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[Article]

Dynamics of a Recovering Lake Trout Population in Eastern Wisconsin Waters of Lake Superior, 1980–2001

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Abstract.—Lake trout *Salvelinus namaycush* are important in Lake Superior because of their economic and ecological value. Lake trout populations collapsed in the early 1950s due to overexploitation by the commercial fishery and predation by sea lampreys *Petromyzon marinus*. Efforts to rehabilitate a self-sustaining lake trout population included stocking of hatchery-reared lake trout, control of sea lamprey populations, and closure of the lake trout fishery. To quantify and describe the dynamics of the recovering lake trout population in eastern Wisconsin waters of Lake Superior between 1980 and 2001, we used statistical catch-at-age analysis to estimate abundance, recruitment, mortality, and fishery selectivity of wild and stocked lake trout. We found that estimated wild lake trout abundance increased, whereas estimated stocked lake trout abundance decreased. Estimated wild lake trout recruitment was erratic, while estimated stocked lake trout recruitment decreased until stocking was discontinued in 1996. Natural mortality was the largest component of estimated wild lake trout total mortality, where commercial fishing mortality was the largest component of estimated stocked lake trout total mortality. Wild lake trout abundance in Wisconsin waters of Lake Superior is on par with precollapse abundance levels, and total mortality rates are below rehabilitation target levels; however, wild lake trout recruitment is still below the level thought necessary to sustain the population.

Population dynamics is the engine of fisheries management because resource managers must understand underlying processes that drive a fish population if they hope to effectively solve problems that arise within the population. Current theories of fish population dynamics postulate that changes in abundance are caused by recruitment balanced against fishing and natural mortality (Hilborn and Walters 1992). Knowledge of each of these processes is therefore required to understand the abundance and structure of a population.

The lake trout *Salvelinus namaycush* is a species of great interest to Lake Superior fisheries managers because of its importance as a food source, as the focus of a recreational fishery, and as the top predator in the Lake Superior ecosystem. Lake Superior supported an average annual lake trout harvest of 2 million kg from 1913 to 1950 (Baldwin et al. 1979). Lake trout stocks collapsed in the early 1950s due to the combined effects of fishery exploitation and predation by sea lampreys *Petromyzon marinus* (Pycha and King 1975; Pycha 1980; Swanson and Swedberg 1980). The Wisconsin commercial fishery for lake trout was closed in 1962 as a result of the collapse (Pycha and King 1975). At the same time, a free permit system was initiated to regulate the Wisconsin recreational fishery for lake trout.

Efforts to rehabilitate lake trout populations in Lake Superior began soon after stocks collapsed. Interagency management goals specific to lake trout initially were formulated by the Lake Superior Lake Trout Technical Committee and were based on use of historic stock sizes as recovery reference points (LSLTT 1986; Hansen 1996; Horns et al. 2003). Fisheries managers in Wisconsin and other areas of Lake Superior attempted to meet these goals by stocking hatchery-reared lake trout to bolster natural recruitment,

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reducing sea lamprey-based mortality through control of the parasite's abundance, and reducing fishing mortality by setting stricter regulations on fisheries. Initial reports showed that wild lake trout abundance in Wisconsin waters of Lake Superior remained relatively constant and then increased slowly after 1970 (Hansen 1990, 1999; Hansen et al. 1994b). Reports also revealed a decline in stocked lake trout abundance in Wisconsin waters despite consistent stocking rates between 1963 and 1986 (Hansen et al. 1994a, 1994b); the decline was later attributed to commercial large-mesh gill-net fishing effort (Hansen et al. 1996). Early stock–recruitment analyses showed that stocked fish in Wisconsin waters had fueled recovery and that wild fish had contributed little between 1959 and 1993 (Hansen et al. 1995, 1997). This finding concerned fisheries managers because wild lake trout were expected to support a self-sustaining population as recovery progressed. In contrast, Schram et al. (1995) found that wild adult lake trout abundance explained most of the recruitment variation in Wisconsin's Gull Island Shoal refuge during that same period. The progress and mechanisms of lake trout recovery in Wisconsin waters of Lake Superior were uncertain owing to the mixed results of rehabilitation efforts.

Statistical catch-at-age analysis (SCAA) is a stock assessment technique that can provide insight into the recovery of the lake trout population in Wisconsin waters of Lake Superior. Statistical catch-at-age analysis is already being used to manage stocks of lake trout and lake whitefish *Coregonus clupeaformis* in some Michigan waters of the upper Great Lakes (MSC 2005) and can be a versatile tool to manage lake trout in Wisconsin. The primary advantage of SCAA is that it provides estimates of absolute abundance at age and key demographic characteristics, such as age-specific mortality rates, using fishery catch-at-age data (Fournier and Archibald 1982; Megrey 1989). Statistical catch-at-age analysis can be improved by incorporating additional information such as fishery-independent survey abundance indices and fishery effort data (Deriso et al. 1985). By use of SCAA, Wisconsin fisheries managers will be able to explicitly account for uncertainty in their data and determine the effect of that uncertainty on the estimation of important lake trout population attributes (Megrey 1989). The Wisconsin waters of Lake Superior provided us with a unique opportunity to compare the dynamics of wild and stocked lake trout by separately analyzing these two components of the population. Such a comparison between wild and stocked lake trout has not been conducted before using SCAA.

