam 1994), which was calculated as

$$\alpha_f = xp/b_f, \tag{5}$$

where $x$ is the mean productivity of females producing at least one offspring. Female productivity is the number of young an individual needs to produce for at least one individual from the brood to be recruited into the adult population. The variable $p$ is the proportion of females producing young. We estimated that recruitment of adult fish was equal to the mortality rate because no immigration or emigration was occurring, and, thus, stable population size at carrying capacity required that recruitment be balanced by mortality. For the SLMP, there is a lag time of 5 years, so productivity was calculated as the number of 4-year-old fish recruited into the adult population divided by the number of age-0 recruits. The variable $b_f$ is the Poisson-distributed proportion of females producing no young. Nunney and Elam (1994) provided the equation: $x = b_f/[1 - \exp(-b_f)]$, to estimate the expected value of $b_f$. Using values of 0.1 for $x$, 1.5179 for $p$, and 0.902 for $b_f$ based on the observed mortality rate, we estimated the value of $I_{bf}$ to be 4.94. Using values of 0.2 for $x$, 1.6161 for $p$, and 1.0513 for $b_f$ based on two times the observed mortality rate, we estimated the value of $I_{bf}$ to be 2.25. Standardized variance of male reproductive success was calculated as

$$I_{bm} = K + (1 - \alpha_m)/\alpha_m, \tag{6}$$

where $K$ is a correction factor and $\alpha_m$ is the proportion of males attempting to spawn. We assumed the lottery polygyny model (Nunney and Elam 1994) adequately represents the mating system of the SLMP. Under this system, females mate once per season but males attempt to mate many times. Though females are known to have two distinct egg-laying periods during spawning and, thus, the likelihood of having two different male partners, the very low survival rate of offspring that grow to reproductive age makes it a reasonable assumption that only one of the spawning periods was successful. Males on the other hand, stay on spawning grounds and attempt to breed with as many females as possible. We calculated $K$ as

$$K = r/[(1 - r)\alpha_f]. \tag{7}$$

Under the lottery polygyny model, $\alpha_m$ is equal to 1. Based on the observed mortality rate, we used a value of 0.5 for $r$ and 0.1682 for $\alpha_f$ to calculate $K$ as 5.94 and estimate the value of $I_{bm}$ to be 5.94. Based on two times the observed mortality rate, we used a value of 0.5 for $r$ and 0.3074 for $\alpha_f$ to calculate $K$ to be 3.25 and estimate the value of $I_{bm}$ to be 3.25.

The procedures detailed above resulted in two estimates of the ratio $N_e/N$. For the observed mortality rate, our estimate of $N_e/N$ was 0.66. For two times the observed mortality rate, our estimate of $N_e/N$ was 0.75. These estimates are comparable to the mean $N_e/N$ value of 0.73 reported by Nunney and Elam (1994) based on a compilation of previous studies of crustaceans, birds, and mammals. We used our estimated $N_e/N$ values as multipliers to convert simulated population-size estimates to simulated effective population sizes.

## Results

One-hundred-year simulations of effective population size based on the population size and habitat area at the beginning of the companion study (Frohnauer et al. 2007) resulted in annual values ranging from 276 to 872 (Figure 1). At current levels of natural and fishing mortality, effective population size was well above the threshold level of 500 in all years, ranging from 629 to 852 (Figure 1a, b). Higher recruitment variability increased the range of yearly variability in simulated effective population size, but at no time did effective population size approach the threshold level. At the current level of natural mortality and a hypothetical low level of fishing mortality, simulated effective population size fluctuated above and below the threshold level, ranging from 407 to 684 (Figure 1c, d). The percentage of years the simulated effective population size was below 500 was higher with low recruitment variability (47%) than with high recruitment variability (15%). At the current level of natural mortality and a hypothetical higher level of fishing mortality, simulated effective population size was below the threshold level in all years, ranging from 276 to 451 (Figure 1e, f). At two times the current level of natural mortality and the current level of fishing mortality, effective population size was well above the threshold level of 500 in all years, ranging from 654 to 872 (Figure 1 g, h). Higher recruitment variability increased the range of yearly variability in simulated effective population size, but at no time did effective population size approach the threshold level. At two times the current level of natural mortality and a hypothetical low level of fishing mortality, effective population size was above the threshold level in all years, ranging from 511 to 674 (Figure 1i, j). Higher recruitment variability increased the range of yearly variability in simulated effective population size, and at one point during the simulation the effective population size came very close to the threshold level. At two times the current level of natural mortality and a hypothetical higher level of fishing mortality, simulated effective population size was below the threshold level in all years with low recruitment variability, ranging from 411 to 498, and in most years (80%) with high recruitment variability, ranging from 385 to 548 (Figure 1k, l).

