

Population Dynamics and Angler Exploitation of the Unique Muskellunge Population in Shoepack Lake, Voyageurs National Park, Minnesota

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Abstract.—A unique population of muskellunge *Esox masquinongy* inhabits Shoepack Lake in Voyageurs National Park, Minnesota. Little is known about its status, dynamics, and angler exploitation, and there is concern for the long-term viability of this population. We used intensive sampling and mark–recapture methods to quantify abundance, survival, growth, condition, age at maturity and fecundity and angler surveys to quantify angler pressure, catch rates, and exploitation. During our study, heavy rain washed out a dam constructed by beavers *Castor canadensis* which regulates the water level at the lake outlet, resulting in a nearly 50% reduction in surface area. We estimated a population size of 1,120 adult fish at the beginning of the study. No immediate reduction in population size was detected in response to the loss of lake area, although there was a gradual, but significant, decline in population size over the 2-year study. Adults grew less than 50 mm per year, and relative weight (W_p) averaged roughly 80. Anglers were successful in catching, on average, two fish during a full day of angling, but harvest was negligible. Shoepack Lake muskellunge exhibit much slower growth rates and lower condition, but much higher densities and angler catch per unit effort (CPUE), than other muskellunge populations. The unique nature, limited distribution, and location of this population in a national park require special consideration for management. The results of this study provide the basis for assessing the long-term viability of the Shoepack Lake muskellunge population through simulations of long-term population dynamics and genetically effective population size.

Muskellunge *Esox masquinongy* is a well-studied species in North America owing to its large size and popularity as a sport fish. Muskellunge often attain lengths well over 1 m, weights greater than 18 kg, and are long-lived, frequently reaching 15 years of age with some individuals reaching 30 years (Casselman and Crossman 1986; Casselman et al. 1999). Age of sexual maturity is dependent on growth rates, with males reaching maturity between 3 and 6 years and females reaching maturity between 4 and 8 years (Cook and Solomon 1987). Muskellunge are broadcast spawners and commonly spawn in water less than 1 m deep when temperatures reach 9.4–15.0°C in the spring (Scott and Crossman 1973). The spring spawning

period sometimes occurs in two or more pulses (LeBeau 1991). Newly hatched muskellunge feed on zooplankton for the first 1–3 weeks, and then switch to a piscivorous diet (Cook and Solomon 1987). Muskellunge are nonselective feeders, preying on available fish species, with yellow perch *Perca flavescens* and white sucker *Catostomus commersonii* being the most common prey species (Engstrom-Heg et al. 1986; Cook and Solomon 1987; Bozek et al. 1999). Muskellunge densities are low relative to those of most species. For example, Hanson (1986) reported fewer than 1.5 fish/ha in eight Wisconsin Lakes.

Muskellunge are popular sport fish because of their large size, ferocious strike, and elusiveness (Crossman 1986). Angling for muskellunge is increasing in popularity and is supported by numerous clubs and tournaments in both the United States and Canada (Simonson 2003; Younk and Pereira 2003). Muskellunge anglers typically practice catch-and-release fishing and many are well informed about muskellunge

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biology and management (Sandell 1994; Simonson and Hewett 1999; Margenau and Petchenik 2004).

Voyageurs National Park (VNP) in northern Minnesota contains a population of muskellunge that is restricted to the small, geographically isolated Shoepack Lake. The Shoepack Lake muskellunge population (SLMP) is of special concern for VNP for several reasons. First, this population 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 a unique recreational opportunity for park visitors. Sport fishing is an important component of recreational activity in national parks (Panek 1994) and the principal visitor activity in VNP (Kallemeyn et al. 2003), and thus management of fishery resources such as the SLMP is a high priority. Third, the legislation establishing VNP specifically states that the Minnesota Department of Natural Resources (MNDNR) has the right to use the Shoepack muskellunge strain as broodstock for future hatchery operations. Although this is unlikely, availability of sound biological and angler use data will help ensure wise management of the SLMP by all stakeholder agencies in the future.

Little is known about the population status of the SLMP. Without knowledge of the population size and dynamics, managers cannot assess current and future threats. Effective management of the SLMP will require information on the population size, population dynamics, growth, survival, natural mortality, and angler exploitation. The purpose of this study was to assess the population status, dynamics, and angler exploitation of the SLMP. We used intensive sampling and mark-recapture methods to quantify abundance, survival, growth, condition, age at maturity and fecundity. We used angler surveys to quantify angler pressure, catch rates, and exploitation.

Study Site

Shoepack Lake (48°30'N, 92°53'W) is on the forested, roadless Kabetogama Peninsula in Voyageurs National Park, Minnesota. Access to Shoepack Lake is possible only by floatplane or a rugged 5-km hiking trail. The lake has several small inlet streams from nearby lowland areas and one from Little Shoepack Lake, which is fed by surrounding wetland areas. A single outlet stream flows from Shoepack Lake into Rainy Lake. Barriers to upstream fish movement from Rainy Lake include several beaver dams and a 50-m-long rock slab known as the "bear slide," over which

the Shoepack Lake outlet stream flows as a thin film. This rock slab is apparently a highly effective barrier, since northern pike *Esox lucius*, which are abundant in Rainy Lake and most of the other VNP lakes, do not occur upstream from it in the Shoepack Lake drainage. Of the 26 interior lakes in VNP, Shoepack Lake and Little Shoepack Lake are the only lakes containing muskellunge.

The water level in Shoepack Lake is significantly affected by the activity of beavers *Castor canadensis*. At the beginning of this study, a large beaver dam with a 2.16-m head above the bedrock sill was located at the outlet. Remnant beaver dams were also evident near the outlet. Before July 23, 2001, Shoepack Lake had a surface area of 234 ha, including flooded shoreline areas and wetlands adjoining the lake that were used by fish. On July 23, 2001, the large beaver dam at the outlet of Shoepack Lake was breached owing to high water from a 12.5-cm rain event, causing the water level to drop 1.8 m and engendering the loss of roughly 2.16×10^6 kL of water. After the beaver dam failure, Shoepack Lake stabilized at a new surface area of 125 ha, or 53% of its previous area. This reduced surface area is the basin as determined by the bedrock sill at the outlet. In addition to surface area reduction, many of the previously flooded lake margins that provide complex littoral zone habitat were above water due to the lower water level and no longer accessible by fish.

