GREAT LAKES FISHERY COMMISSION

2004 Project Completion Report[1]

Effects of Mortality Sources on Population Viability of Lake Sturgeon: A Stage-Structured Model Approach

by:

Trent M. Sutton[2], Barry L. Johnson[3], Terry D. Bills[3], Cynthia S. Kolar[3]

[2]Purdue University
Department of Forestry and Natural Resources
195 Marsteller Street
West Lafayette, Indiana 47907-1159

[3]U.S. Geological Survey
Upper Midwest Environmental Sciences Center
2630 Fanta Reed Road
La Crosse, Wisconsin 54603

December 2003

[1]Project completion reports of Commission-sponsored research are made available to the Commission's cooperators in the interest of rapid dissemination of information that may be useful in Great Lakes fishery management, research, or administration. The reader should be aware that project completion reports have not been through a peer review process and that sponsorship by the Commission does not necessarily imply that the findings or conclusions are endorsed by the Commission.

PROJECT COMPLETION REPORT

Effects of Mortality Sources on Population Viability of Lake Sturgeon: A Stage-Structured Model Approach

Submitted to:
Executive Secretary
Great Lakes Fishery Commission
2100 Commonwealth Boulevard, Suite 209
Ann Arbor, Michigan 48105-1563

Submitted by:
Trent M. Sutton
Purdue University
Department of Forestry and Natural Resources
195 Marsteller Street
West Lafayette, Indiana 47907-1159

Barry L. Johnson, Terry D. Bills, and Cynthia S. Kolar
U.S. Geological Survey
Upper Midwest Environmental Sciences Center,
2630 Fanta Reed Road
La Crosse, Wisconsin 54603

December 2003

ABSTRACT

We used a stage-structured, life-history model (MOCPOP 2.0) to examine the impacts of lampricide applications and sea lamprey *Petromyzon marinus* parasitism on the population viability of lake sturgeon *Acipenser fulvescens* in the Laurentian Great Lakes basin. Population abundance, the number of age-1 recruits, and reproductive potential of lake sturgeon exhibited relative percentage decreases with increasing mortality of age-0 juvenile fish (range, 0 to 100%) as a result of lampricide applications at four-year treatment intervals. When larval sea lamprey mortality (range, 100 to 0%) following lampricide treatments was incrementally decreased, lake sturgeon mortality from increased sea lamprey parasitism for both the low and high mortality simulation scenarios resulted in relative percentage decreases in population abundance, the number of age-1 recruits, and reproductive potential from baseline conditions. Incremental increases in sea lamprey-induced lake sturgeon mortality (range, 0 to 22%) as estimated from wounding rate data resulted in relative percentage decreases in population abundance, the number of age-1 recruits, and reproductive potential from baseline conditions. Based on the results of our model simulations, it appears that mortality agents, such as sea lamprey parasitism, that influence subadult and adult lake sturgeon have a greater impact on the long-term population viability of this species than mortality factors that affect early life stages (i.e., lampricide applications). As a result, we do not recommend that lampricide-application strategies for the control of larval sea lamprey populations in tributaries containing lake sturgeon continue to follow the no effect protocol in order to allow for the long-term rehabilitation and management for this species.

INTRODUCTION

Lake sturgeon *Acipenser fulvescens* were historically one of the most abundant fishes in the Laurentian Great Lakes, utilizing the productive nearshore waters and adjoining tributaries as spawning, nursery, and feeding areas (Auer 1999a; Thuemler et al. 1999). Abundance of lake sturgeon throughout the basin declined dramatically during the 1800s, and populations were reduced to remnant levels by the early 1900s (Wells and McLain 1973). Factors directly attributed to these declines include reductions in water quality, alterations to physical habitat, impediments to migration, and commercial overexploitation (Harkness and Dymond 1961; Smith 1968; Rochard et al. 1990).

Although basin-wide improvements in water quality and reductions in harvest have allowed for some recovery of lake sturgeon stocks, abundance still remains low, with current population estimates at 1% of their historical levels (Hay-Chmielewski and Whelan 1997). Because population recovery has been limited, lake sturgeon are listed as an endangered, threatened, or special concern species by the eight states bordering the Great Lakes and as a species of special interest by the U.S. Fish and Wildlife Service (Johnson 1987; Booker et al. 1993; Auer 1999a). As a result, significant efforts have been undertaken by state, federal, and tribal natural resources management agencies to protect and rehabilitate remaining populations. By identifying and addressing critical information needs and ongoing impediments to rehabilitation, it is anticipated that long-term sustainability and recovery can occur for lake sturgeon, allowing for their delisting as an imperiled species in the Great Lakes basin.

The current limited level of recovery by lake sturgeon populations throughout the Great Lakes basin has largely been attributed to habitat fragmentation and degradation in tributaries used as spawning and nursery areas (Rochard et al. 1990; LaHaye et al. 1992; Auer 1996a;

Thuemler et al. 1999). However, other factors may also contribute to the lack of successful rehabilitation. For example, early life stages of lake sturgeon are sensitive to lampricides (3-trifluoromethyl-4-nitrophenol [TFM] and 2’, 5-dichloro-4’-nitrosalicylanilide [niclosamide]) that are used to control larval sea lamprey *Petromyzon marinus* populations in Great Lakes tributaries. According to Bills et al. (2000) and Boogaard et al. (2003), swim-up larvae and small (< 100 mm) juvenile lake sturgeon exposed to TFM and TFM/1% niclosamide in laboratory toxicity experiments experienced greater than 50% mortality at the minimum lethal concentration (MLC) required for effective sea lamprey control. In contrast, yolk-sac larvae and larger (> 100 mm) juvenile lake sturgeon exhibited low sensitivity to lampricides at standard treatment concentrations (Johnson et al. 1999; Boogaard et al. 2003). Therefore, lampricide applications in streams containing swim-up larvae and small juvenile lake sturgeon may negatively impact recruitment, rehabilitation, and sustained viability of this species in the Great Lakes.

To minimize mortality of lake sturgeon early life stages during lampricide applications, the U.S. Fish and Wildlife Service implemented a no observable effect (i.e., no mortality) treatment protocol in 1989 for streams suspected or known to support spawning populations of this species (Klar and Schleen 1999). Beginning in 1998, this protocol was amended so that the maximum lampricide treatment concentration that could be applied to streams supporting lake sturgeon would not exceed 1.0 times the MLC. Further, these systems are not to be treated until after 01 August to allow age-0 lake sturgeon to grow to at least 100 mm in length (Bills et al. 2000). Although these measures appear to have been successful in protecting early life stages of lake sturgeon, the overall effectiveness of lampricide treatments may be diminished because greater numbers of parasitic-phase sea lampreys may be produced from tributaries through inefficient or failed lampricide treatments (W. Swink, U.S. Geological Survey, personal communication). As a result, there is potential for increased parasitism-induced mortality on lake sturgeon and other fishes such as lake trout *Salvelinus namaycush*. Therefore, continued use of the no observable effect (herein referred to as no effect) treatment protocol in streams supporting lake sturgeon may not allow the desired level of protection needed to rehabilitate and maintain viable populations of this species in the Great Lakes basin.

For this study, we used a stage-structured, life-history model to examine the impacts of lampricide applications and sea lamprey parasitism on lake sturgeon populations in the Great Lakes basin. The specific objectives of this research were to: (1) examine incremental changes in lampricide- and sea lamprey-induced mortality on the abundance, recruitment, and reproductive potential of lake sturgeon; (2) determine which mortality factor has the greatest potential to negatively influence lake sturgeon population viability; and (3) identify deficiencies in lake sturgeon life-history information needed for improvement of the population model. With this information, we will discuss the implications of each lampricide treatment strategy within the context of minimizing effects on lake sturgeon populations while ensuring sea lamprey control at levels consistent with fisheries management objectives in the Great Lakes basin.

MATERIALS AND METHODS

For this study, data from published and unpublished studies on the life history and population dynamics of lake sturgeon in the Great Lakes basin was incorporated into a stage-structured simulation model. When data for lake sturgeon were not available, we substituted information collected from studies on other sturgeon species. We used the modeling software MOCPOP (Beamesderfer 1991) to determine which life-stage mortality source (i.e., lampricide application or sea lamprey parasitism) most strongly influenced abundance of subadult and adult fish, recruitment to age 1 (i.e., the number of age-1 recruits), and reproductive potential (i.e., the number of adult, female fish) for a generalized population of lake sturgeon in a Great Lakes tributary. For these simulations, model outputs were generated for each of the different levels of lake sturgeon mortality resulting from lampricide applications and sea lamprey parasitism separately as defined below under *Mortality sources*.