Our objective was to quantify and describe the dynamics of the recovering lake trout population in eastern Wisconsin waters of Lake Superior between 1980 and 2001 by addressing two questions. First, how have abundance, recruitment, and mortality of wild and stocked lake trout changed over time? Second, how do current levels of abundance, recruitment, and mortality of wild lake trout relate to established recovery goals? To answer these questions, we used SCAA to estimate abundance, recruitment, mortality, and fishery selectivity of wild and stocked lake trout.

Methods

Study area.—Lake Superior is highly oligotrophic; Wisconsin waters are among the more productive areas of the lake. The southern shore of Lake Superior has surface water temperatures ranging from 2°C to 11°C annually (Bennett 1978). Wisconsin waters are shallow (depth < 100 m) relative to other areas of Lake Superior; the substrate is primarily sandy, and the habitat is highly complex due to the presence of the 22 Apostle Islands (Johnson et al. 2004). Concentrations of major ions are lower than lakewide averages (Weiler 1978), and mean phytoplankton biomass is 196.65 mg/m^3 (Munawar and Munawar 1978).

The Wisconsin waters of Lake Superior are divided into two lake trout management units (Figure 1). Most fishing activity, stocking, and surveys occur within the eastern management unit (WI-2). The WI-2 unit has a surface area of 4,474 km^2 and includes the Apostle Islands. Shallow, rocky reefs (depth = 3–30 m) along the shoreline of the mainland and islands provide spawning grounds for lake trout (Coberly and Horrall 1980). The WI-2 unit contains two lake trout refuges that are closed to commercial and recreational fishing. The Gull Island Shoal refuge has a surface area of 336 km^2, and the Devils Island Shoal refuge has a surface area of 283 km^2.

Data collection.—We compiled harvest, effort, and age distribution data for commercial and recreational lake trout fisheries in WI-2 from unpublished records maintained by the Wisconsin Department of Natural Resources (WDNR), and the Red Cliff and Bad River bands of Lake Superior Chippewa for use in SCAA. We used age distribution and catch-per-unit-effort (CPUE) data from WDNR large-mesh and graded-mesh gill-net surveys to provide fishery-independent indices of relative abundance for our SCAA.

In Wisconsin waters of Lake Superior, the WDNR surveyed the angling fishery annually to estimate effort and harvest, whereas state and tribal commercial gill-net fisheries were required to report harvest and effort as part of license requirements. The WDNR and the Red Cliff Band also monitored state and tribal commercial fisheries. We used the percentage of wild fish caught in the large-mesh gill-net survey to estimate

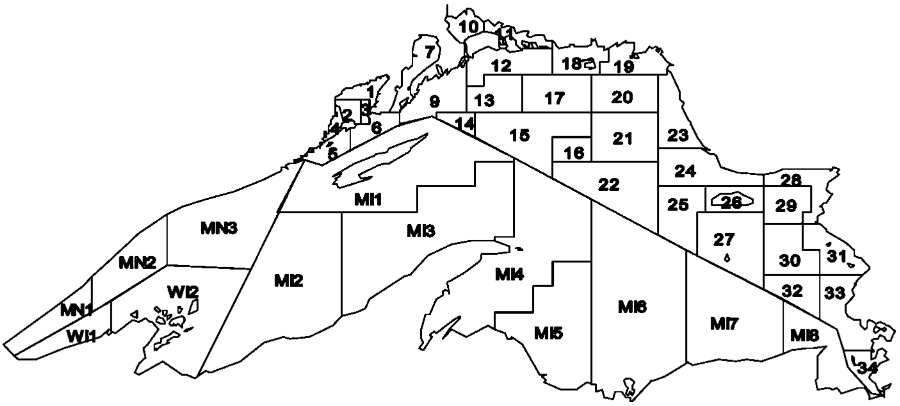

FIGURE 1.—Map of Lake Superior, showing lake trout management units. The U.S. management units are marked by state (MI = Michigan; MN = Minnesota; WI = Wisconsin). Canadian management units are marked only by numbers.

separate harvests of wild and stocked lake trout. We applied year-specific age–length keys from the large-mesh gill-net survey to recreational and commercial monitoring data to develop age distributions for the two fisheries because no age data were collected from the fisheries (Ricker 1975). We included commercial and recreational fishery data in our SCAA from 1980 to 2001 for ages 4–15+, where the age-15+ group included all fish ages 15 and older. Data for age-15+ fish were pooled because those fish constituted a small proportion of the fishery harvest. The WDNR also provided yearling stocking data from 1977 to 1995, when yearlings were last stocked, and fall fingerling stocking data from 1976 to 1985, when fall fingerlings were last stocked.