Before the beaver dam failure, Shoepack Lake's maximum depth was 7.3 m and the mean depth was 2.9 m. The water, which is heavily stained (Hazen color value = 80 platinum-cobalt units), is soft, with a total alkalinity of 4.1 mg/L (Payne 1991). Chlorophyll *a* concentrations were 2.2–4.7 µg/L (Payne 1991), reflecting low primary production and low densities of zooplankton (Lillie and Mason 1983). Shoepack Lake supports little aquatic vegetation (Anderson 2000).

The fish species found in Shoepack Lake in addition to muskellunge are yellow perch, white sucker, blacknose shiner *Notropis heterolepis*, golden shiner *Notemigonus crysoleucas*, finescale dace *Phoxinus neogaeus*, northern red belly dace *Phoxinus eos*, johnny darter *Etheostoma nigrum*, mottled sculpin *Cottus bairdii*, and Iowa darter *Etheostoma exile* (Anderson 2000).

Methods

Access.—The remote location of Shoepack Lake placed limitations on the study. All equipment and personnel were transported to and from the lake by floatplane, with the exceptions of a small boat and fyke nets, which were towed in by a snowmobile in the late winter before the beginning of the study. Floatplane access during the study prevented us from using

electrofishing gear, large boats, large motors, and other heavy gear. Equipment and methods described below reflect this limitation.

Fish sampling.—We collected fish using fyke nets (Hubert 1996). Nets were constructed of 2.5-cm-bar nylon mesh wrapped around two square aluminum frames (1.0 m × 1.0 m) and three hoops of 0.75-m diameter or 1.3-cm-bar nylon mesh wrapped around two rectangular steel frames (1.0 m × 1.5 m) and three hoops of 0.50-m diameter.

A crew of three workers sampled muskellunge nondestructively during the spawning period using the 2.5-cm-bar mesh fyke nets. Fyke nets were fished in the early spring from ice-out (late April to early May) until after the peak of spawning (approximately 2 weeks) in the springs of 2001, 2002, and 2003. The nets were set in locations that appeared to have good spawning habitat or would intercept fish moving to spawning areas. Up to eight locations could be sampled simultaneously with the available gear.

Additional sampling periods occurred in 1-week time intervals during June, July, August, and September of 2001 and June, July, and August of 2002. A map of the lake was divided into 100-m × 100-m squares and sampling sites were determined by choosing squares randomly. During the summer periods, four to six single fyke nets and two tandem fyke nets were set each day. Fyke nets were deployed with lead and cab fully extended. Fyke nets were set perpendicular to the shore with the lead attached to the shore and the end of the cab was anchored with a buoy attached. Tandem fyke nets were also deployed with leads and cabs fully extended and with anchors and buoys attached to both ends. Fyke net leads were joined using plastic zip ties. Tandem fyke nets were set parallel to the shoreline. All fyke nets were set for approximately 24 h. Experimental gill nets (20-, 25-, 32-, 38- and 51-mm-bar mesh panels) were used in June and July of 2001 but were discontinued due to high mortality rates of captured fish. Seining techniques were also employed, targeting younger fish in the population in June and September 2002 sampling periods.

Fish handling.—All captured fish were handled with extreme care using mesh cradles and tubs of fresh lake water (Kelsch and Shields 1996). Upon capture, fish were measured to the nearest millimeter total length (TL) and weighed to the nearest 0.1 kg. Newly captured individuals were tagged, the left side pelvic fin clipped, sexed, and scale samples taken. Sex was determined from external characteristics or extrusion of gametes (LeBeau and Pageau 1989). Fish were dually marked with a month-specific fin clip and an individually numbered Floy tag. Scales were removed

nonlethally with the point of a knife from the area above the lateral line and in front of the dorsal fin. Captured fish were processed within 5 min and released back into the lake alive. Abnormalities, obvious injuries due to capture, poor fish condition, and other observations were also recorded.

Bone structures and other tissue samples requiring destructive sampling were obtained from a small number (<20) of female fish sacrificed during the spawning seasons of 2001 and 2002 and from fish that died as a result of injuries during capture. Females were sacrificed during spawning for gonad examination to verify sex and estimate fecundity (Crim and Glebe 1990). Otoliths and cleithra were extracted from all of these fish.

Angler pressure and harvest surveys.—Voyageurs National Park maintains a rowboat on Shoepack Lake for visitors and monitors usage by checkout records at visitor centers. Angler pressure was assessed by angler surveys (Malvestuto 1996). Angler surveys were made mandatory by VNP and distributed at park visitor centers, by a commercial pilot who flew anglers into Shoepack Lake, and from a drop box located at Shoepack Lake. Survey questions included number of anglers fishing, number of hours fished, number of fish caught, number of fish harvested, how they got to the lake, where they fished, whether the fish were marked or unmarked, tag number, and comments offered by anglers.

Catch per unit effort (CPUE), the number of harvestable fish caught, and the number of fish harvested were calculated from returned surveys. The CPUE was calculated as

$$CPUE = \sum x / \sum yz, \quad (1)$$

where CPUE is number of fish caught per angler per hour, x is the number of reported fish caught in a survey, y is the number of reported anglers in a survey, and z is the number of reported angling hours in a survey. The CPUE was calculated by month and year. All fish longer than the 762-mm TL length limit were considered harvestable. The harvest rate was determined as the number of fish reported kept in a given year.

Tag loss and mortality experiments.—We were able to detect tag loss because we marked fish with both Floy tags and fin clips. Tag loss proportion was assessed by dividing the number of tags lost by the total number of tagged fish from 2001 and 2002. Fish were monitored in an observation pen to assess handling mortality. The observation pen was 1.5 m square by 3 m deep. Fish collected during the first 2 d of a sampling period were put into the pen and

observed for 5 d. Handling mortality proportion was calculated as the number of fish found dead divided by the total number of fish placed in the pen. This was done in May 2001, June 2001, and May 2002.

Mark-recapture analysis.—Abundance and survival were estimated using mark-recapture techniques (Van den Avyle 1993) and the population analysis software MARK (Cooch and White 2001). Developed by wildlife statisticians, MARK is part of a suite of sophisticated mark-recapture techniques that have recently become prevalent in fisheries research (Pine et al. 2003). The Jolly-Seber model was used in MARK to analyze mark-recapture data. The model contains four parameters: survival, capture probability, population rate of change, and population size. We condensed the summer sampling periods in 2001 (June–September) and 2002 (June–August) into two annual “summer” capture periods. The May 2001, May 2002, and May 2003 sampling periods were considered “spawning” capture periods. This yielded a total of five mark-recapture periods (May 2001, summer 2001, May 2002, summer 2002, and May 2003) for the MARK analysis. Time differences between capture periods were taken into account within MARK. Capture histories were entered into MARK as live recaptures (Cooch and White 2001). For example, a fish caught in May 2001 and July 2002 would have a 10010 capture history. Capture histories include both netting data and data collected from anglers. This was justified because summer sampling times occurred during the angling season and the recapture probabilities of a tagged fish subsequently captured again were not significantly different ($\chi^2 = 1.554$, $df = 1$, $P = 0.2126$) between angling and netting.