Life-history parameters. – The model was comprised of the following linked, lake sturgeon life-stage groups: (1) eggs, larvae, and age-0 juveniles; (2) juveniles (ages 1 to 6); and (3) subadults (ages 6 to 25) and adults (ages 25+). Life stage and population parameter data that were used to conduct the model simulations are shown in Table 1. We relied largely on the published studies of Harkness and Dymond (1961) and Auer (1999b) that were completed on lake sturgeon populations in the Lake Nipigon and Sturgeon River watersheds, respectively, of Lake Superior. Unpublished lake sturgeon data collected from U.S. waters of the St. Marys River (Lake Huron watershed) by T. Sutton (Purdue University, West Lafayette, Indiana) was also used to augment information from these two sources. Based on population abundance and age distribution data from these studies, the number of lake sturgeon in each age class (N) during a particular year was estimated as:

$$N_{(x+1,\, t+1)} = (N_{x,\, t})(S_x),$$

where x was the age, t was the year, and S_x was the age-specific survival rate for that population (Ricker 1975). Age-specific annual survival was calculated as:

$$S_x = 1 - [m_x + n_x - (m_x)(n_x)],$$

where m_x was the conditional fishing mortality rate and n_x was the conditional natural mortality rate. The ratio of males to females was fixed at 1.85:1, which was the mean gender ratio estimated from data collected from 1991 through 1995 (range, 1.25:1 to 2.7:1; Auer 1999b). Female age-at-reproductive maturity and the maximum age of lake sturgeon were set at 25 and 100, respectively, for all model simulations (Harkness and Dymond 1961; Scott and Crossman 1973; Becker 1983). The relationship between wet weight and total length (kg and cm, respectively) was calculated using data from Harkness and Dymond (1961), Auer (1999b), and Sutton (unpublished data; Figure 1). Based on this relationship, we generated a least-squares regression equation between absolute female lake sturgeon fecundity and total length (cm) using the fecundity and weight data in Harkness and Dymond (1961; Figure 2). Following the procedures described in Van Den Avyle and Hayward (1999), we fitted a von Bertalanffy growth curve to the lake sturgeon mean length-at-age data from Harkness and Dymond (1961; Figure 3).

Several studies have examined spawning populations of lake sturgeon in tributaries of the Great Lakes, Lake Winnebago, and the St. Lawrence River (Priegel and Wirth 1977; Folz and Meyers 1985; LaHaye et al. 1992; Fortin et al. 1993; Lyons and Kempinger 1993; Auer 1996b, 1999b). However, little information exists on the number of female spawners, percent females that successfully spawn, or early life stage mortality rates. Auer (1999b) annually observed between 13 and 52 female lake sturgeon on the spawning grounds in the Sturgeon River between 1991 and 1995. However, the author was unable to determine the percentage of these fish that successfully spawned in a given year. Because the spawning periodicity of female lake sturgeon ranges from 4 to 6 years (mean = 5 years; Priegel and Wirth 1977; Auer 1999b), we estimated that between 15 and 25% (mean = 20%) of the reproductively mature female fish in a population spawn each year (Table 1). Although these estimates are higher than those reported by Pine et al. (2001) for Gulf of Mexico sturgeon *A. oxyrhinchus desotoi* in the

Suwannee River, Florida (range, 3 to 10%), they are consistent with observations of other spawning populations of lake sturgeon in Green Bay tributaries of Lake Michigan (R. Elliott, U.S. Fish and Wildlife Service, personal communication). These data were used to estimate the reproductive potential of each lake sturgeon age class (P_x) at or above the age of female maturity as:

$$P_{x,\,t} = (N_{x,\,t})(F_x)(pf)(ps_x),$$

where F_x was the age-specific fecundity of females, pf was the proportion of the population that was female, and ps_x was the age-specific proportion of female lake sturgeon that spawn in any year. The net reproductive potential (P) of all age classes of lake sturgeon in any given year was determined as:

$$P = \Sigma\,(P_x),$$

where P_x was as described previously.

Lake sturgeon egg production was simulated using the following density-dependent relationship between female reproductive potential and egg survival (Beverton and Holt 1993):

$$R = \frac{p}{[1 - A\,(1 - p/P_r)]}\,,$$

where R and p were the realized (i.e., actual) and potential (i.e., based on the fecundity-total length relationship) egg deposition per female, respectively, A was the parameter that determined the shape of the stock-recruitment relationship, and P_r represented the reproductive potential of the population at equilibrium conditions. Parameter estimates for A and P_r were obtained from Pine et al. (2001) as determined for Gulf of Mexico sturgeon (Table 1) because these data is not available for lake sturgeon populations. According to Ricker (1975), this model is the most appropriate stock-recruitment relationship for long-lived fishes, such as lake sturgeon, that have low population abundance and exhibit little intraspecific competition for resources.

Mortality sources. – We used information from various sources to assess the impacts of mortality agents on lake sturgeon population viability (Tables 1, 2, and 4). Specific mortality factors that were examined during model simulations, and their targeted life stage(s) (in parentheses), were as follows: (1) natural mortality (eggs, larvae, and all ages of juveniles); (2) lampricide application (small [< 100 mm] age-0 juveniles); and (3) sea lamprey parasitism (subadults and adults). Because the effects of commercial, tribal, and recreational harvest on Great Lakes lake sturgeon populations have not been quantified and appear to be limited, we did not include fishing mortality in our model simulations (Slade and Auer 1997; Auer 2003).

Natural mortality resulting from predators, parasites, and pathogens remain largely unknown for lake sturgeon populations (Holey et al. 2000; Auer 2002). Because early life-stage survival for most fish populations is very low (Cushing 1995), we used the same egg and larval life-stage mortality rate (mean = 99.93%; range = 99.86 to 100%) reported by Pine et al. (2001) for Gulf of Mexico sturgeon (Table 1). We also used the same annual mortality rate and range of variability (mean = 25%; range = 16 to 34%) for all ages of juvenile lake sturgeon that was attributed to natural sources by Pine et al. for Gulf of Mexico sturgeon (2001). Because of their large body size, subadult and adult lake sturgeon appear to not have predators other than sea lamprey, silver lamprey *Ichthyomyzon unicuspis*, and chestnut lamprey *I. castaneus*. As a result, we assumed that natural mortality for subadult and adult life stages, excluding that induced by sea lamprey parasitism, was negligible (0%).

In addition to mortality from natural sources, survival of lake sturgeon in the model simulations was also based on life stage, body length, and lampricide-treatment strategy (Table

2). At the standard protocol, small (< 100 mm) juveniles suffered lampricide-induced mortality once every four years, which corresponded to a four-year treatment periodicity for larval sea lamprey control in Great Lakes tributaries. Although Bills et al. (2000) and Boogaard et al. (2003) reported that small juveniles experienced greater than 50% mortality following lampricide exposures in toxicology experiments, we allowed annual mortality of small juvenile lake sturgeon to range from 0 to 100% at 10%-mortality increments to simulate the potential variability that might be expected following stream applications. During years between lampricide treatments, mortality of small age-0 juveniles only resulted from natural sources. Larger (> 100 mm) juveniles, subadults, and adults did not experience lampricide-induced mortality at the standard-treatment protocol. For the no effect treatment protocol, mortality of lake sturgeon following lampricide applications was fixed at 0%, regardless of life stage or body length (Johnson et al. 1999; Bills et al. 2000; Boogaard et al. 2002).

Although the effects of sea lamprey parasitism on lake sturgeon survival are unknown, it is likely that control efforts have minimized the extent of this mortality source (Auer 2002). However, the no effect treatment protocol may allow for increased escapement of parasitic-phase sea lampreys, thereby increasing the potential for parasitism-induced mortality on lake sturgeon. To simulate mortality resulting from sea lamprey predation, we incorporated information on percent sea lamprey transformer escapement (i.e., survival) following lampricide treatments, sea lamprey wounding rate on lake sturgeon, and the probability that a host lake sturgeon survives a sea lamprey attack.

During the year prior to transformation, there is no difference in percent survival of sea lamprey larvae between the standard and no effect treatment protocols (1 to 10% and 0 to 16%, respectively; W. Swink, U.S. Geological Survey, unpublished data). Further, transformer sea lampreys do not exhibit greater survival than untransformed larvae following 12-hr lampricide exposures to TFM and TFM/1% niclosamide (M. Boogaard, U.S. Geological Survey, personal communication). However, there is a greater probability that an unsuccessful treatment will result from the no effect protocol than the standard protocol (23% and 6%, respectively; J. Adams, U.S. Geological Survey, unpublished data). Because the life span of a lake sturgeon can reach 100 years, a stream supporting populations of lake sturgeon and sea lampreys would be treated approximately 25 times during that period, assuming a four-year lampricide application cycle. Based on the probabilities for a failed lampricide treatment, we would expect 5.75 and 1.5 unsuccessful treatment events at the no effect and standard treatment protocols, respectively, during this 100-year period. As a result, our estimated rates of subadult and adult lake sturgeon mortality from sea lamprey parasitism due to a failed treatment necessitate an adjustment of both the wounding rate and survival probability data.