The WDNR conducted large-mesh gill-net surveys to provide an index of relative abundance and age distribution data for lake trout in Wisconsin waters of Lake Superior. This survey was conducted using standardized bottom-set gill nets (114-mm stretched mesh; 210/2 multifilament nylon twine; 18 meshes deep). The nets were hung on the one-half basis, set for an average of three nights, and fished from late April to early June. We defined CPUE as the number of fish caught per 305 m (1,000 ft) of net because nets were not of uniform length. We calculated mean annual large-mesh survey CPUE as a geometric mean. The WDNR estimated ages from scales or otoliths removed from a subsample of fish caught in gill nets; we then used year-specific age–length keys to expand estimated ages to the entire catch (Ricker 1975; Hansen et al. 1994a, 1995). Prior to 1987, the WDNR collected only scales from lake trout, whereas from 1987 onward, they collected scales from lake trout shorter than 58.4 cm and otoliths from lake trout 58.4 cm and longer. Stocked fish were identified by year-class-specific fin clip patterns. We calculated separate survey CPUEs and age distributions for wild and stocked lake trout. We used large-mesh gill-net survey data from 1981 to 2001 for ages 4–15+ in our SCAA.

The WDNR conducted graded-mesh gill-net surveys to provide another index of relative abundance and age distribution data for lake trout in Wisconsin waters of Lake Superior. The graded-mesh survey tended to sample the younger fish in the lake trout population. The WDNR used nets with stretched mesh ranging from 38 to 178 mm in 12.7-mm increments; nets were hung on the one-half basis, set for approximately 24 h, and fished during July–August. The WDNR used multifilament nylon nets prior to 1991 and monofilament nylon nets from 1991 to 2001. We assumed the difference in efficiencies between the two net types to be negligible when calculating graded-mesh survey CPUE. The graded-mesh survey was conducted in WI-2 in alternate years beginning in 1980. We defined CPUE as the number of fish caught per 305 m of net. We calculated mean annual graded-mesh survey CPUE as a geometric mean. The WDNR estimated ages from scales or otoliths removed from a subsample of fish caught in gill nets; we used year-specific age–length keys to expand estimated ages to the entire catch. We calculated separate CPUEs and age distributions for wild and stocked lake trout. We used graded-mesh gill-net survey data from 1980 to 2001 for ages 4–10+ in our SCAA.

Statistical catch-at-age models.—Separate SCAA models were built for wild and stocked lake trout in WI-2 using AD Model Builder software (Otter Research Ltd. 2002). Models were not constructed for WI-1 due to insufficient data. We initially attempted to model lake trout within the WI-2 refuges as separate subpopulations because of differences in observed lake trout age composition between refuge and nonrefuge areas. The resulting model failed to converge to a solution; the model was overparameterized because survey CPUE and age distribution were the only data sources for refuge lake trout. Therefore, we estimated parameters for the nonrefuge portion of WI-2 by only including survey data from large-mesh and graded-mesh gill-net survey sites outside of the refuges. We know that lake trout move between management units (Kapuscinski et al. 2005), but we lack sufficient data to explicitly account for that movement. Consequently, we assumed net lake trout movement between the refuge and nonrefuge portions of WI-2 and between WI-2 and adjacent management units to be nil (i.e., immigration and emigration were assumed to be equal). If emigration exceeded immigration, then our analysis would underestimate recruitment or overestimate mortality to account for fish leaving the population. If immigration exceeded emigration, then our analysis would overestimate recruitment or underestimate mortality to account for fish entering the population. The models were used to estimate abundance, recruitment, mortality, and fishery selectivity from 1980 to 2001 for lake trout of ages 4–15+ by fitting predicted fishery harvest, survey CPUE, and age distributions to observed data. For the following model descriptions, symbols used in the equations are found in Table 1.

The heart of SCAA is the simultaneous estimation of age-specific fishery harvest and the abundance required to produce that harvest. We calculated commercial and recreational fishery harvests using Baranov's catch equation (Ricker 1975):

$$\hat{C}_{i,y,a} = \frac{F_{i,y,a}}{Z_{y,a}} N_{y,a}(1 - e^{-Z_{y,a}}).$$

We calculated age distributions of the commercial and recreational harvests as proportions at age by dividing the catch at age by the total annual harvest. We calculated abundance using the exponential population equation (Ricker 1975; Quinn and Deriso 1999),

$$N_{y+1,a+1} = N_{y,a} e^{-Z_{y,a}},$$

for all years after 1980 and all ages greater than age 4. We estimated a series of deviations around a mean of zero for recruitment of the age-4 fish in each year and for each additional age-class in 1980. We constrained these deviations to sum to zero. We estimated a population scaling parameter to scale the deviations to an appropriate population size. In the stocked lake trout model, we based predicted numbers of age-4 fish on the observed number of yearlings stocked 3 years before and the observed number of fall fingerlings stocked 4 years before. We assumed fall fingerling overwinter survival to be 40% (Elrod et al. 1988) based on the approach of Sitar et al. (1999). We estimated mortality from age 1 to 4 as yearly deviations around a mean instantaneous mortality, which scaled the number of yearlings stocked to account for age-4 predicted abundance.