Parameter index matrices were constructed in MARK to form a suite of models. These a priori candidate models included survival, recapture, Lambda (finite rate of population increase), and initial population size parameters. In addition to investigating constant parameters, we varied survival and recapture probabilities by time and season. Lambda was assumed to be constant in these models because the study was not long enough to detect significant differences in population size between time periods. This assumption was based on several factors. First, muskellunge are long-lived and do not exhibit rapid changes in population size. Second, the SLMP is a native population experiencing minimal human impact, so we assumed that the population is at or near the carrying capacity of the lake. Third, muskellunge populations have low recruitment rates. Recruitment will vary from year to year depending on environmental conditions but likely does not vary dramatically. Annual fluctuations in year-class strength would not be

likely to cause significant population size changes within the study period. In contrast, the 47% reduction in lake surface area due to the beaver dam failure was considered capable of eliciting a strong effect on population size. Thus, another set of models incorporating varying Lambda were run to evaluate the potential effect of the reduction in surface area.

Global model goodness of fit was tested using the program RELEASE within MARK and examining the variance inflation factor, \hat{c} . Goodness of fit is a procedure that examines the assumptions underlying the model we were trying to fit to the data; \hat{c} quantifies the amount of binomial variation in the data. Models were compared in terms of QAIC_c, a modification of Akaike's information criterion (AIC; Burnham and Anderson 1998). This method uses quasi-likelihood adjustments to correct for overdispersion in the data and improve the overall fit of the model (Cooch and White 2001). Akaike's information criterion is designed to select the best-fitting model without overfitting the data through the use of numerous parameters. Models were ranked according to their Δ QAIC_c values, that is, the difference between their own QAIC_c values and the lowest QAIC_c value; models with a Δ QAIC_c value less than 2.0 were considered to fit the data well. Weighted parameter estimates were calculated using model averaging to account for uncertainty in model selection (Burnham and Anderson 1998). In addition, we specifically compared models that incorporated Lambda varying by time and a surface area reduction effect (before and after beaver dam failure) to test whether the beaver dam failure and reduction of lake surface area resulted in a loss of fish sufficient to have a significant effect on the population vital rates during the study period.

Age, growth, and condition.—Scales and fin rays were collected from every captured fish for use as aging structures. However, age could not be determined from these structures because annuli were unrecognizable. Otoliths and cleithra were collected from sacrificed fish. Annuli in cleithra could be accurately read to age 8. Beyond age 8, cleithra annuli were spaced closely and were indistinguishable. Otoliths proved to be the best structure for estimating terminal age but lacked a definitive focus. Otoliths were first mounted in epoxy, then a thin section from the middle of the otolith was obtained using an Isomet low speed saw. Sections were mounted on slides, buffed using very fine grit sandpaper, and examined under a compound microscope.

Growth was examined in two ways in this study. The first was by directly calculating known changes in length of fish captured in two or more sampling periods. Calculations for growth were restricted to

recaptures that spanned approximately a year so that both summer (positive) growth and winter (zero or negative) growth were accounted for in the calculation. To standardize rates, growth was first calculated as millimeters per day and then multiplied by 365 to represent annual growth. Since ages could not be determined for live fish, these growth rates were reported by size at first capture.

Additional growth rates were determined by back-calculation of lengths at previous ages and then calculating annual growth increments (DeVries and Frie 1996). Otoliths and cleithra could not be used individually for reasons outlined above, so we used them in combination. We were unable to back-calculate lengths using otoliths because they lacked a definitive focus, so we used terminal ages from otoliths. We then used the matching cleithra to back-calculate growth up to age 8, the point where additional annuli became undistinguishable. For example, we aged an individual at 16 years old from the otolith and were able to determine length-at-age for years 1 to 8 from the cleithrum.

The average length-at-age estimates derived from this combination of methods were then used in the Fisheries Analysis and Simulation Tools (FAST) software package (Slipke and Maceina 2000) to calculate a von Bertalanffy growth function (VBGF) for each sex. The VBGF is

$$L_t = L_\infty \left[1 - e^{-K(t+t_0)} \right], \quad (2)$$

where L_t is length at age t , L_∞ is maximum length, K is the growth coefficient, t is age in years, and t_0 is the time in years when length = 0. We compared female and male growth rates at age using t -tests.

Condition was determined as relative weight (W_r) for each fish at time of capture using length and weight data with the standard weight equations for muskellunge (Neumann and Willis 1994). The standard weight equation used for females was

$$\log_{10} W_S = -6.105 + 3.34 \log_{10} L, \quad (3)$$

and that for males was

$$\log_{10} W_S = -5.823 + 3.245 \log_{10} L, \quad (4)$$

where W_S is standard weight (g) and L is length (mm). Condition was then calculated as

$$W_r = 100(W/W_S), \quad (5)$$

where W_r is relative weight and W is weight (g). The values of W_r were averaged for each month. We used a least-squares means comparison with a Tukey-Kramer adjustment to test for condition differences by month.

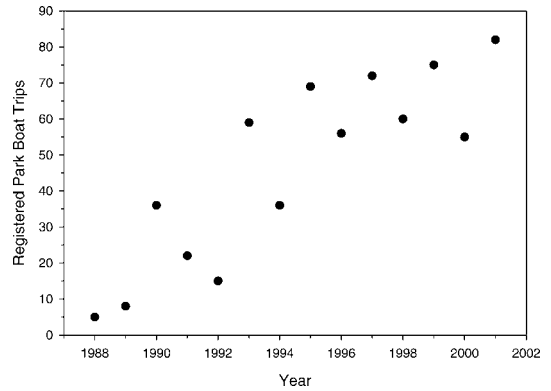


FIGURE 1.—Annual public use of the boat provided by Voyageurs National Park from 1988 to 2001 on Shoepack Lake, Minnesota. Boat use was compiled from visitor center checkout records.

Age of maturity and fecundity.—Age of maturity was determined from fish captured during the spring sampling periods, when fish were spawning. Lengths of spawning fish were used in a rearrangement of the appropriate VBGF, solving for age. Age of maturity was estimated as the earliest age of spawning fish predicted by length using the rearranged VBGFs.