Sea lamprey wounding rate on subadult and adult lake sturgeon in the St. Marys River was estimated at 22% from 2000 through 2002 (T. Sutton, Purdue University, unpublished data). Because lampricide treatments were initiated in the St. Marys River during 1997 (Schleen et al. 2003), we have assumed that this wounding rate estimate represents those that would occur following a standard lampricide treatment. Therefore, we would expect to observe a higher sea lamprey wounding rate for lake sturgeon following use of the no effect protocol due to the greater probability of an unsuccessful treatment. To adjust the wounding rate to account for greater sea lamprey transformer escapement following a no effect treatment, the relative difference in mortality between a successful and unsuccessful lampricide application was computed as $((Y_S - Y_U)/Y_S) \cdot 100$, where Y_S was the percent mortality of larval sea lampreys following a successful treatment (i.e., 85 to 100% mortality) and Y_U was the percent mortality of larval sea lampreys during an unsuccessful treatment (i.e., 60 to 80% mortality). For example, to adjust for a 60% larval sea lamprey mortality rate resulting from an unsuccessful treatment relative to an 85% mortality rate resulting from a successful treatment, we would estimate a 5.88% correction factor. Multiplying this value by the 22% lake sturgeon wounding rate resulting from sea lamprey parasitism would increase the wounding rate 1.29% to 23.29% (Table 3). Using these differences in larval sea lamprey mortality between the two lampricide-treatment protocols, we adjusted the wounding rate for lake sturgeon using a 4 x 5 correction-factor matrix (Table 3).

Swink (1990, 2002) and Greig et al. (1992) determined the following relationship between lake trout total length and the probability of surviving a sea lamprey attack (in parentheses): (1) < 432 mm (1.00); (2) 432 to 533 mm (0.35); (3) 534 to 635 mm (0.45); and (4) > 635 mm (0.55). Because the life-history strategy of lake trout is similar to lake sturgeon (i.e., delayed sexual maturation, long life span, and large body size), it is reasonable to apply these data to lake sturgeon in the absence of that information for the latter species. However, lake sturgeon grow much larger than lake trout and may reach a size at which they are no longer vulnerable to direct or indirect mortality resulting from sea lamprey parasitism. Due to the uncertainty associated with lake sturgeon vulnerability to sea lamprey parasitism, particularly for large (> 635 mm) individuals, we conducted three different series of simulations to model the probability that a lake sturgeon would survive a sea lamprey attack (Table 4). For simulation 1 (i.e., low sturgeon mortality), the adjusted wounding rate data estimated using the correction-factor matrix was multiplied by the probability that a subadult or adult lake sturgeon would survive a sea lamprey attack following the survival schedule provided above for fish ranging from 432 to 635 mm. For this simulation, fish larger than 635 mm were not considered vulnerable to sea lamprey parasitism and therefore were assigned a probability of surviving a sea lamprey attack of 1.00. For simulation 2 (i.e., high sturgeon mortality), a similar survival schedule was followed as the previous simulation with the exception that lake sturgeon greater than 635 mm in length had an identical survival probability following a sea lamprey attack as large lake trout (0.55). We also conducted a third simulation (i.e., variable sturgeon mortality) where subadult and adult lake sturgeon mortality was allowed to range from 0 to 22% at 2.2%-mortality increments (where each 2.2%-mortality increment represented a 10% increase in the sea lamprey wounding rate) to simulate a broader range in potential variability as a result of sea lamprey parasitism. The data for this simulation were based on the original wounding rate observations for lake sturgeon in U.S. waters of the St. Marys River.

Model-simulation procedures. – The influence of lampricide applications and sea lamprey parasitism on lake sturgeon population viability was examined by comparing the percent relative change of the model-output parameters from baseline conditions. For all model simulations, baseline conditions represented a scenario where mortality of lake sturgeon was strictly from natural sources, i.e., not as a result of lampricide treatments or parasitism-induced mortality by sea lampreys. Percent relative change for lake sturgeon population abundance, the number of age-1 recruits, and reproductive potential was computed as $[(Y_i - Y_b/Y_b] \cdot 100$, where Y_i was the predicted model output value for the *i*th input value that was changed and Y_b was the predicted model output value under baseline conditions. Model outputs for each simulation scenario were determined from the average of ten replicates, with each simulation run being conducted over a 100-year period at one-year increments.

Biological-probability analyses. - The probability of significantly affecting lake sturgeon population viability was determined given biologically realistic changes in derived mortality variables. For these simulations, we examined how incremental changes in lampricide use, transformer escapement rates, lake sturgeon wounding rates, and the probability of lake sturgeon surviving a sea lamprey attack affect population abundance, number of age-1 recruits, and reproductive potential of lake sturgeon. This information was used to evaluate which mortality factors were most influential on lake sturgeon population viability, and to aid the identification of deficiencies in lake sturgeon life-history information necessary for the improvement of the population model.

RESULTS AND DISCUSSION

Population abundance, the number of age-1 recruits, and reproductive potential of lake sturgeon exhibited relative percentage decreases from baseline conditions with increasing mortality of age-0 juveniles as a result of lampricide applications at four-year treatment intervals (Figure 4). Relative percent changes from baseline conditions declined similarly for population abundance and the number of age-1 recruits, ranging from -0.14 and -0.52%, respectively, to -3.07 and -2.98%, respectively, as age-0 juvenile lake sturgeon mortality was increased from 10 to 100% every four years. However, relative percent changes in reproductive potential from baseline conditions were generally greater as age-0 juvenile mortality was increased from 0 to 100%, ranging from -0.12 to -9.90%. The greatest relative percent changes in the three output parameters occurred as age-0 juvenile mortality was increased from 50 to 60% for population abundance (-48%), 40 to 50% for the number of age-1 recruits (-42%), and 90 to 100% for reproductive potential (-55%).

When the percentage of larval sea lamprey mortality following lampricide treatments was incrementally decreased, lake sturgeon mortality from increased sea lamprey parasitism for both the low and high mortality simulation scenarios (simulations 1 and 2) resulted in relative percentage decreases in population abundance, the number of age-1 recruits, and reproductive potential from baseline conditions (Figure 5). For the low lake sturgeon mortality simulation, population abundance and the number of age-1 recruits exhibited similar declines in relative percent changes from baseline conditions, ranging from -2.46 and -1.64%, respectively, to -6.10 and -4.37%, respectively, as the percentage of larval sea lamprey mortality following lampricide treatments was decreased from 100 to 60%. Similarly, population abundance and the number of age-1 recruits also exhibited similar declines in relative percent changes from baseline conditions for the high lake sturgeon mortality simulation, ranging from -19.47 and -17.94%, respectively, to -20.43 and -22.33%, respectively, as the percentage of larval sea lamprey mortality following lampricide treatments was decreased from 100 to 60%. Relative percent changes in reproductive potential from baseline conditions were generally greater for both the low and high lake sturgeon mortality simulation as the percentage of larval sea lamprey mortality following lampricide treatments was decreased from 100 to 60%, ranging from -5.51 to -9.85% and -24.70 and -28.87%, respectively. Overall, mean relative percent change was always greater for the high than the low lake sturgeon mortality simulation for population abundance (-3.57 and -17.95%, respectively), number of age-1 recruits (-2.71 and -18.44%, respectively), and reproductive potential (-7.65 and -21.16%, respectively).

Incremental increases in sea lamprey-induced lake sturgeon mortality as estimated from wounding rate data (simulation 3) resulted in relative percentage decreases in population abundance, the number of age-1 recruits, and reproductive potential from baseline conditions (Figure 6). Population abundance and the number of age-1 recruits exhibited similar declines in relative percent changes from baseline conditions, ranging from -4.48 and -3.91%, respectively, to -39.60 and -48.70%, respectively, as the mortality of those subadult and adult lake sturgeon wounded by sea lampreys was increased from 10 to 100%. Relative percent changes in reproductive potential from baseline conditions were generally greater as the mortality of subadult and adult lake sturgeon wounded by sea lampreys was increased from 0 to 100%, ranging from -7.76 to -58.92%. The greatest relative percent changes in the three output parameters occurred as the mortality of subadult and adult lake sturgeon wounded by sea lampreys was increased from 30 to 40% for population abundance (-46%), 50 to 60% for the number of age-1 recruits (-68%), and 70 to 80% for reproductive potential (-67%).