TABLE 1.—Description of equation symbols used in analysis of lake trout population dynamics in Wisconsin waters of Lake Superior.

Symbol	Description
$\bar{A}$	Mean coded age
A	True age
b_1	First inflection point of selectivity curve
b_2	First slope of selectivity curve
b_3	Second inflection point of selectivity curve
b_4	Second slope of selectivity curve
$\hat{c}$	Vector of predicted catch at age
$\tilde{c}$	Vector of predicted catch at age adjusted for age estimation error
C	Observed fishery catch
$\hat{C}$	Predicted fishery catch
$\tilde{C}$	Predicted fishery catch adjusted for age estimation error
E	Fishing effort
F	Instantaneous fishing mortality
F_C	Instantaneous commercial fishing mortality
F_R	Instantaneous recreational fishing mortality
L	Log-likelihood component
λ	Log-likelihood emphasis factor
M	Instantaneous natural mortality
M_L	Instantaneous sea lamprey-based mortality
N	Numbers of fish
n	Number of years in model
N_E	Effective sample size of age-estimated fish
p	Probability of surviving sea lamprey attack
P	Observed proportion of fish at age
$\hat{P}$	Predicted proportion of fish at age
q	Catchability
s	Fishery selectivity
t	Time of survey as proportion of year
T'	Transpose of age estimation error matrix
U	Observed survey CPUE
$\hat{U}$	Predicted survey CPUE
W	Estimated average sea lamprey wounding rate
Z	Instantaneous total mortality
α	Shape parameter for true versus coded age curve
β	Shape parameter for true versus coded age curve
ε	Deviations in fishing mortality–effort relationship
σ	Log-scale SD
a	Age index
i	Fishery–survey index
l	Length index
y	Year index

We partitioned total mortality into natural mortality, sea lamprey-based mortality, and fishing mortality:

$$Z_{y,a} = M + M_{Ly,a} + F_{y,a}.$$

We calculated an initial value of 0.19 for natural mortality (from which the final natural mortality was estimated) by use of Pauly's equation (Pauly 1980; Quinn and Deriso 1999). We estimated the von Bertalanffy growth parameters (asymptotic length L_∞

= 83.3 cm; $K = 0.15$ per year) for Pauly's equation separately from the SCAA models using mean length-at-age data from the large-mesh gill-net survey and the lakewide average water temperature of 6°C (Bennett 1978). We separated sea lamprey-based mortality from natural mortality due to the impact that sea lampreys have on lake trout abundance (Pycha and King 1975; Pycha 1980; Swanson and Swedberg 1980). We used a logistic model to estimate the number of sea lamprey wounds on lake trout as a function of lake trout length (Eshenroder and Koonce 1984; Ebener et al. 2003; Rutter and Bence 2003). The logistic model was used separately from the SCAA models because of the small sample sizes of large lake trout used for wounding rate estimation. The predicted wounding rates were then used to estimate length-specific sea lamprey-based mortality separately from the SCAA model (Sitar et al. 1999; Bence et al. 2003):

$$M_{Ly,l} = W_{y,l}\left(\frac{1 - p_l}{p_l}\right).$$

The probability of surviving a sea lamprey attack is summarized in Greig et al. (1992) from a laboratory study conducted by Swink (1990). Sea lamprey-based mortality was converted from length-specific to age-specific values using large-mesh survey age–length keys.

We separated fishing mortality into two components for the commercial and recreational fisheries:

$$F_{y,a} = F_{Cy,a} + F_{Ry,a}.$$

We assumed fishery-specific fishing mortality to be separable into age and year effects (Doubleday 1976; Quinn and Deriso 1999):

$$F_{i,y,a} = s_{i,a} q_i E_{i,y} \varepsilon_{i,y}.$$

The age effect was fishery selectivity, and the year effect consisted of observed fishery effort and annual deviations in the fishing mortality–effort relationship. Catchability represented the overall scalar between fishing mortality and observed effort. Annual deviations in the fishing mortality–effort relationship represented a combination of observation error in fishery effort and annual variation in catchability. We constrained annual deviations in the fishing mortality–effort relationship to sum to zero. We estimated fishery selectivity using a double logistic function (Bence et al. 1993):

$$s_{i,a} = \frac{1}{1 + e^{-b_{2,i}(a - b_{1,i})}}\left[1 - \frac{1}{1 + e^{-b_{4,i}(a - b_{3,i})}}\right].$$

We normalized the selectivity curve to the age of estimated maximum selectivity to uniquely parameterize the age and year effects of fishing mortality (Doubleday 1976; Bence et al. 1993).