Fecundity was determined using both volumetric and gravimetric calculations and then averaging the results. In the volumetric method, the total volume of eggs from a female was measured. Next, the volume of 100 randomly selected eggs was measured. These measurements were used to calculate the total number of eggs as

$$X = 100 \cdot V/v, \quad (6)$$

where X is the estimated total number of eggs, V is the volume of all eggs, and v is the volume of the sample of 100 eggs. In the gravimetric method, the total weight of eggs from a female was measured. Next, the weight of 100 randomly selected eggs was measured. These weights were used to calculate the total number of eggs as

$$X = 100 \cdot W/w, \quad (7)$$

where W is the weight of all eggs and w is the weight of the sample of 100 eggs. Three replicate estimates were obtained for each method, and all six values were averaged to give the final estimate of fecundity.

Results

Angler Pressure and Harvest

Use of the public rowboat on Shoepack Lake has increased steadily over the last decade (Figure 1).

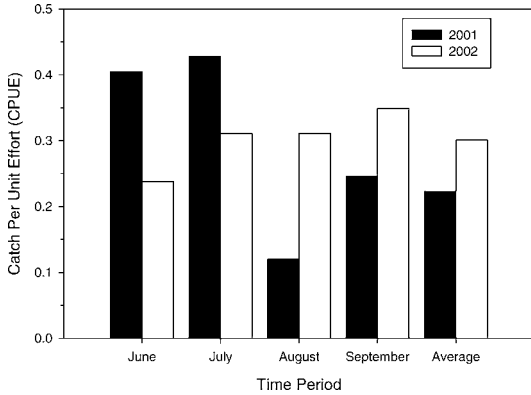


FIGURE 2.—Muskellunge catch per unit effort on Shoepack Lake, Minnesota, in 2001 and 2002 as calculated from returned angler surveys.

Annual usage was fewer than 10 trips per year in the late 1980s and has increased to more than 80 trips in 2001. Data in Figure 1 are records of boat use only, not angling. However, the increased boat use implies an increase in angler pressure over this period.

In 2001, 29 fishing parties returned usable surveys and reported fishing 736.3 h on Shoepack Lake and catching 164 muskellunge. Catch per unit effort averaged 0.22 fish per angler per hour in 2001, although there was a dramatic drop in CPUE from July to August, which coincided with the beaver dam failure (Figure 2). Of the fish caught, five (~3%) were above the 762-mm minimum harvest length limit. Anglers reported keeping no fish in 2001.

In 2002, 29 fishing parties returned usable surveys and reported fishing 481.8 h on Shoepack Lake and catching 145 muskellunge. Catch per unit effort averaged 0.30 fish per angler per hour and was relatively consistent from May through September (Figure 2). Of the fish caught, six (~4%) were above the 762-mm minimum length limit. Anglers reported keeping two fish, or less than 2% of all fish caught.

Tag Loss and Handling Mortality

Only 4 of the 320 fish that were recaptured had lost their tags, a loss rate of 1.25%. Of these, three were initially captured in 2001 and the fourth in 2002.

Seventy-three fish were held in the holding pen and 6 of these fish died. Three deaths were attributed to nonhandling effects, where fish were found either tangled in the corners or wedged into small holes in the holding net. The other three mortalities, which we assumed to result from handling stress, resulted in a mortality estimate of 4.1%. Recapture probabilities of tagged fish originally caught by anglers and caught in

nets were not significantly different ($\chi^2 = 1.554$, $df = 1$, $P = 0.2126$), so we assumed mortality rate for these two groups were similar. Therefore, we used the 4.1% estimate of handling mortality derived from our holding pen as an estimate of handling mortality for angler-caught fish.

Mark-Recapture Population and Survival Estimates

A total of 1,056 fish captures were recorded between May 2001 and May 2003. The number of captured fish ranged from 241 to 347 during the three spawning periods and from 8 to 57 in the seven nonspawning periods. During the study, 736 unique fish were caught, with 320 recaptures and 74 mortalities (sacrificed and sampling) (Table 1). The total number of tagged fish minus known mortalities left an estimated 672 tagged fish in Shoepack Lake in May 2003. The size of the muskellunge caught ranged from 469 to 820 mm TL, 78% of the fish being in the 560–680-mm range.

The fully time-dependent Jolly-Seber model failed to converge in MARK, so survival was constrained to seasons for the global model. Program RELEASE goodness-of-fit statistics ($\chi^2 = 15.0512$, $df = 8$, $P = 0.0582$) indicated adequate fit and some evidence of overdispersion ($\hat{c} = 2.18$). This overdispersion was corrected by using 2.18 as a \hat{c} adjustment. Four models had ΔQAIC_c values less than 2.0 and were used to calculate the parameter estimates (Table 2). Models with time-varying and surface-area-reduction Lambdas had ΔQAIC_c values that were greater than 5.0 and thus were excluded from consideration.

The estimated population size of fish greater than 450 mm at the beginning of the study was 1,120 (95% confidence interval, 842–1,399), with a summer survival rate of 0.987 (0.752–0.999) and a winter survival rate of 0.963 (0.845–0.992) (Table 2). The finite rate of population change for the Shoepack Lake muskellunge population, 0.974 (0.842–0.996), indicated a population in decline.

Age, Growth, and Condition

Based on the changes in length of tagged individuals, growth rates for both females and males declined with increasing size (Figures 3, 4). Female growth rates were less than 50 mm a year with little or no growth beyond 722 mm. Male growth rates were less than 50 mm a year with little or no growth beyond 663 mm. Growth rates of both sexes were much lower than those reported for lakes in Ontario (Casselman et al. 1999) and Wisconsin (Hanson 1986) (Figures 3 and 4).

The VBGF parameter estimates for females were $L_\infty = 749$, $K = 0.231$, and $t_0 = 0.628$, and those for males were $L_\infty = 683$, $K = 0.297$, and $t_0 = 0.305$ (Figures 5, 6). Female and male lengths for ages 1–6 years did not

TABLE 1.—Numbers of fish in various categories in muskellunge sampling from May 2001 to May 2003 in Shoepack Lake, Minnesota. Data are shown for both individual sampling periods and the condensed periods used in a MARK analysis.