Based on the results of our model simulations, we determined that mortality agents, such as sea lamprey parasitism, that influence subadult and adult lake sturgeon had a greater impact on abundance, the number of age-1 recruits, and reproductive potential than those mortality factors that affected early life stages of this species (i.e., lampricide applications). Because small (i.e., 10%) increases in the rate of mortality of subadult and adult life stages were more detrimental to long-term viability of lake sturgeon populations than increases in early life stage mortality, the survival of older life stages is more important for population persistence of this species in the Great Lakes than recruitment of age-0 fish. As a consequence, any factor that increases subadult and adult mortality will cause more severe declines in population abundance than changes in recruitment rates. Further, the percentage of spawning females in the population (i.e., reproductive potential) and subsequent subadult and adult female survival were always most strongly influenced by mortality factors examined in model simulations. Given the low number of female lake sturgeon that spawn in Great Lakes tributaries on an annual basis (Auer 1999a), the loss of any immature and/or mature females from a population would negatively affect recruitment and subsequently limit rehabilitation. Therefore, the development of management plans for the restoration of lake sturgeon populations in the Great Lakes basin should protect subadult and adult fish in order to ensure successful long-term recovery of this unique species.

According to Winemiller and Rose (1992), lake sturgeon are classified as periodic strategists, exhibiting life-history attributes such as long life span, large adult body size, delayed age at reproductive maturity, long intervals between repeat spawning events, and high fecundity. Although these adaptations improve spawning success and survival of early life stages during years with optimal environmental conditions, these same traits jeopardize long-term viability of fishes such as lake sturgeon when mortality factors reduce the population abundance of subadult and adult life stages (Beamesderfer and Farr 1997). As a result, sea lamprey parasitism, which has a direct affect on the survival of subadult and adult lake sturgeon, has the potential to limit the success of rehabilitation efforts for this species. Because of this, our data support the conclusion of Beamesderfer and Farr (1997) that rehabilitation and management strategies for sturgeon species must minimize mortality factors which target older life stages.

Because information on the effects of sea lamprey parasitism on mortality of subadult and adult lake sturgeon was not available, the model that we used to conduct simulations could only be used to predict relative percent changes, not absolute changes, in population abundance, the number of age-1 recruits, and reproductive potential. Further, information on lake sturgeon population biology and dynamics was collected from several different sources or, in some cases, data on the population dynamics of other sturgeon species was incorporated into the model simulations. Although we do not believe that these shortcomings in our input parameters have resulted in inaccurate predictions in model-output trends, the inclusion of more detailed and species-specific information will only enhance the robustness of future modeling efforts. When specific information becomes available regarding the biological attributes of lake sturgeon populations or the effects of mortality factors on population persistence, these data can be incorporated into the model and used to more accurately predict changes in the model outputs examined in this study.

Mortality of subadult and adult lake sturgeon resulting from sea lamprey parasitism had a greater impact on population abundance, the number of age-1 recruits, and reproductive potential than mortality on age-0 juvenile lake sturgeon following lampricide applications. Therefore, those mortality agents which influence older life stages will more strongly regulate long-term population viability of lake sturgeon in the Great Lakes basin than those sources that affect early life stages. Based on these results, we do not recommend that lampricide application strategies for the control of larval sea lamprey populations in tributaries containing lake sturgeon continue to follow the no effect protocol. Because the probability of a failed lampricide application is nearly four times greater for the no effect than the standard treatment strategy (J. Adams, U.S. Geological Survey, unpublished data), long-term rehabilitation and management objectives for lake sturgeon or other fishes, such as lake trout, in the Great Lakes basin could be compromised as a result of increased numbers of parasitic-phase sea lampreys.

FUTURE RESEARCH

Although the effects of sea lamprey predation on lake trout, rainbow trout *Oncorhynchus mykiss*, and burbot *Lota lota* have been well documented (Swink and Hanson 1986, and 1989; Swink 1990, 1991, 1993; Swink and Fredricks 2000; Swink 2003), there have been no similar studies to date which have examined the influence of sea lamprey parasitism on lake sturgeon (Slade and Auer 1997; Auer 2003). Because the results of our model simulations indicated that sea lamprey parasitism on subadult and adult lake sturgeon has the potential to significantly affect long-term population viability in the Great Lakes, field and laboratory studies should be conducted to examine this relationship. Specifically, field studies involving lake sturgeon should document the incidence of sea lamprey scars and classify these wounds based on established criteria (King 1980). This information will not only all for the determination of the incidence of sea lamprey attacks on lake sturgeon, but it will also allow for the examination of size-related trends in wound frequency on lake sturgeon. To determine the relationship between wounding rate and mortality of lake sturgeon, laboratory experiments should be conducted to examine host-size selection by parasitic-phase sea lampreys on lake sturgeon, the effects of body size and water temperature on survival of lake sturgeon, and the influence of wound frequency (i.e., single versus multiple wounds) on a single fish on growth and survival of lake sturgeon. Therefore, accurate estimates of lake sturgeon mortality from sea lamprey parasitism will require better knowledge of these relationships in order to ensure that sea lamprey control strategies are meeting long-term goals for rehabilitation of lake sturgeon populations in the Great Lakes.

Additional information on lake sturgeon population biology in the Great Lakes also should be collected in order to ensure that management and recovery efforts for this species are meeting their desired goals. Further, by gaining a better understanding of the biology and ecology of lake sturgeon stocks, modeling efforts involving this species should more accurately portray population dynamics and trends in abundance. For example, little information exists on the population abundance of lake sturgeon using spawning tributaries, the number of female spawners that use these tributaries on an annual basis, and the percentage of females that successfully spawn each year (Slade and Auer 1997; Holey et al. 2000). As a result, increased assessment efforts will be required to document the current level of abundance of self-sustaining populations of lake sturgeon, as well as determine the number of female spawners and reproductive success on an annual basis. Although quantifying the nature and extent of natural mortality factors influencing fish populations is difficult, small changes in mortality during the egg, larval, and juvenile life stages will strongly affect recruitment to subadult and adult life stages (Houde 1987). Therefore, field and laboratory studies should be conducted to examine mortality factors and rates of mortality on early life stages (Auer 2003). Further, how abiotic and biotic factors influence recruitment of larval and juvenile lake sturgeon to existing populations should be identified and understood within the context of subsequent year-class strength determination (Holey et al. 2000; Auer 2003). Because factors influencing older life stages of lake sturgeon have significant implications for long-term population viability, estimates of subadult and adult mortality rates from natural and fishing sources should be identified and quantified in order to ensure successful long-term rehabilitation. Although harvest of lake sturgeon in recreational, commercial, and tribal fisheries in the Great Lakes basin occurs on a limited basis and is highly regulated (Baker 1980; Bruch 1999; Auer 2003), our model simulations demonstrated that those factors that increase mortality rates of older life stages have significant effects on population abundance. However, it is not known if indirect harvest sources, such as by-catch of lake sturgeon in gill or trap nets that target other Great Lakes fishes such as lake trout, lake whitefish *Coregonus clupeaformis*, and lake herring *C. artedi*, has any effect on fishing mortality rates of this species. Therefore, dedicated studies should be developed to address the influence of these mortality sources on lake sturgeon population viability in the Great Lakes.

LITERATURE CITED

Auer, N. A. 1996a. Importance of habitat and migration to sturgeons with emphasis on lake sturgeon. Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):152-160.

Auer, N. A. 1996b. Response of spawning lake sturgeon to change in hydroelectric facility operation. Transactions of the American Fisheries Society 125:66-77.

Auer, N. A. 1999a. Lake sturgeon: a unique and imperiled species in the Great Lakes. Pages 515-536 *in* W.W. Taylor and C.P. Ferreri, editors. Great Lakes fisheries policy and management: a binational perspective. Michigan State University Press, East Lansing.

Auer, N. A. 1999b. Population characteristics and movements of lake sturgeon in the Sturgeon River and Lake Superior. Journal of Great Lakes Research 25:282-293.

Auer, N. A, editor. 2003. A lake sturgeon rehabilitation plan for Lake Superior. Great Lakes Fishery Commission Miscellaneous Publication 2003-02, Ann Arbor, Michigan.

Baker, J. P. 1980. The distribution, ecology, and management of lake sturgeon (*Acipenser fulvescens* Rafinesque) on Michigan. Michigan Department of Natural Resources, Fisheries Research Report 1883, Lansing.

Beamesderfer, R. C. 1991. MOCPOP 2.0: a flexible system for simulation of age-structured populations and stock-related functions. Oregon Department of Fish and Wildlife, Information Report 91-4, Portland.

Beamesderfer, R. C. P., and R. F. Farr. 1997. Alternatives for the protection and restoration of sturgeons and their habitat. Environmental Biology of Fishes 48:407-417.

Becker, G. C. 1983. Fishes of Wisconsin. The University of Wisconsin Press, Madison.

Beverton, R. J. H., and S. J. Holt. 1993. On the dynamics of exploited fish populations. Chapman and Hall, Fish and Fisheries Series, United Kingdom.