We calculated CPUEs and age distributions for the large-mesh and graded-mesh surveys as

$$\hat{U}_{i,y,a} = s_{i,a} q_i N_{i,y,a},$$

where population abundance at the time of the survey was employed. We estimated selectivity for the surveys using the double logistic function described for the commercial and recreational fisheries. We calculated large-mesh and graded-mesh survey age distributions as proportions at age by dividing the age-specific CPUE by the total annual CPUE for the year.

In our SCAA, a method developed by Weeks (1997) was used to account for lake trout age estimation errors, which affect the observed fishery catch-at-age and age-specific survey CPUE data. We built two age estimation error matrices separately from the SCAA models to account for the change in age estimation techniques that occurred in 1987. We used age estimation data from fin-clipped hatchery lake trout, whose ages were known with a high degree of confidence. The WDNR assigned coded ages to each fin-clipped fish by use of both scales and otoliths. We calculated the observed mean coded age assigned to each true age (i.e., ages as determined by fin clips). We used a simple power function ($\alpha = 1.53$; $\beta = 0.79$) to estimate mean coded ages from true ages:

$$\bar{A} = \alpha A^{\beta}.$$

This method was used because of the small sample sizes available for calculating observed mean coded ages of older fish. We assumed that the probability of assigning a coded age to a given fish in our SCAA was normally distributed around our estimated mean coded age for that fish's true age. We developed separate distributions for the probability of assigning coded ages for each age in our model. We determined a single SD for all of the coded age assignment distributions by averaging the SDs of all observed mean coded ages. We built the first matrix using only coded ages estimated from scales and applied the matrix to the model time series when only scales were used to assess ages (1980–1986). We built the second matrix using coded ages estimated from scales for ages 4–8 and coded ages estimated from otoliths for ages 9–15+. Age 9 was chosen for the transition to otolith-estimated ages because the mean length of age-9 lake trout was approximately 58.4 cm. The second matrix was applied to the model time series when both scales and otoliths were used to assess ages (1987–2001). We applied the age estimation error matrices to predicted catch at age within the models as follows (using matrix notation):

TABLE 2.—Log-scale estimated parameter values and asymptotic SDs for a statistical catch-at-age model of wild lake trout in Wisconsin waters of Lake Superior. Model parameters include the population scaler (N_P) and population deviations ($\zeta_{y,a}$). All other parameters are described in Table 1.

Parameter	Value(s) (SD)
N_P	11.51 (0.49)
$[\zeta_{y,4}]_{y=1980}^{2001}$	1.14 (0.22), 0.83 (0.23), 0.75 (0.22), 1.13 (0.22), 1.51 (0.20), 0.96 (0.22), 0.79 (0.23), 1.38 (0.20), 0.77 (0.24), 1.47 (0.21), 1.11 (0.24), 1.35 (0.22), 1.20 (0.22), 0.98 (0.22), 0.84 (0.23), 1.30 (0.23), 1.04 (0.24), 1.65 (0.24), 0.79 (0.29), 1.80 (0.28), 1.00 (0.32), 1.17 (0.61)
$[\zeta_{1980,a}]_{a=5}^{15+}$	−0.19 (0.29), 0.37 (0.31), −1.69 (1.75), −0.59 (0.52), −4.31 (2.97), −1.07 (0.45), −4.47 (2.92), −3.81 (3.04), −2.30 (1.78), −3.04 (2.80), −3.87 (2.94)
$[b_{i,C}]_{i=1}^{4}$	1.87 (0.01), 0.74 (0.04), −5.00 (0.19), −1.16 (0.12)
q_C	−18.21 (0.50)
$[\varepsilon_{C,y}]_{y=1980}^{2001}$	0.60 (0.20), 0.37 (0.18), 0.13 (0.17), 0.16 (0.16), 0.02 (0.16), 0.10 (0.16), 0.08 (0.15), −0.12 (0.15), −0.28 (0.15), −0.49 (0.15), −0.50 (0.15), −0.25 (0.15), −0.13 (0.14), −0.10 (0.14), −0.04 (0.15), 0.04 (0.15), 0.24 (0.15), 0.13 (0.16), 0.06 (0.17), 0.02 (0.18), 0.02 (0.19), −0.08 (0.20)
$[b_{i,R}]_{i=1}^{4}$	1.83 (0.01), 1.11 (0.06), 1.50 (0.001), −1.19 (0.13)
q_R	−16.62 (0.51)
$[\varepsilon_{R,y}]_{y=1980}^{2001}$	−0.11 (0.37), −0.81 (0.36), −0.80 (0.36), −0.86 (0.36), −0.93 (0.36), −0.52 (0.36), −0.02 (0.35), 0.07 (0.36), −0.14 (0.35), 0.06 (0.35), 0.12 (0.35), 0.40 (0.36), 0.22 (0.35), 0.18 (0.35), 0.22 (0.36), 0.16 (0.35), 0.39 (0.35), 0.53 (0.35), 0.59 (0.36), −0.07 (0.36), 0.52 (0.37), 0.80 (0.37)
M	−1.71 (0.06)
$[b_{i,LM}]_{i=1}^{4}$	1.89 (0.01), 0.76 (0.04), 1.00 (0.001), −0.86 (0.10)
q_{LM}	−11.31 (0.53)
$[b_{i,GM}]_{i=1}^{4}$	1.44 (0.01), 2.00 (0.001), −5.00 (0.45), −0.03 (0.07)
q_{GM}	−13.26 (0.55)