One-hundred-year simulations of effective population size based on the reduced habitat area after the beaver dam failure and our assumption of a proportional reduction in average population size (Frohnauer et al. 2007) also resulted in a variety of annual values, from 134 to 489 (Figure 2). There was a striking difference between these simulations and the previous set; effective population size in every simulation was below the threshold level 100% of the time. Regardless of the level of recruitment variability, the combination of reduced habitat area and a hypothetical higher level of fishing mortality had a particularly deleterious effect on effective population size (Figure 2e, f, k, l). Effective population size in these four simulations ranged from 134 to 344, well below the threshold value of 500.

## Discussion

Our simulations identified two potential threats to the long-term viability of the SLMP, reduction in habitat area and exploitation. Habitat area reduction was observed in dramatic fashion during the companion

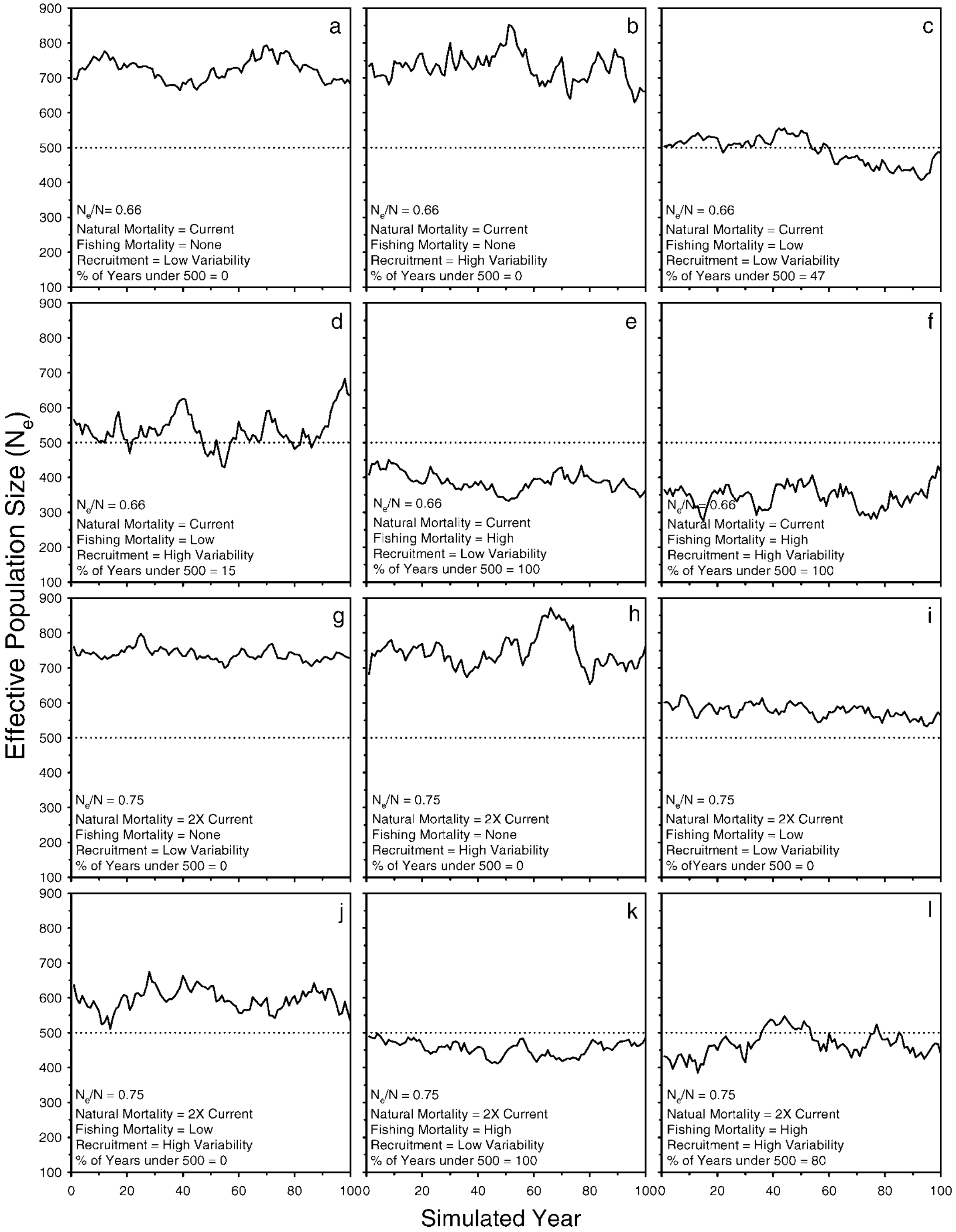

FIGURE 1.—Simulations of effective population size ($N_e$) initially parameterized to generate a population of 1,120 muskellunge (the number observed at the beginning of a companion study [Frohnauer et al. 2007]) in Shoepack Lake, Minnesota. Model parameters are discussed in the text. The dotted lines indicate the threshold $N_e$ level of 500 fish.