Category	Condensed period for MARK analysis									
	1		2		3		4		5	
	Sampling period ^a									
	1	2	3	4	5	6	7	8	9	10
Total caught	327	57	40	43	8	241	37	39	20	244
Previously tagged	0	17	15	8	2	89	15	20	12	142
Newly tagged	327	40	25	35	6	152	22	19	8	102
Total dead	22	13	14	1	0	8	14	2	0	0
Tagged dead	2	5	13	1	0	3	12	2	0	0
Nontagged dead	20	8	1	0	0	5	2	0	0	0
Tagged in lake	325	360	372	380	386	535	545	562	570	672

^a Sample periods are as follows: 1 = May 2001, 2 = June 2001, 3 = July 2001, 4 = August 2001, 5 = September 2001, 6 = May 2002, 7 = June 2002, 8 = July 2002, 9 = August 2002, and 10 = May 2003.

vary significantly ($P = 0.5562, 0.4531, 0.4300, 0.1750, 0.3870,$ and 0.6788). Female ultimate length was greater than that of males. Length at age was less than for other muskellunge populations reported in the literature, diverging dramatically after age 5 (Figure 7).

The W_r averaged 79.8 (SE = 0.3) for males and 82.6 (SE = 0.4) for females (Figure 8). Literature estimates of muskellunge W_r averaged 93.2 with a 1.2 SE (Neumann and Willis 1994). Both female and male average W_r values were significantly lower ($P < 0.0001$) than the literature average. There were no significant differences ($\alpha > 0.05$) between May 2002 and May 2003 in average W_r for both females ($P = 0.1963$) and males ($P = 0.3762$). May 2002 and May 2003 W_r were significantly higher than in May 2001 in both females ($P < 0.0001$ and $P = 0.0227$ respectively) and males ($P < 0.0001$, and $P < 0.0001$ respectively).

TABLE 2.—MARK estimates of parameters from mark-recapture data collected from May 2001 to May 2003 for muskellunge in Shoepack Lake, Minnesota. Parameter estimates were derived from weighted models with $\Delta QAIC_c$ values less than 2. The periods in this table are the condensed periods shown in Table 1.

Parameter	Estimate	SE	95% Confidence limits	
			Lower	Upper
Survival				
Summer	0.987	0.0124	0.752	0.999
Winter	0.963	0.0247	0.845	0.992
Capture probability				
Period 1	0.303	0.0388	0.222	0.399
Period 2	0.158	0.0218	0.116	0.212
Period 3	0.258	0.0331	0.187	0.343
Period 4	0.137	0.0209	0.098	0.189
Period 5	0.267	0.0460	0.181	0.374
Lambda	0.974	0.0193	0.842	0.996
Population size	1,120	130	842	1,399

Fecundity and Age of Maturity

Based on the length of fish caught during the spawning periods, females reach sexual maturity between ages of 6 and 7. Males reach sexual maturity between ages of 4 and 5. This is similar to other muskellunge populations, where a majority of females have been reported to mature between 6 and 8 years and males between 5 and 6 years (Cook and Solomon 1987). Females averaged 14,306 eggs per kg and ranged from 22,239 to 28,537 eggs per female. The

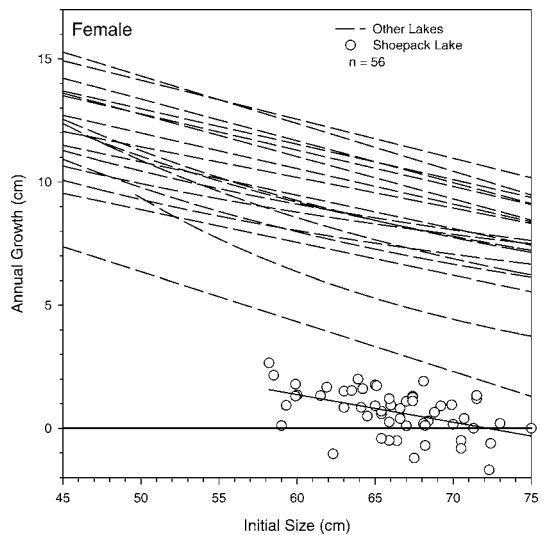


FIGURE 3.—Annual growth in relation to length at the start of the growing season for female muskellunge in Shoepack Lake, Minnesota. Annual growth rates are the differences in the total lengths of fish captured in two or more sampling periods standardized to 1 year. Growth rates from other lakes (Hanson 1986; Casselman et al. 1999) are shown for comparison.

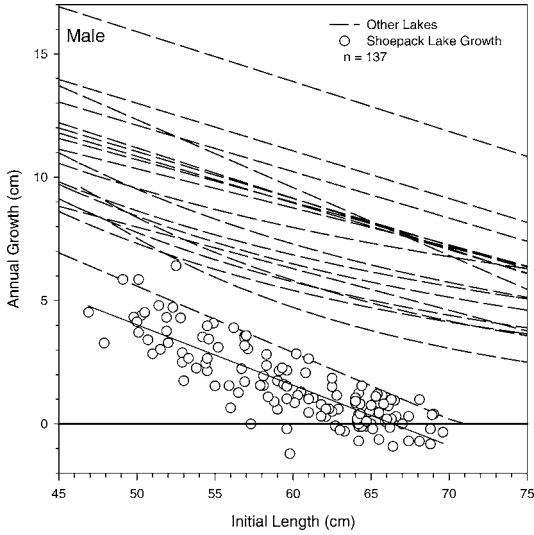


FIGURE 4.—Annual growth in relation to length at the start of the growing season for male muskellunge in Shoepack Lake, Minnesota. Annual growth rates are the differences in the total lengths of fish captured in two or more sampling periods standardized to 1 year. Growth rates from other lakes (Hanson 1986; Casselman et al. 1999) are shown for comparison.

sample size of four females was small due to the ineffective preservation of samples collected the first year. Females ranged from 619 to 669 mm in length and from 1.55 to 2.3 kg in weight.

Discussion

Our results demonstrated the unique nature of the muskellunge population in Shoepack Lake, both in terms of population characteristics and angler exploitation. The SLMP has slower growth rates, lower condition, higher densities, and higher angler CPUE than other muskellunge populations. These differences, combined with its genetic uniqueness, limited distribution and susceptibility to dramatic changes in habitat area, have potential consequences for the long-term viability of the SLMP.