$$\tilde{c}_{i,y} = T'_y \hat{c}_{i,y}.$$

We used the same age estimation error matrices in both wild and stocked lake trout models.

Model parameters were estimated on the log scale using a quasi-Newton iterative algorithm with Bayesian-based likelihood methods (i.e., prior densities were assigned to some parameters) that fit model predictions to observed data (Tables 2, 3). We obtained parameter estimates by minimizing the negative log-likelihood function, which was formulated as

$$L = \sum_i \lambda_i L_i,$$

where an emphasis factor (λ_i) was used to adjust the weight of each negative log-likelihood component and

TABLE 3.—Log-scale estimated parameter values and asymptotic SDs for a statistical catch-at-age model of hatchery lake trout in Wisconsin waters of Lake Superior. Model parameters included the population scaler (N_P), population deviations ($\zeta_{y,a}$), mean instantaneous mortality of stocked yearlings ($\bar{S}$), and yearly deviations in mortality of stocked yearlings (ψ_y). All other parameters are described in Table 1.

Parameter	Value(s) (SD)
$\bar{S}$	−0.59 (0.29)
$[\psi_y]_{y=1980}^{1998}$	−1.85 (1.07), −5.40 (2.67), −5.34 (2.67), 0.76 (0.30), 0.54 (0.30), 1.23 (0.29), 0.77 (0.29), 1.67 (0.29), 1.36 (0.29), 0.72 (0.29), 1.17 (0.29), 1.70 (0.29), 1.00 (0.29), 1.54 (0.29), 1.32 (0.29), 0.90 (0.29), 1.27 (0.28), −0.12 (0.27), −3.21 (3.11)
N_P	8.87 (0.77)
$[\zeta_{1980,a}]_{a=5}^{15+}$	3.56 (0.73), 1.94 (2.07), 0.81 (5.19), 2.08 (1.37), −1.55 (4.08), 1.81 (0.90), −0.99 (4.26), −0.26 (2.23), −2.26 (3.62), −2.07 (2.90), −3.07 (3.21)
$[b_{i,C}]_{i=1}^{4}$	1.39 (5.14), 4.59 (1030.2), 2.59 (0.03), 0.89 (0.41)
q_C	−17.19 (0.05)
$[\varepsilon_{C,y}]_{y=1980}^{2001}$	−0.30 (0.14), −0.48 (0.13), −0.55 (0.13), −0.39 (0.12), −0.17 (0.12), 0.06 (0.12), 0.07 (0.13), −0.33 (0.13), −0.11 (0.13), −0.03 (0.13), −0.17 (0.13), 0.03 (0.14), 0.38 (0.14), 0.26 (0.14), 0.39 (0.14), 0.85 (0.14), 1.07 (0.14), 0.69 (0.15), −0.14 (0.16), −0.37 (0.15), −0.25 (0.16), −0.49 (0.16)
$[b_{i,R}]_{i=1}^{4}$	1.46 (0.003), 2.00 (0.0002), 2.00 (4.51), −3.00 (0.002)
q_R	−15.61 (0.09)
$[\varepsilon_{R,y}]_{y=1980}^{2001}$	−0.96 (0.35), −1.58 (0.35), −1.34 (0.34), −1.18 (0.33), −0.99 (0.33), −0.51 (0.32), −0.05 (0.33), −0.14 (0.33), −0.01 (0.33), 0.47 (0.34), 0.36 (0.35), 0.58 (0.35), 0.64 (0.34), 0.48 (0.35), 0.57 (0.36), 0.87 (0.36), 1.11 (0.37), 1.02 (0.36), 0.43 (0.38), −0.45 (0.36), 0.25 (0.36), 0.44 (0.36)
M	−1.84 (0.05)
$[b_{i,LM}]_{i=1}^{4}$	1.45 (0.003), 2.00 (0.0002), 2.55 (0.04), −0.11 (0.35)
q_{LM}	−9.94 (0.21)
$[b_{i,GM}]_{i=1}^{4}$	1.41 (0.01), 2.00 (0.002), −5.00 (0.34), −0.10 (0.08)
q_{GM}	−11.76 (0.40)