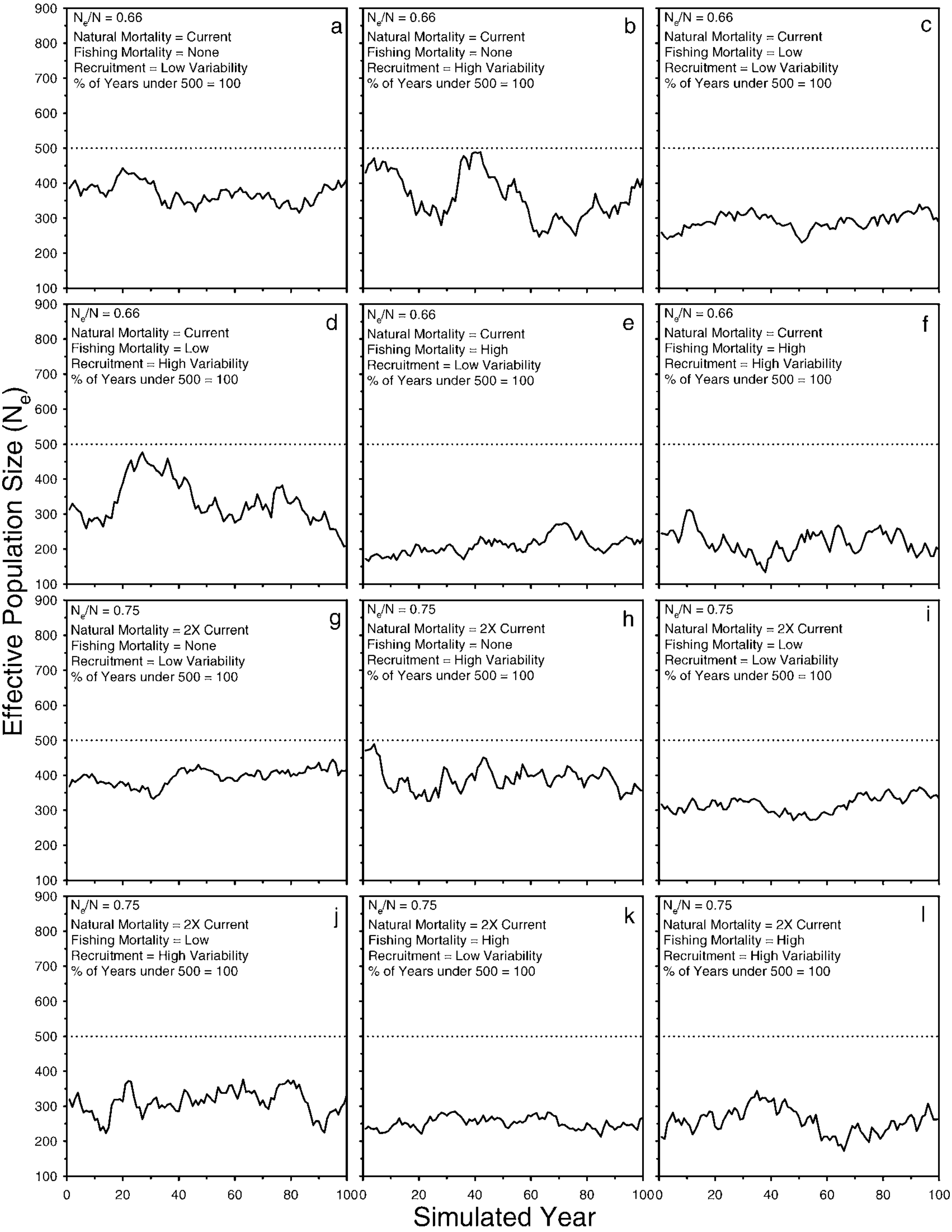

FIGURE 2.—Simulations of effective population size ($N_e$) initially parameterized to generate a population of 600 muskellunge (a hypothetical number reflecting the reduction in population owing to reduced habitat area) in Shoepack Lake, Minnesota. See Figure 1 for additional details.

study (Frohnauer et al. 2007) and therefore must be considered a realistic threat. Exploitation is negligible at present but could emerge as a significant threat if harvest and associated hooking mortality increase in the future, perhaps as consequences of a continued upward trend in boat use on Shoepack Lake. Although initially the latter threat appears more amenable to management than the former, there may be ways to reduce the potential for harmful loss of effective population size from both of these threats.

A critical assumption in our simulations of the effect of reduced habitat area is the long-term proportionality of population size to habitat area. Several lines of evidence support this assumption. Meta-analysis of data from a wide variety of insect, mammal and bird species indicated that, on average, population densities were positively correlated with area (Connor et al. 2000). Carlander (1955) analyzed the relationship of fish standing crop biomass with lake area for a large data set from lakes and reservoirs and concluded that, on average, there was no significant relationship of standing crop biomass with area. These synoptic studies imply that, all other factors being equal, numbers of individuals or the total weight in a population decline with declining area. A good example of this phenomenon is represented in Figure 2 in Tonn (1985). In fact, a significant body of theory in fisheries management is based on this observed proportionality. Empirical models of fish biomass, production and yield (Ryder et al. 1974; Matuszek 1978; Hanson and Leggett 1982) are area-specific (e.g., kg/ha), tacitly assuming proportionality in the numbers or weight of fish with lake area. The fact that the portion of habitat area lost in Shoepack Lake due to the beaver dam failure was the shallow littoral zone containing much of the available cover (Frohnauer et al. 2007) suggests that the remaining habitat area would be of poorer quality for an extended period of time, increasing the likelihood of reduced population size. A final consideration is the time scale of population size reduction in response to habitat area reduction. Frohnauer et al. (2007) reported no immediate population reduction after the dam failure but did find evidence for a gradual decline in population size over the course of their field study. The available evidence suggests that population size is roughly proportional to habitat area but that a population response to an abrupt change such as the one that occurred in Shoepack Lake would require several years, perhaps even a decade or more.