Bills, T. D., M. A. Boogaard, and M. L. Hanson. 2000. Toxicity of TFM and a combination of TFM/1% Niclosamide to early life stages of lake sturgeon (*Acipenser fulvescens*). Great Lakes Fishery Commission, Completion Report, Ann Arbor, Michigan.

Boogaard, M. A., T. D. Bills and D. A. Johnson. 2003. Acute toxicity of TFM and a TFM/1% niclosamide mixture to selected species of fish and mudpuppies in laboratory and field exposures. Journal of Great Lakes Research (In press).

Booker, W. V., F. A. Chapman, S. P. Filipek, L. K. Graham, A. A. Rakes, J. L. Rasmussen, K. J. Semmens, R. A. St. Pierre, and T. J. Smith. 1993. Framework for the management and conservation of paddlefish and sturgeon species in the United States. National Paddlefish and Sturgeon Steering Committee, U.S. Fish and Wildlife Service, Washington, D.C.

Bruch, R. M. 1999. Management of lake sturgeon on the Winnebago system: long-term impacts of harvest and regulations on population structure. Journal of Applied Ichthyology 15:142-152.

Cushing, D. 1995. Population production and regulation in the sea: a fisheries perspective. Cambridge University Press, United Kingdom.

Folz, D. J., and L. S. Meyers. 1985. Management of the lake sturgeon, *Acipenser fulvescens*, population in the Lake Winnebago system, Wisconsin. Pages 135-146 *in* F. P. Binkowski and S. I. Doroshov, editors. North American sturgeons. Dr. W. Junk Publishers, The Netherlands.

Fortin, R., J. R. Mongeau, G. Desjardins, and P. Dumont. 1993. Movements and biological statistics of lake sturgeon (*Acipenser fulvescens*) populations from the St. Lawrence and Ottawa River systems. Canadian Journal of Zoology 71:638-650.

Greig, L., D. Meisner, and G, Christie. 1992. Manuel for the management protocol for the implementation of integrated management of sea lamprey in the Great Lakes basin. Version 1.1. Great Lakes Fishery Commission Report, Ann Arbor, Michigan.

Harkness, W. J. K., and J. R. Dymond. 1961. The lake sturgeon: the history of its fishery and problems of conservation. Ontario Department of Lands and Forests, Ottawa.

Hay-Chmielewski, E. M., and G. E. Whelan. 1997. State of Michigan lake sturgeon rehabilitation strategy. Michigan Department of Natural Resources, Fisheries Special Report Number 18, Lansing.

Holey, M. E., E. A. Baker, T. F. Thuemler, and R. F. Elliott. 2000. Research and assessment needs to restore lake sturgeon in the Great Lakes. Great Lakes Fishery Trust Workshop Results, Muskegon, Michigan.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. American Fisheries Society Symposium 2:17:29.

Johnson, D. A., J. W. Weisser, and T. D. Bills. 1999. Sensitivity of lake sturgeon (*Acipenser fulvescens*) to the lampricide TFM in field and laboratory exposures. Great Lakes Fishery Commission Technical Report Number 62, Ann Arbor, Michigan.

Johnson, J. E. 1987. Protected fishes of the United States and Canada. American Fisheries Society, Bethesda, Maryland.

King, E L., Jr. 1980. Classification of sea lamprey (*Petromyzon marinus*) attacks on Great Lakes lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 37:1989-2006.

Klar, G. T., and L. P. Schleen. 1999. Standard operating procedures for application of lampricides in the Great Lakes Fishery Commission integrated management of sea lamprey (*Petromyzon marinus*) control program. Special Report 92-001.3. U.S. Fish and Wildlife Service Sea Lamprey Control, Marquette, Michigan.

LaHaye, M., A. Branchaud, M. Gendron, R. Verdon, and R. Fortin. 1992. Reproduction, early life history, and characteristics of the spawning grounds of the lake sturgeon (*Acipenser fulvescens*) in the Des Prairies and L'Assomption Rivers, near Montreal, Quebec. Canadian Journal of Zoology 70:1681-1689.

Lyons, J., and J. J. Kempinger. 1992. Movements of adult lake sturgeon in the Lake Winnebago system. Wisconsin Department of Natural Resources Research Report 156, Madison.

Pine, W. E., III, M. S. Allen, and V. J. Dreitz. 2001. Population viability of the Gulf of Mexico sturgeon: inferences from capture-recapture and age-structured models. Transactions of the American Fisheries Society 130:1164-1174.

Priegel, G. R., and T. L. Wirth. 1977. The lake sturgeon: its life history, ecology, and management. Wisconsin Department of Natural Resources Publication 4-3600(77), Madison.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin 191 of the Fisheries Research Board of Canada.

Rochard, E., G. Castelnaud, and M. Lepage. 1990. Sturgeons (Pisces: Acipenseridae); threats and prospects. Journal of Fish Biology 37(Suppl. A):123-132

Schleen, L. P., G. C. Christie, J. W. Heinrich, R. A. Bergstedt, R. J. Young, T. J. Morse, D. S. Lavis, T. D. Bills, J. E. Johnson, and M. P. Ebener. 2003. Development and implementation of an integrated program for control of sea lampreys in the At. Marys River. Journal of Great Lakes Research (In press).

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Ottawa.

Slade, J. W., and N. A. Auer. 1997. Status of lake sturgeon in Lake Superior. Great Lakes Fishery Commission, Lake Superior Technical Committee, Ann Arbor, Michigan.

Smith, S. H. 1968. Species succession and fishery exploitation in the Great Lakes. Journal of the Fisheries Research Board of Canada 25:667-693.

Swink, W. D. 1990. Effect of lake trout size on survival after a single sea lamprey attack. Transactions of the American Fisheries Society 119:996-1002.

Swink, W. D. 1991. Host-size selection by parasitic sea lampreys. Transactions of the American Fisheries Society 120:637-643.

Swink, W. D. 1993. Effect of water temperature on sea lamprey growth and lake trout survival. Transactions of the American Fisheries Society 122:1161-1166.

Swink, W. D. 2003. Host selection and lethality of attacks by sea lampreys (*Petromyzon marinus*) in laboratory studies. Journal of Great Lakes Research (In press).

Swink, W. D., and K. T. Fredricks. 2000. Mortality of burbot from sea lamprey attack, an dinitial analyses of burbot blood. Pages 147-154 *in* V. L. Paragamian and D. W. Willis, editors. Burbot: biology, ecology, and management. American Fisheries Society, Bethesda, Maryland.

Swink, W. D., and L. H. Hanson. 1986. Survival from sea lamprey (*Petromyzon marinus*) predation by two strains of lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 43:2528-2531.

Swink, W. D., and L. H. Hanson. 1989. Survival of rainbow trout and lake trout after sea lamprey attack. North American Journal of Fisheries Management 9:35-40.

Thuemler, T. F., E. A. Baker, and R. F. Elliott. 1999. Draft lake sturgeon plan for the Green Bay basin. Green Bay Basin Sturgeon Work Group, Peshtigo, Wisconsin.

Van Den Avyle, M. J., R. S. Hayward. 1999. Dynamics of exploited fish populations. Pages 127-166 *in* C. C. Kohler and W. A. Hubert, editors. Inland fisheries management in North America, second edition. American Fisheries Society, Bethesda, Maryland.

Wells, L., and A. L. McLain. 1973. Lake Michigan: man's effects on native fish stocks and other biota. Great Lakes Fishery Commission Technical Report No. 20, Ann Arbor, Michigan.

Winemiller, K. O., and K. A. Rose. 1992. Patterns of life history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49:2196-2218.

Table 1. Life history and population parameters used to assess lake sturgeon population viability. Notations in the variable column (i.e., LKS = lake sturgeon; GMS = Gulf of Mexico sturgeon) indicate the species that served as the data source.

Variable	Value(s)	Data source
Female age at sexual maturity (LKS)	Age 25	Harkness and Dymond (1961); Becker (1983)
Maximum age of females (LKS)	Age 100	Scott and Crossman (1973)
Percent of population that is female (LKS)	35%	Auer (1999b)
Percent mature females that spawn each year (LKS)	20%	Priegel and Wirth (1977); Auer (1999b)
Beverton-Holt density-dependent relationship between reproductive potential and realized egg deposition (GMS)	A = 0.2; P_r = 2,370,334	Pine et al. (2001)
Wet weight (WT) - total length (TL) relationship (LKS)	$WT = 1.77 \times 10^{-6} \cdot TL^{3.28}$	Harkness and Dymond (1961); Auer (1999b); Sutton (unpublished data)
Fecundity (FC) - total length (TL) relationship (LKS)	$FC = 3.76 \times 10^{-3} \cdot TL^{3.59}$	Harkness and Dymond (1961)
von Bertalanffy growth equation (LKS)	$L_t = 228.638 \cdot [1-e^{-0.023(t+4.713)}]$	Harkness and Dymond (1961)
Natural mortality		
Egg and larval life stages (GMS)	99.93% (range, 99.86 to 100%)	Pine et al. (2001)
Juvenile life stage (GMS)	25% (range, 16 to 34%)	Pine et al. (2001)
Subadult and adult life stages (LKS)	0%	This study

Table 2. Mortality rates used for simulations involving juvenile, subadult, and adult lake sturgeon life stages as a result of lampricide applications for the control of sea lamprey populations according to the standard and no effect treatment protocols.