negative log-prior density (Methot 1990). We included eight negative log-likelihood components in the wild lake trout model for commercial and recreational fishery harvests and age distributions and large-mesh and graded-mesh gill-net survey CPUEs and age distributions. We included four negative log-prior densities in the wild lake trout model for commercial and recreational fishing effort, natural mortality, recruitment, and abundance in the first year. The stocked lake trout model also included a negative log-prior density for poststocking mortality. We assumed that negative log-likelihood components for fishery harvest followed lognormal distributions of the form

$$L_i = \frac{1}{2\sigma_i^2} \sum_y \left[\left(\log_e \frac{C_{i,y}}{\tilde{C}_{i,y}} \right)^2 \right] + n \log_e \sigma_i .$$

Negative log-likelihood components for commercial and recreational fishery harvest were weighted by their associated variances ($\sigma_C^2 = 0.02$; $\sigma_R^2 = 0.16$), which were derived from the expert opinion of WDNR and tribal managers. We assumed that negative log-likelihood components for survey CPUE followed lognormal distributions of the form

$$L_i = \sum_y \left[\frac{1}{2\sigma_{i,y}^2} \left(\log_e \frac{U_{i,y}}{\hat{U}_{i,y}} \right)^2 + \log_e \sigma_{i,y} \right] .$$

Negative log-likelihood components for large-mesh and graded-mesh survey CPUE were weighted by their associated variances, which were calculated for each year from the raw survey data. We assumed that negative log-likelihood components for fishery and survey age distributions followed multinomial distributions of the form

$$L_i = -\sum_y N_{E,i,y} \sum_a (P_{i,y,a} \log_e \hat{P}_{i,y,a}),$$

as was recommended by Methot (1990). Negative log-likelihood components for fishery and survey age distributions were weighted by the effective sample size, which was the number of fish for which ages were estimated each year up to a maximum of 200 fish (Sitar et al. 1999). Negative log-prior densities for commercial and recreational fishing effort assumed that variability in the relationship between fishing mortality and fishing effort was lognormally distributed. The negative log-prior density for natural mortality assumed that the deviation between the prior natural mortality value (i.e., from Pauly's equation) and the predicted natural mortality value was lognormally distributed. The negative log-prior density for recruitment of the first age in each year and abundance of each age in the first year assumed that variability in recruitment and abundance in the first year was lognormally distributed. In the stocked lake trout model, the negative log-prior density for poststocking mortality was lognormally distributed. All negative log-prior densities were weighted by their associated variances, which were derived from the expert opinion of WDNR and tribal managers.

Negative log-likelihood components and negative log-prior densities are naturally weighted by the variances or effective sample sizes of the individual components. Emphasis factors provide a convenient means of adjusting these natural weights. We set all emphasis factors to a value of 1.0, which assumes that the variances and effective sample sizes were correctly specified, except for the emphasis factors for commercial and recreational fishing effort. Observed fishing effort was not directly related to lake trout fishing mortality: commercial fishing effort targeted lake whitefish while avoiding lake trout as bycatch, whereas recreational fishing effort targeted several other species in addition to lake trout. The poor fit of predicted to observed commercial and recreational harvest when the fishing effort emphasis factors were set to 1.0 was evidence that we had underestimated the fishery effort variances. Therefore, we allowed estimated fishing mortality to deviate further from observed fishing effort by setting commercial and recreational fishing effort emphasis factors to 0.1, which effectively increased the variances associated with commercial and recreational fishing effort by a factor of 10 ($\sigma_C^2 = 0.22$; $\sigma_R^2 = 0.63$).

We judged a model run to have converged on a solution when the maximum gradient component was less than 1×10^{-4}, which is the default convergence criterion for AD Model Builder. To evaluate model robustness, we tested the sensitivity of SCAA model output to changes in model assumptions. We individually doubled and halved each likelihood emphasis factor and estimated model parameters after each adjustment. We measured model sensitivity as percent difference between adjusted and unadjusted model values for total abundance, fully selected commercial fishing mortality, and fully selected recreational fishing mortality averaged over the most recent 3 years of data.