Growth in the SLMP was much slower than that documented in other muskellunge populations. Survey data from MNDNR indicated that Shoepack muskellunge were smaller than other strains of muskellunge (Anderson 2000). Observed slow growth in Shoepack Lake muskellunge progeny led the MNDNR to terminate its use of the Shoepack strain for stocking and switch to a Mississippi River strain from Leech Lake, which has much faster growth (Younk and Strand 1992). Younk and Strand's (1992) study provided information on growth and survival of

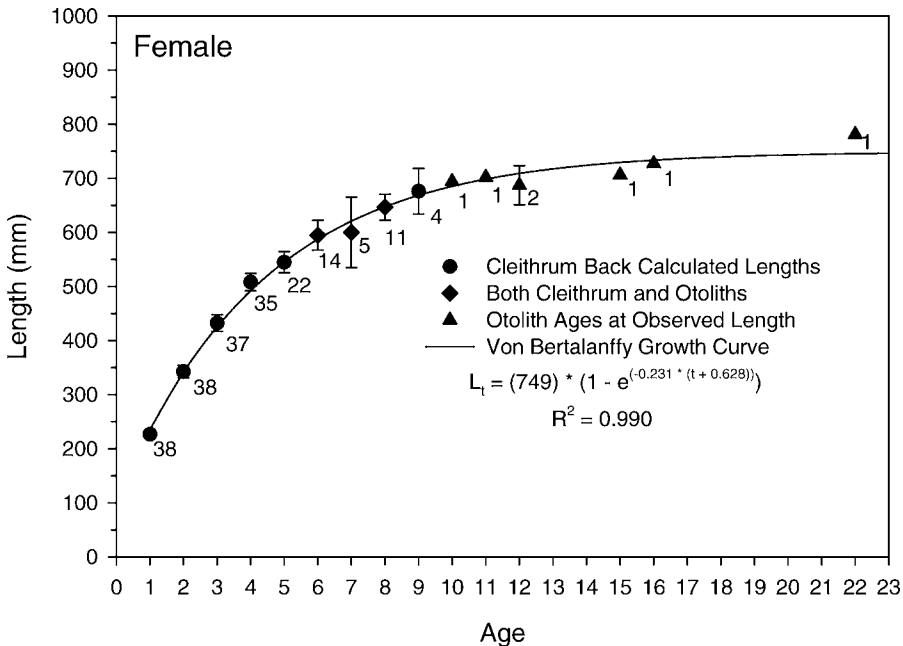


FIGURE 5.—Length at age of female muskellunge from Shoepack Lake, Minnesota. Means are from cleithrum back-calculated lengths or lengths at observed otolith ages. Also shown are the sample size and 95% confidence limits for each mean and the von Bertalanffy growth curve calculated from these means.

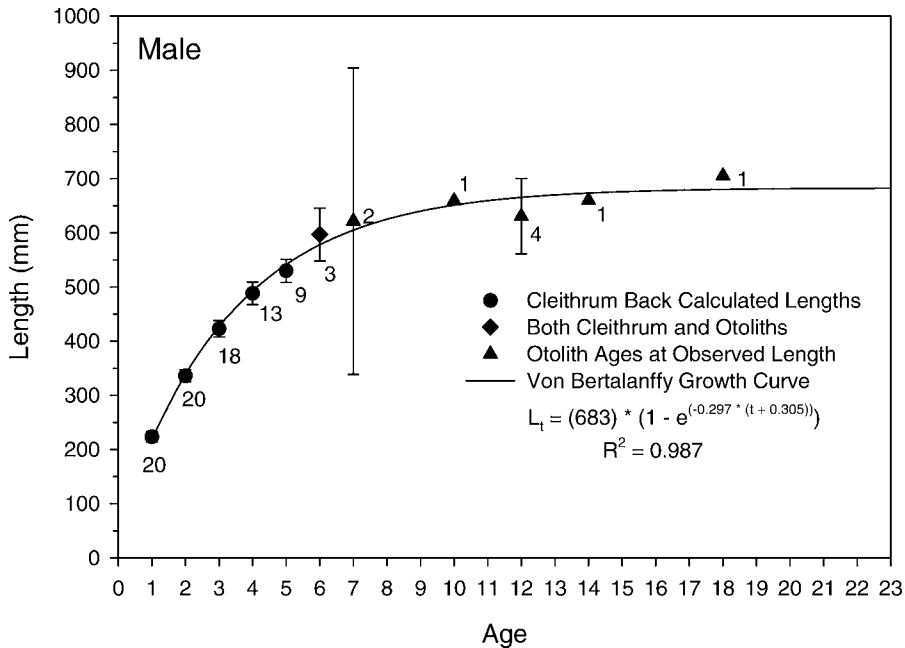


FIGURE 6.—Length at age of male muskellunge from Shoepack Lake, Minnesota. Means are from cleithrum back-calculated lengths or lengths at observed otolith ages. Also shown are the sample size and 95% confidence limits for each mean and the von Bertalanffy growth curve calculated from these means.

Shoepack strain muskellunge, but it was not conducted in Shoepack Lake. They found that the Shoepack strain grew more slowly than other strains stocked in Minnesota. Shoepack strain muskellunge grew faster and attained greater ultimate lengths in other lakes than they do in Shoepack Lake, although their growth was still slower than other strains. The evidence to date suggests that slow growth of the SLMP is due to a combination of genetic and environmental factors. As discussed below, high population density could be an important factor contributing to slow growth.

The condition of Shoepack muskellunge was also low. As with growth, the low condition of muskellunge in Shoepack Lake could be a reflection of high population density. Condition correlates positively with food availability in other species (Liao et al. 1995; Porath and Peters 1997), and although we did not assess food availability in this study, circumstantial evidence suggests it may have played a role in Shoepack Lake. The largest monthly increase in condition of both male and female muskellunge corresponded with the beaver dam failure in late July, 2001, and subsequent surface area reduction and dewatering of littoral habitat. Increased vulnerability of available prey fish was a likely consequence of this, which might explain the increase in muskellunge

condition. The coincident decrease in angler CPUE from July to August 2001 supports this interpretation. An increase in effectively available food by this mechanism would likely be short-lived, and rather than increasing food availability and condition, a long-term consequence of this change in the physical environment could be a reduced carrying capacity for the SLMP, with food availability, condition and population size adjusting accordingly.