Water level is an important determinant of habitat area for muskellunge in Shoepack Lake, and beavers regulate it through the construction and maintenance of the outlet dam. Beaver populations have fluctuated greatly in this region, as they have in all of North America, and this fluctuation has apparently resulted in water level fluctuation and ultimately habitat area fluctuation for the SLMP. Before European settlement, the North American beaver population was estimated to lie between $60 \times 10^6$ and $400 \times 10^6$ animals (Seton 1929). Trapping and forest clearing depleted this population to near extinction by 1900 (Jenkins and Busher 1979). Recent estimates of the North American beaver population range from $6 \times 10^6$ to $12 \times 10^6$ animals (Naiman et al. 1986). On the Kabetogama Peninsula in VNP, which contains Shoepack Lake, beaver abundance has followed a similar trend over the last century. Beaver were rare on the peninsula in 1900 due to trapping and extensive logging, but reached a population density of roughly one colony per km$^2$ by the late 1980s (Broschart et al. 1989) due to a combination of cessation of trapping, re-growth of forests, and establishment of Voyageurs National Park in 1975. Aerial photographs of Shoepack Lake in 1927, 1936, 1972 and 1981 showed no outlet beaver dam and reduced surface area (Voyageurs National Park, unpublished data). Photographs taken in 1988 showed a slight increase in surface area, and by 1995 aerial photographs documented an expanded surface area comparable with what we encountered in May 2001 (Frohnauer et al. 2007). This history of changing beaver presence in Shoepack Lake suggests that habitat area for the SLMP has changed similarly over time. We speculate that during the thousands of years between the last glaciation and the decline in beavers associated with trapping and European settlement, habitat area in Shoepack Lake was probably similar to what we encountered in May 2001. However, it is also likely that occasional extreme rain events during this time may have lead to periodic dam failures followed by relatively rapid dam rebuilding. For the SLMP, this scenario suggests a habitat area and population size similar to what we encountered in May 2001 for most of the postglacial period, punctuated by occasional habitat area bottlenecks. Whether these bottlenecks lasted long enough to result in population bottlenecks is unknown. In contrast to our speculation about the early history of the SLMP, evidence is clear that habitat area was reduced from at least the early 1900s until the 1980s. If population size was reduced in response to reduced habitat area, then based on our simulations we believe the SLMP may have already lost significant genetic variation. The steepness of the probability of persistence curves between populations of 600 and 1,120 in Figure 18.1 in Hallerman (2003) support our contention that reduced population size should be viewed as a significant threat to the long-term viability of the SLMP.

Fishing mortality is also a significant threat to the SLMP. Although exploitation is negligible at present (Frohnauer et al. 2007), there are two reasons for concern that exploitation and hooking mortality could increase in the future. First, boat use on Shoepack Lake has been increasing steadily over the last decade, and most of the users of the public boat are anglers fishing for muskellunge. Catch rates are high on Shoepack Lake, and if boat use continues to increase fishing mortality resulting from exploitation and hooking stress is likely to increase. Second, even if boat use and fishing pressure remained at 2001 levels, if population size adjusted downward in response to reduced habitat area as hypothesized in our second set of simulations, the fishing mortality rate would probably increase primarily as a result of the stress associated with hooking and releasing fish from a smaller population.

Recruitment variability had a relatively minor effect on effective population size in our simulations. Recruitment variability is widely recognized as a major determinant of biomass and yield in marine fisheries (Rothschild 1986; Cowan and Shaw 2002), and is well known to affect abundance of freshwater species such as walleye *Sander vitreus* (Kempinger and Carline 1977; Koonce et al. 1977; Kallemeyn et al. 2003), yellow perch *Perca flavescens* (Koonce et al. 1977; Shroyer and McComish 1998; Kallemeyn et al. 2003), black crappie *Pomoxis nigromaculatus*, and white crappie *P. annularis* (Mitzner 1991; Guy and Willis 1995). Muskellunge typically exist in low density, are long lived (up to 30 years) and mature late (ca. age 6) compared with most exploited freshwater fishes, and this life history inertia probably results in weaker adult population response to recruitment variability than in other freshwater species. Based on our simulation results we tentatively conclude that interannual recruitment variability probably has a minor effect on effective population size of the SLMP compared with reduction in habitat area and exploitation, but we caution that because of the lack of recruitment data on muskellunge populations, including the SLMP, this conclusion is far from certain.