Mortality rate and life stage	Values	Data source
Lampricide-induced mortality		
Standard treatment protocol		
Small (< 100 mm) juveniles	0 to 100% at 10%-mortality increments every four years and 0% during non-treatment years	Bills et al. (2000); Boogaard et al. (2003)
Large (> 100 mm) juveniles	0%	
Subadults and adults	0%	Johnson et al. (1999); Bills et al. (2000); Boogaard et al. (2002)
No effect treatment protocol		
All life stages	0%	Johnson et al. (1999); Bills et al. (2000); Boogaard et al. (2002)

Table 3. Adjusted lake sturgeon wound rate (%) data to account for greater sea lamprey transformer escapement for an unsuccessful lampricide treatment relative to a successful lampricide treatment. Criteria for determination of successful versus unsuccessful larval sea lamprey treatment events are based on those from J. Adams (U.S. Geological Survey, unpublished data).

Successful lampricide treatment	Unsuccessful lampricide treatment				
	80%	75%	70%	65%	60%
85%	22.31	22.62	22.93	23.24	23.55
90%	22.59	22.88	23.17	23.47	23.76
95%	22.83	23.11	23.39	23.69	23.94
100%	23.06	23.32	23.58	23.85	24.11

Table 4. Mortality rates for subadult and adult lake sturgeon as a result of sea lamprey parasitism for three different series of model simulations. For simulations 1 and 2, the adjusted wounding rate data estimated using the correction-factor matrix was multiplied by the probability that a subadult or adult lake sturgeon would survive a sea lamprey attack following the survival schedule derived for lake trout.

Mortality rate	Values	Data source
Low sturgeon mortality (simulation 1)	Lake sturgeon total length: (1) < 432 mm (1.00); (2) 432 to 533 mm (0.35); (3) 534 to 635 mm (0.45); and (4) > 635 mm (1.00)	Swink (1990, 2002); Greig et al. (1992); This study
High sturgeon mortality (simulation 2)	Lake sturgeon total length: (1) < 432 mm (1.00); (2) 432 to 533 mm (0.35); (3) 534 to 635 mm (0.45); and (4) > 635 mm (0.55)	Swink (1990, 2002); Greig et al. (1992); This study
Variable sturgeon mortality (simulation 3)	0 to 22% at 2.2%-mortality increments (where each 2.2%-mortality increment represented a 10% increase in the sea lamprey wounding rate)	T. Sutton (unpublished data); this study

FIGURE CAPTIONS

Figure 1. Observed wet weight and total length data for Great Lakes lake sturgeon. The line represents the weight-length model fitted to these data and reported in Table 1. Data are from Harkness and Dymond (1961), Auer (1999b), and Sutton (unpublished).

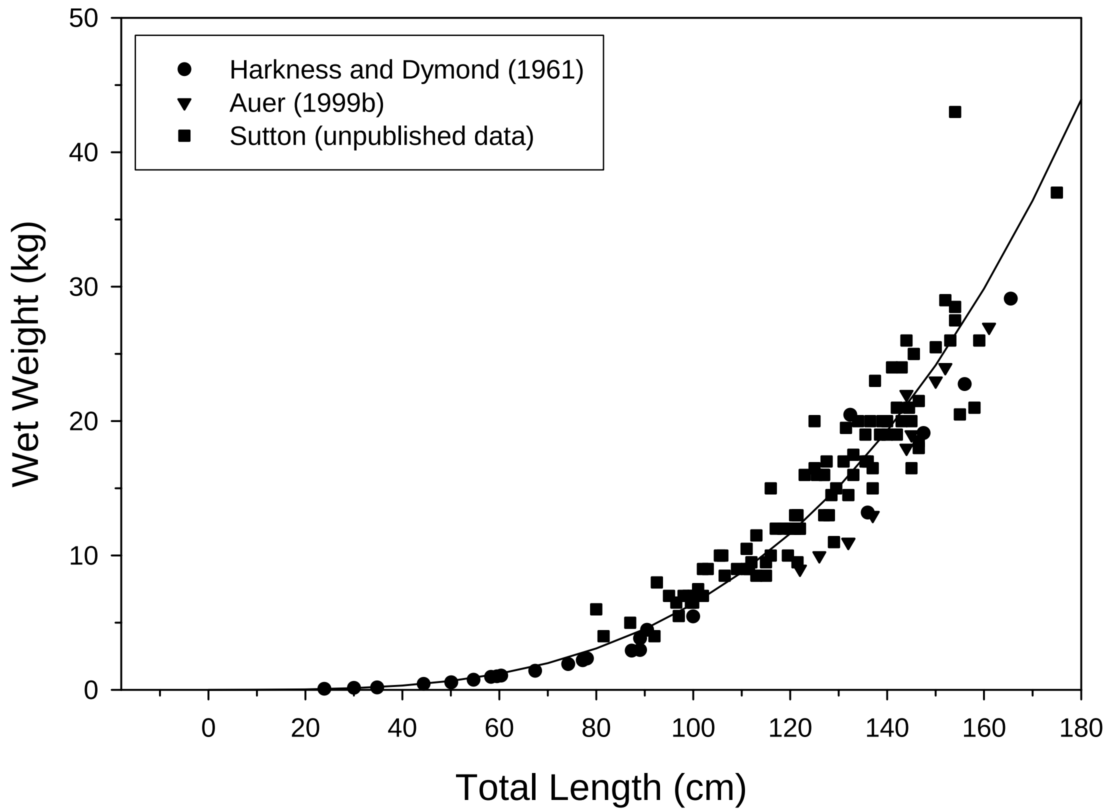
Figure 2. Fecundity and total length data for lake sturgeon in Lake Nipigon. The line represents the fecundity-length model fitted to these data and reported in Table 1. Data are from Harkness and Dymond (1961).

Figure 3. Mean length-at-age data for lake sturgeon in Lake Nipigon. The line represents the von Bertalanffy growth model fitted to these data and reported in Table 1. Data are from Harkness and Dymond (1961).

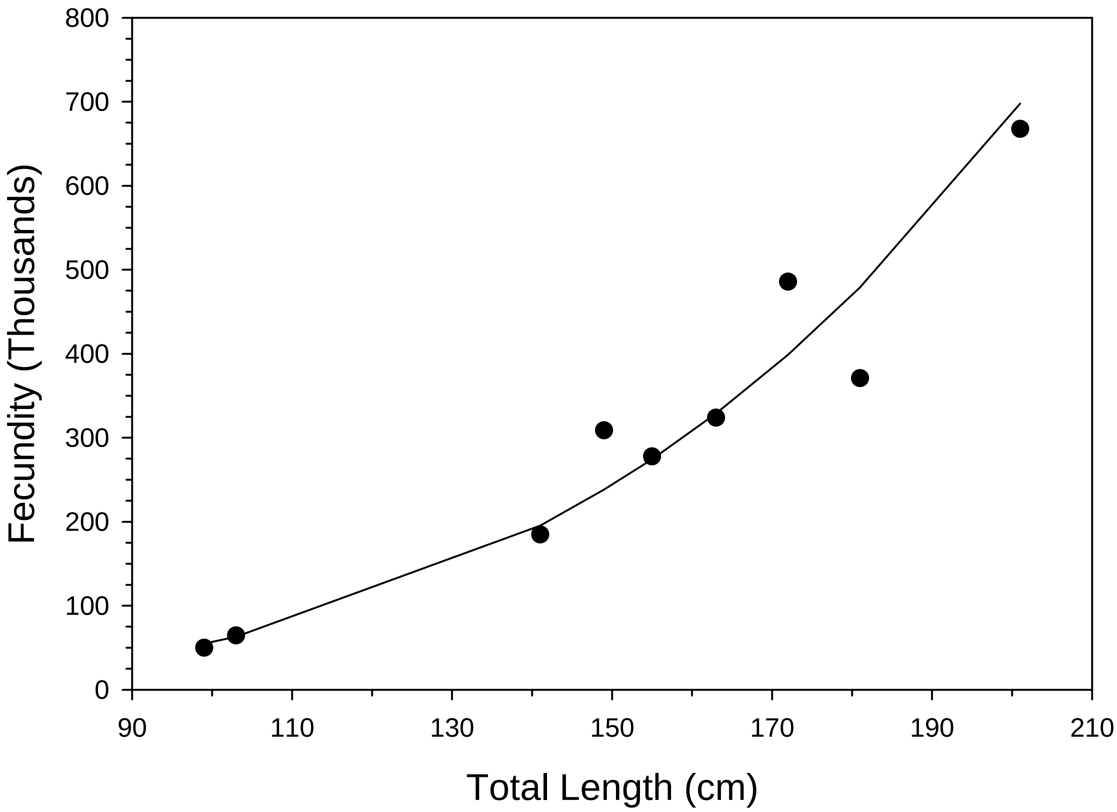
Figure 4. Percent relative change in lake sturgeon (a) population abundance, (b) number of age-1 recruits, and (c) reproductive potential from baseline conditions (as defined in the Methods) resulting from lampricide applications at four-year treatment intervals.