The population density of the SLMP was much higher than that of other documented muskellunge populations. Muskellunge density in Shoepack Lake before the loss of the beaver dam was 4.8 fish/ha, several-fold higher than the range of 0.2–1.5 fish/ha recorded in eight Wisconsin lakes (Hanson 1986). After the beaver dam failure, the muskellunge density of 9.0 fish/ha in Shoepack Lake was roughly an order of magnitude greater than that of other documented populations owing to the 47% reduction in lake surface area but negligible reduction in estimated population size. Biomass differences, although less pronounced due to the smaller size of Shoepack Lake muskellunge, were still considerable with biomass in Shoepack Lake approximately 7.2 kg/ha and 13.5 kg/ha before and after loss of the beaver dam, respectively, compared with an average of 4 kg/ha in the Wisconsin lakes

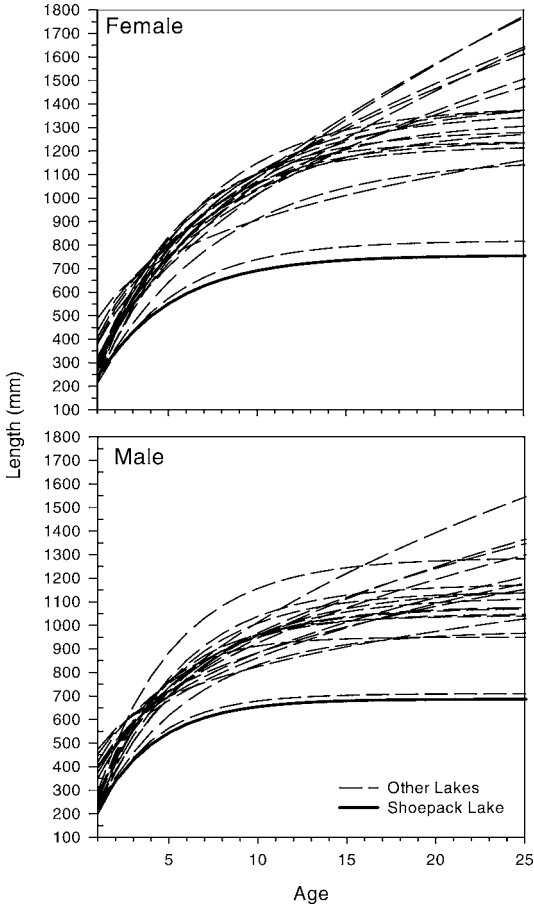


FIGURE 7.—Length-at-age curves for muskellunge in Shoepack Lake, Minnesota, and other muskellunge populations reported in the literature, by sex.

(Hanson 1986). A possible reason for these differences is the low fishing pressure and harvest in relatively remote and inaccessible Shoepack Lake compared with most other studied lakes that are more accessible and receive greater fishing pressure. For example, Hanson (1986) reported fishing pressure in Wisconsin lakes roughly 30 times greater than what we documented in Shoepack Lake, and a mean exploitation rate of roughly 27% compared with our negligible rate of exploitation. Regardless of the reason for the high muskellunge density in Shoepack Lake, it is reasonable to question whether this high density can be sustained. Long-term monitoring of the SLMP would be required to verify the population response to this reduction in habitat area. In the absence of empirical evidence, we think it is reasonable to speculate that population size roughly tracks habitat area over time, with lags of several years due to the inertia inherent in the

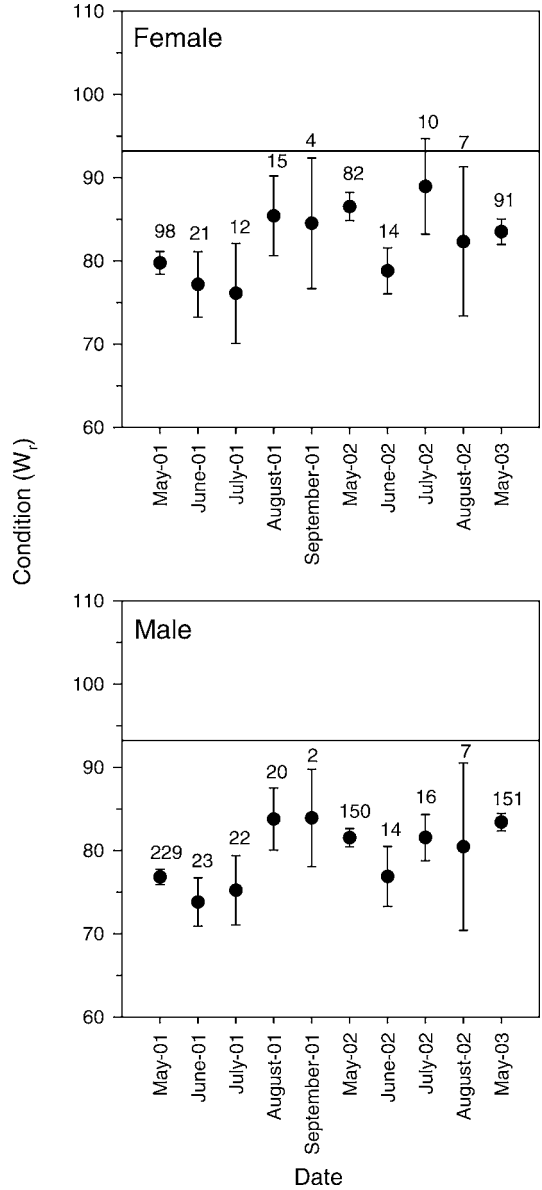


FIGURE 8.—Monthly condition of muskellunge in Shoepack Lake, Minnesota, from May 2001 to May 2003, as represented by mean relative weight (W_r). The sample size and 95% confidence limits are shown for each estimate. The published average (Neumann and Willis 1994) is indicated by a horizontal line for comparison.

muskellunge life history. If this speculation is accurate, population size during periods of reduced surface area might be approximately 600 adult fish.

Although documented fishing pressure and harvest rates were much lower in Shoepack Lake than in other muskellunge populations, catch rates were an order of

magnitude greater than elsewhere. The mean catch rates of 0.04 fish/angler-hour reported from northern Wisconsin (Simonson 2003), 0.03 fish/angler-hour in Minnesota (Younk and Pereira 2003), 0.04 fish/angler-hour in Ontario (Duffy and Mossindy 2000), and 0.09 fish/angler-hour in Lake St. Clair (Thomas and Haas 2005) are much lower than the average values of 0.22 and 0.30 fish angler-hours we documented in Shoepack Lake in 2001 and 2002. The high catch rates are likely a reflection of the greater population density in Shoepack Lake relative to other lakes. High catch rates could also be a result of greater vulnerability to angling inherent to the Shoepack strain and low angling pressure due to the lake's remoteness. The high catch rates at Shoepack Lake also suggest that the SLMP is potentially susceptible to significant harvest and hooking mortality if fishing pressure increases in the future. The steady upward trend in yearly boat usage over the last decade on Shoepack Lake is reason for concern about the potential effect of increased fishing pressure.