The primary threats to the SLMP based on the simulation results, namely, habitat area reduction and increased exploitation, present different challenges for future management. Prevention of increased exploitation and associated hooking mortality can be addressed with traditional fishery management approaches (Goeman et al. 1995; Noble and Jones 1999). The current muskellunge regulations on Shoepack Lake allow one fish (>762 mm) harvested per day, with no harvest allowed from late February to early June to prevent angling during spawning. These regulations are adequate to minimize fishing mortality at current levels of fishing pressure and population size (Frohnauer et al. 2007). Future adequacy of regulations will require updated information, and we agree with Kallemeyn et al. (2003) who recommended periodic population and creel surveys to monitor abundance and exploitation on Shoepack and other interior VNP lakes. If fishing pressure increases, adoption of no-kill, barbless hook, and perhaps even limited entry regulations should be considered to prevent or at least minimize increases in exploitation and hooking mortality.

Restoration of the pre-July 2001 habitat area and prevention of future habitat area reductions are more uncertain and will require reestablishment and maintenance of the outlet dam by beavers. In addition to roughly doubling the surface area, the outlet dam on Shoepack Lake provided two of the keys to muskellunge habitat management recommended by Dombeck (1986), elevated water level and increased littoral zone woody debris. Beaver density is high on the Kabetogama Peninsula, and the protection offered by the remote location of Shoepack Lake in VNP should favor relatively rapid reestablishment of the outlet dam. Restricting visitors from the area around the lake outlet by posting signs on site and providing information at park visitor centers, as is currently done to restrict visitors from areas near eagles' nests, would reduce human disturbance and facilitate dam reconstruction. Other factors regulating beaver activity such as food dynamics and predators will be difficult, if not impossible, to control in a national park setting. Along with the monitoring recommended by Kallemeyn et al. (2003), we suggest annual aerial monitoring of beaver activity near the outlet and annual inspection of the condition of the outlet dam. This information would help managers assess the status of beaver activity in maintaining the outlet dam, and alert them when the dam is at risk for failure.

Our simulation of the effects of various factors on effective population size is only one of several possible approaches toward understanding and preserving the genetic integrity of the SLMP. Although we used the ecological method for estimating $N_e/N$ ratios (Nunney and Elam 1994), we acknowledge that genetic methods could potentially give different results. Using genetic methods with northern pike *E. lucius* in a lake similar in size to Shoepack Lake, Miller and Kapuscinski (1997) estimated $N_e/N$ ratios ranging from 0.03 to 0.14, much lower than we estimated for the SLMP. If our estimated $N_e/N$ ratios are overestimates, as some studies with fish imply (Miller and Kapuscinski 1997; Turner et al. 2002; Hansen et al. 2006), concerns about potential threats to the long-term viability of the SLMP are even more serious than our results suggest.

Several other approaches, some with software packages, have been developed for PVA (e.g., Lacy 1993; Akçakaya 2000; Sjögren-Gulve and Hanski 2000). Although our approach was unconventional in its combination of a fishery modeling software package and an equation from the conservation literature predicting the $N_e/N$ ratio, we agree with Akçakaya and Sjögren-Gulve (2000) who stated, "There is no single recipe to follow when doing a PVA, because each case is so different in so many respects." Given the lack of agreement in the PVA literature concerning the validity of conventional approaches (Coulson et al. 2001), there appears to be ample room for new approaches to emerge. We do not contend that our approach was better than conventional approaches. Rather, we simply assert that it was adequate and appropriate for meeting our objectives. In addition, by bridging approaches from fishery management and conservation biology, we believe it will serve as a practical example for future application.

Biodiversity ranks high among the resources our national parks are designed to preserve and protect (Stohlgren et al. 1995). As oases of pristine habitat in a desert of altered and degraded landscapes, national parks are among the few places where viable, unexploited populations of many species remain. Limiting access and human exploitation of populations, and restoring and preserving natural habitats and ecosystem functions within parks are important tools in the wise management and preservation of biodiversity. Thus, the unique biodiversity resources known to exist in parks, such as the SLMP, warrant special attention. Our study evaluated potential threats and suggested management actions that should enhance the long-term viability of the SLMP, and illustrates a useful approach for other unique populations.

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