Figure 5. Percent relative change in lake sturgeon (a) population abundance, (b) number of age-1 recruits, and (c) reproductive potential from baseline conditions (as defined in the Methods) due to sea lamprey parasitism. Levels of lake sturgeon mortality (i.e., low and high) were based on the product of the adjusted wounding rate and the probability that a subadult or adult fish would survive a sea lamprey attack following the survival schedule based on fish total length.

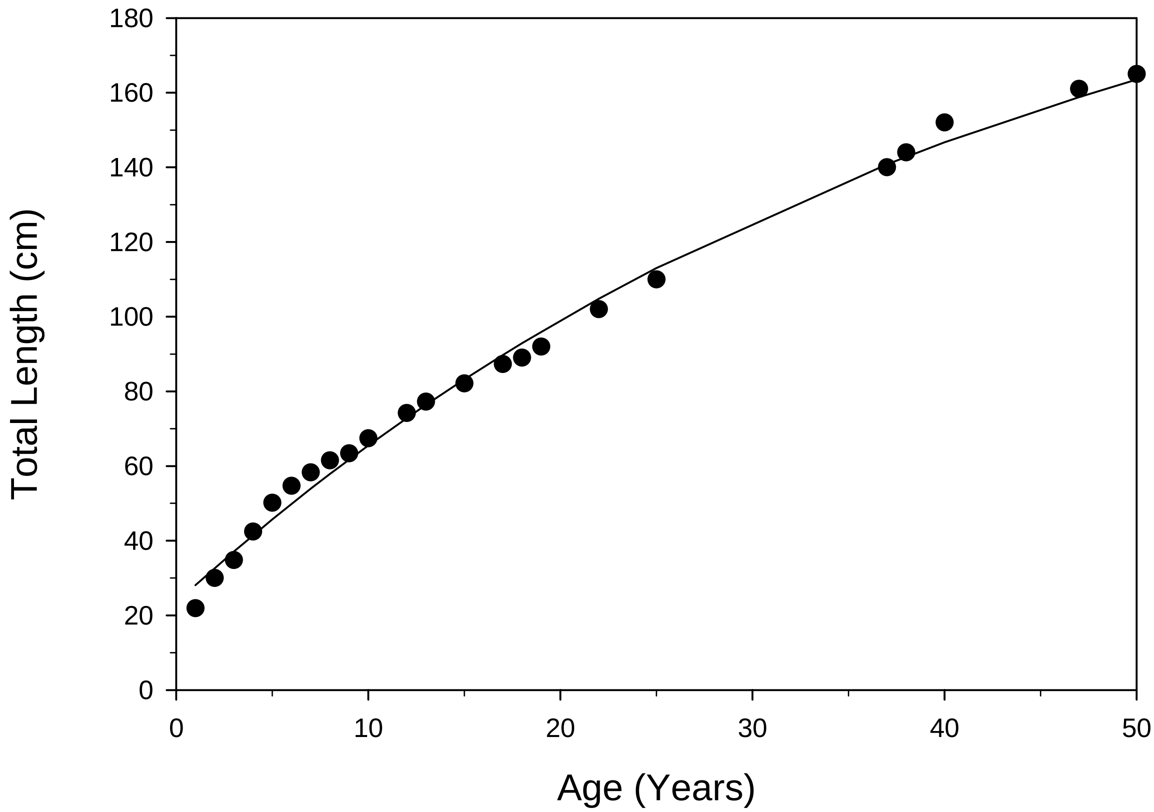
Figure 6. Percent relative change in lake sturgeon (a) population abundance, (b) number of age-1 recruits, and (c) reproductive potential from baseline conditions (as defined in the Methods) due to sea lamprey parasitism. Levels of lake sturgeon mortality were based on incremental changes in sea lamprey wounding rate data.



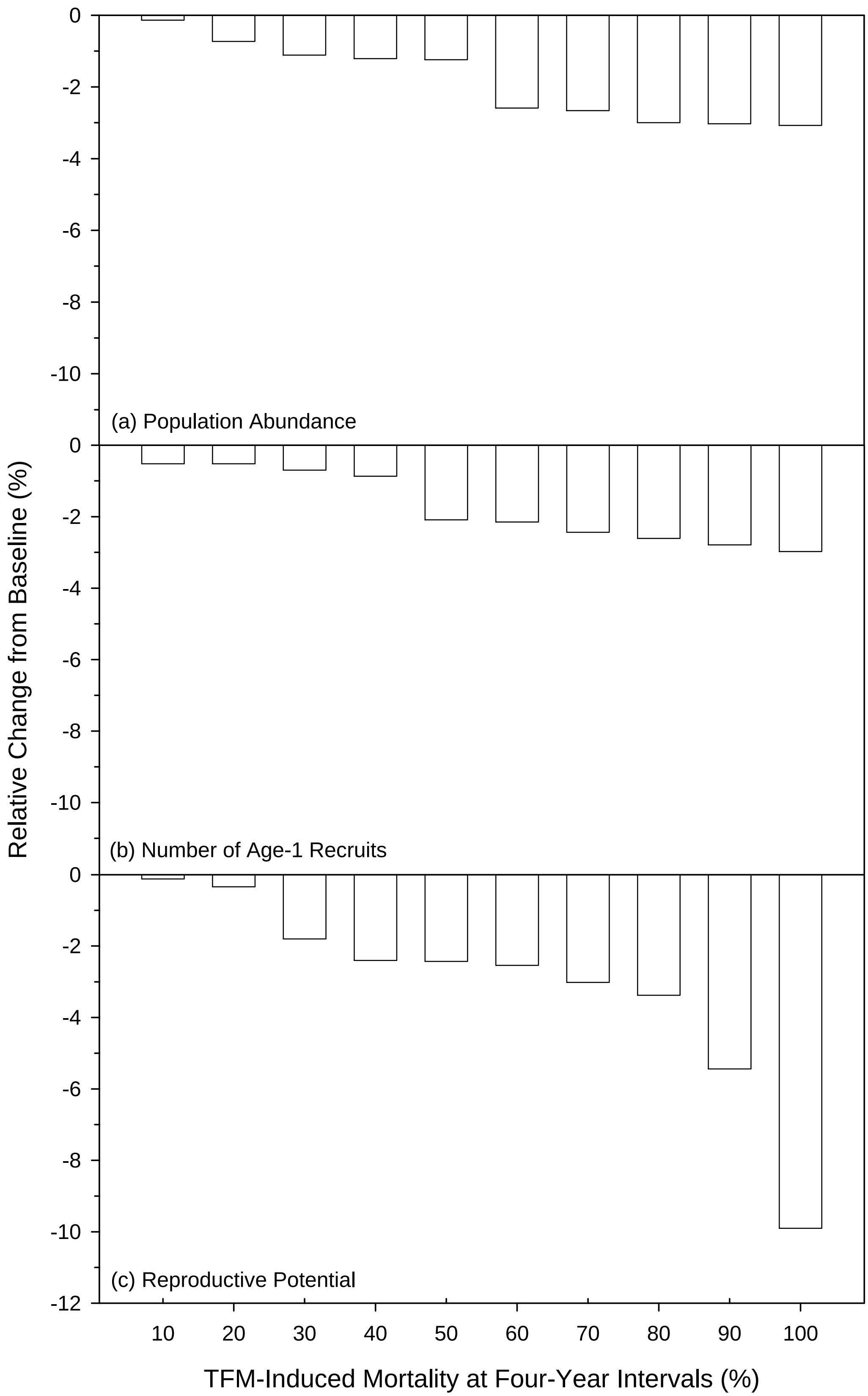
50
40
30
20
10
0
Wet Weight (kg)
0
20
40
60
80
100
120
140
160
180
Total Length (cm)
Harkness and Dymond (1961)
Auer (1999b)
Sutton (unpublished data)