The estimated population size of the SLMP was declining during the study period. This could be due, in part, to the loss of the beaver dam and the consequent reduction in the carrying capacity of the lake. An equally plausible explanation is that it represents a brief snapshot of a long-term series of population fluctuations attributable to a variety of natural causes. Examining factors related to muskellunge population declines elsewhere may suggest factors to consider when assessing potential threats to the long-term viability of the SLMP. Self-sustaining muskellunge populations in many locations within their native range are believed to be declining (Dombeck et al. 1986; Hanson 1986; Zorn et al. 1998). These apparent declines have been attributed to several causes, including competition from northern pike (Oehmeke et al. 1974; Inskip 1986), overharvest (Bimber and Nicholson 1981), and low or variable recruitment (Scott and Crossman 1973; Oehmeke et al. 1974; Porter 1977; Trautman 1981; Dombeck et al. 1984; Hanson 1986; Zorn et al. 1998). Currently, we can rule out the first explanation because Shoepack Lake does not contain northern pike. In the future, however, competition from northern pike should not be discounted as a potential threat because abundant populations exist in nearly all the surrounding lakes. Unauthorized stocking of smallmouth bass *Micropterus dolomieu*, largemouth bass *M. salmoides*, and walleye *Sander vitreus* has occurred elsewhere in VNP. Northern pike or other potential competitors of muskellunge could be introduced from nearby Rainy Lake or Jorgen's Lake by foot or floatplane. Introduction of smallmouth bass into nearby Beast Lake may

have had a negative effect on the native northern pike population (L.W.K., unpublished data). The SLMP could suffer similarly if northern pike or other competitors were introduced into Shoepack Lake.

We can also tentatively rule out overharvest at present because we documented a very low harvest rate, averaging one fish per year. The remoteness of the lake, relatively small size of the fish, the 762-mm minimum length limit, and the trend toward catch-and-release among muskellunge anglers all likely contribute to this low harvest rate. Mortality due to the stress of hooking and handling probably affects a small percentage of the muskellunge caught and released in Shoepack Lake. Muskellunge hooking mortality studies are limited, but have documented 10–13% mortality in Illinois impoundments (Newman and Storck 1986). Physiological analysis suggested that mortality could be as high as 30% in Nogies Creek, Ontario (Beggs et al. 1980). Our postrelease mortality estimate of 4.1% would translate into fewer than ten deaths per year at current catch rates. Thirteen percent mortality would result in roughly 20 deaths per year. These low rates may not be a concern at the current low angler pressure, but if pressure were to increase in the future, hooking mortality combined with increased harvest could become a significant threat to the population status.

Low or variable recruitment in muskellunge could have several potential causes, including exploitation of females before they reach spawning age (Hanson 1986), spawning habitat loss or alteration (Trautman 1981; Dombeck et al. 1984, 1986; Zorn et al. 1998), unfavorable water temperature during spawning (Oehmeke et al. 1974), predation on eggs and juveniles (Scott and Crossman 1973; Oehmeke et al. 1974; Porter 1977), and insufficient food for juveniles (Oehmeke et al. 1974). Exploitation of females is clearly not a factor in Shoepack Lake at present, and it is unlikely to become important in the foreseeable future. Although there appeared to be ample shallow, boggy, littoral zone spawning habitat (Dombeck 1986) at the beginning of our study, much of this habitat was above water after the lake level receded. It is unclear how long it will take vegetation and woody debris to accumulate in these new littoral areas, or how long it will take for beavers to rebuild the dam at the lake outlet and reestablish a higher water level. Regardless, the beaver dam failure significantly reduced spawning habitat for muskellunge in Shoepack Lake, at least in the short term. Shoepack Lake is near the northern limit of the range of muskellunge, and frequent severe cold fronts in the springtime in this part of the range coupled with the reduced thermal inertia of a relatively small lake could contribute to poor reproductive success in

some years. Predation on eggs and juveniles and food supply for juveniles were not investigated, but we have no reason to believe they differ from conditions experienced by other muskellunge populations, nor do we have any reason to believe they are changing with time. Regardless of the specific mechanisms involved, recruitment in muskellunge populations is low compared with that in most freshwater species, and the SLMP appears to be no exception.

Water level reduction can have large impacts on resident fish communities, including reduction in abundance and diversity (Gaboury and Patalas 1984; Paller 1997), loss of spawning habitat (Estes 1972), loss of littoral zone habitat (Nichols 1975; Paller 1997), and changes in water chemistry (Gaboury and Patalas 1984). Despite a tremendous loss of water in a very short time, we detected no immediate reduction in abundance of muskellunge following the beaver dam failure. It is fortuitous that this event occurred during our study because it provides evidence that muskellunge apparently resist the water current produced by such events and maintain position in their resident water body. We speculate that similar beaver dam failures may have occurred periodically in the past, and that rather than displacing fish downstream, these events, like the one we documented in 2001, had the effect of increasing density. The lowered water level not only reduced surface area, but resulted in elimination of the majority of structurally complex littoral zone cover, which before the beaver dam failure consisted of flooded shoreline timber, downed timber, and bog vegetation. As discussed earlier, this apparently resulted in a short-term increase in prey density and vulnerability, but it is unlikely that this condition could be sustained in the long term. We believe that this reduction in the complexity of littoral zone habitat will also reduce reproductive success in the long term.

Our study provided a detailed characterization of the population status, dynamics, and angler exploitation of the SLMP over a 2-year period. Our results clearly define the unique nature of this population, and this uniqueness along with the location of Shoepack Lake in a national park requires that special consideration be given to future management. Although our data and analyses are rigorous, they only support speculative predictions about the long-term viability of the SLMP in the face of numerous potential future threats. Additional work in two areas is needed to translate the results of this study into a robust, objective evaluation of potential threats to long-term viability. First, dynamics of the SLMP must be simulated over a much longer time period than the duration of this study to fully explore potential population responses to environmental conditions and alternative management

scenarios. Results of the present study would provide a suitable foundation for such simulation modeling. Second, simulated future population-size estimates must be viewed in terms of genetically effective population size, which is a more precise estimator of the size of the gene pool and thus a better indicator of potential genetic bottlenecks, and ultimately the best indicator of long-term population viability (Meffe and Carroll 1997). A companion article (Frohnauer et al. 2007, this issue), based on the results reported here, presents a simulation study of genetically effective population size for the SLMP and discusses the implications for long-term viability.

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