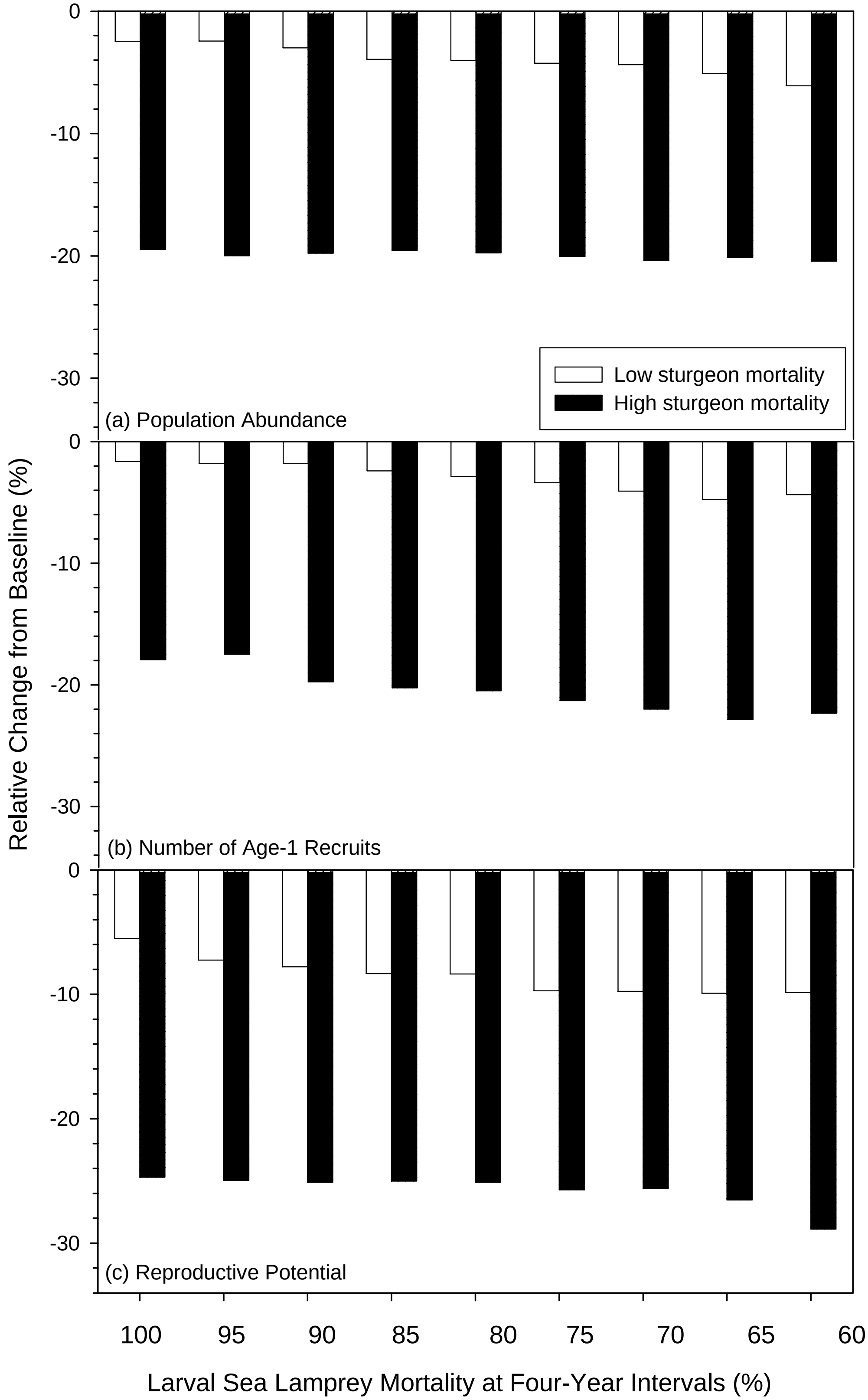


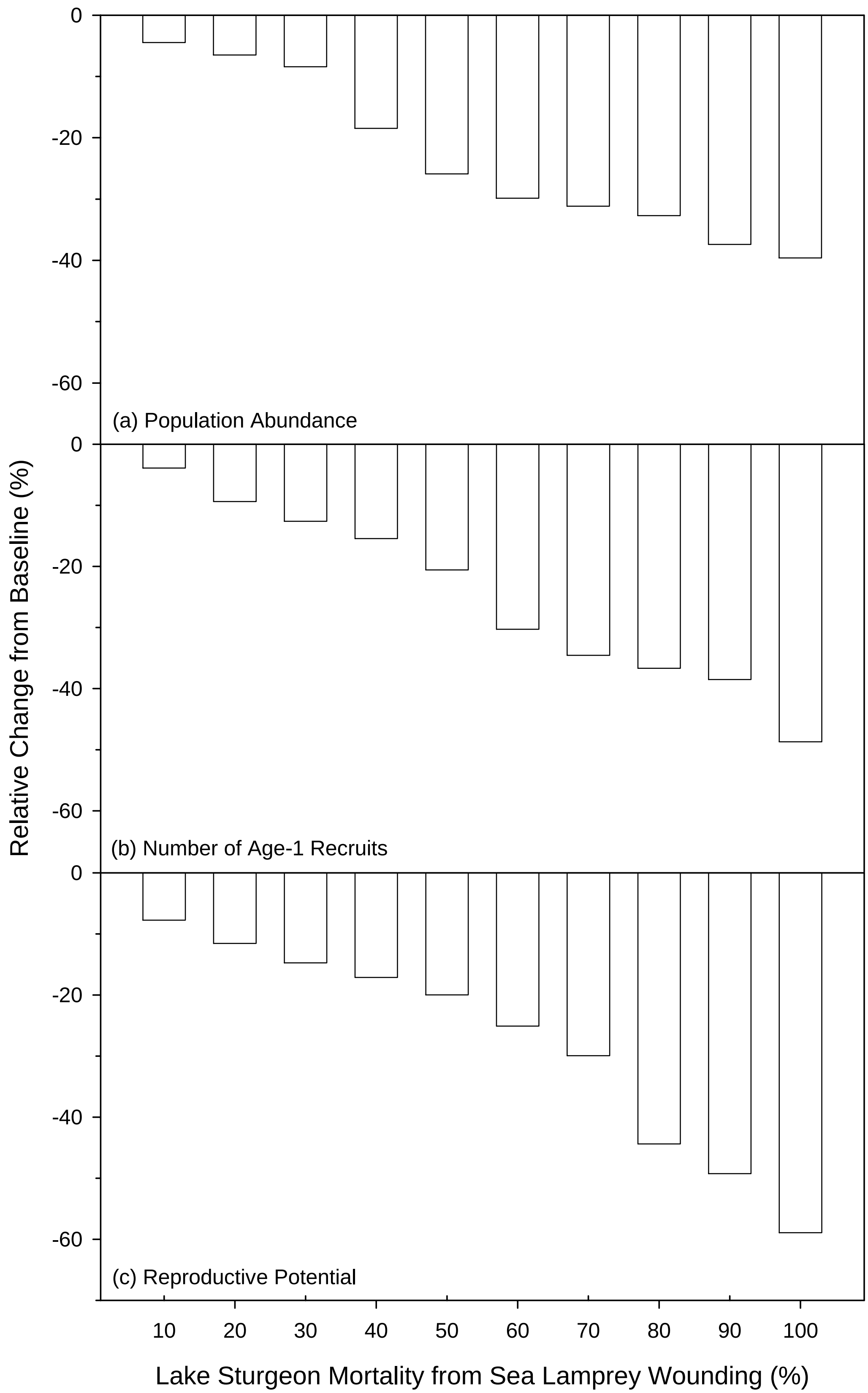
Fecundity (Thousands)
0
100
200
300
400
500
600
700
800
90
110
130
150
170
190
210
Total Length (cm)



180
160
140
120
100
80
60
40
20
0
0
10
20
30
40
50
Total Length (cm)
Age (Years)


(a) Population Abundance
(b) Number of Age-1 Recruits
(c) Reproductive Potential
Relative Change from Baseline (%)
TFM-Induced Mortality at Four-Year Intervals (%)
0
-2
-4
-6
-8
-10
-12
10
20
30
40
50
60
70
80
90
100


0
-10
-20
-30
(a) Population Abundance
Low sturgeon mortality
High sturgeon mortality
(b) Number of Age-1 Recruits
(c) Reproductive Potential
Relative Change from Baseline (%)
100
95
90
85
80
75
70
65
60
Larval Sea Lamprey Mortality at Four-Year Intervals (%)


0
-20
-40
-60
(a) Population Abundance
0
-20
-40
-60
(b) Number of Age-1 Recruits
0
-20
-40
-60
(c) Reproductive Potential
10
20
30
40
50
60
70
80
90
100
Relative Change from Baseline (%)
Lake Sturgeon Mortality from Sea Lamprey Wounding (%)