Results

Wild and stocked lake trout models successfully converged on solutions. Predictions of commercial and recreational fishery harvests, commercial and recreational fishery age distributions, large-mesh and graded-mesh survey CPUEs, and large-mesh and graded-mesh survey age distributions for wild and stocked lake trout from the SCAA models were consistent with observed data. Predicted commercial harvest for wild lake trout

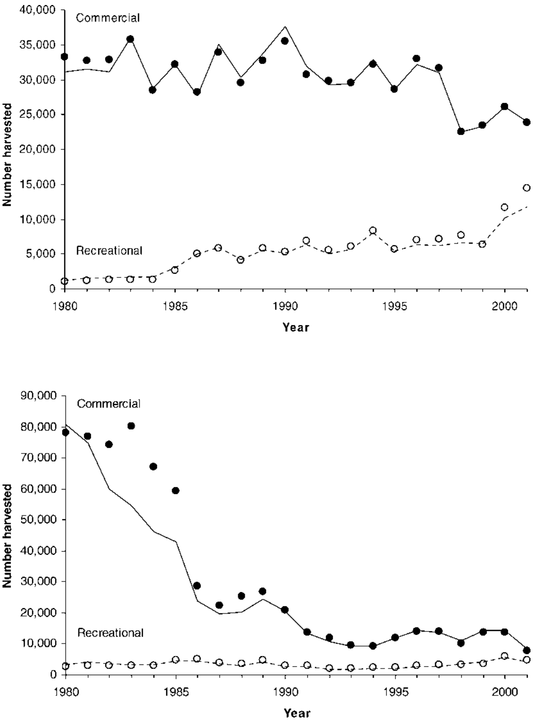

FIGURE 2.—Commercial fishery harvest (observed = solid circles; predicted = solid line) and recreational fishery harvest (observed = open circles; predicted = dashed line) of wild (upper panel) and stocked lake trout (lower panel) in Wisconsin management unit 2 of Lake Superior between 1980 and 2001.

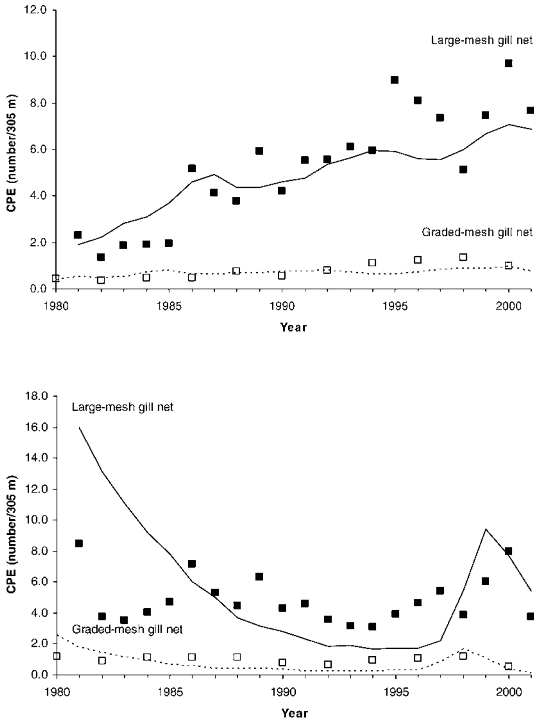

FIGURE 3.—Wild (upper panel) and stocked (lower panel) lake trout catch per unit effort in large-mesh (observed = solid squares; predicted = solid line) and graded-mesh (observed = open squares; predicted = dashed line) gill-net surveys conducted within Wisconsin management unit 2 of Lake Superior between 1980 and 2001.

and recreational harvest for wild and stocked lake trout closely fit observed harvest (Figure 2). Predicted commercial harvest for stocked lake trout consistently underestimated observed harvest prior to 1990 and closely fit observed harvest thereafter. Trends in predicted large-mesh and graded-mesh gill-net surveys matched observed trends in both surveys (Figure 3). Predicted mean age did not systematically differ from observed mean age for the commercial fishery, recreational fishery, large-mesh survey, or graded-mesh survey for either wild or stocked lake trout (Figures 4, 5). Predicted average total abundance, fully selected commercial fishing mortality, and fully selected recreational fishing mortality for wild and stocked lake trout were most sensitive (>17% difference) to adjustments in the likelihood emphasis factors for commercial and recreational fishing effort, commercial and recreational fishery age distributions, and the graded-mesh gill-net survey age distribution. Changes in remaining likelihood emphasis factors led to only small changes (<10% difference) in wild and stocked lake trout model output quantities. The stocked lake trout model failed to converge to a solution when adjustments were made in the likelihood emphasis factors for commercial fishery harvest and age distribution, and the graded-mesh gill-net survey age distribution.

For wild lake trout, commercial fishery harvest declined from 1980 to 2001, while recreational fishery harvest increased over the same period (Figure 2). Predicted commercial harvest of wild lake trout declined from 31,160 fish in 1980 to 23,991 fish in 2001; the maximum harvest of 37,672 fish occurred in 1990. Predicted recreational harvest of wild lake trout increased from 1,130 fish in 1980 to a maximum of 11,774 fish in 2001.

For stocked lake trout, commercial fishery harvest declined form 1980 to 2001, while recreational fishery harvest remained relatively constant over the same period (Figure 2). Predicted commercial harvest of stocked lake trout declined from 80,829 fish in 1980 to 8,224 fish in 2001. Predicted recreational harvest of stocked lake trout was highest in 2000 (5,756 fish) and lowest in 1992 (1,749 fish).

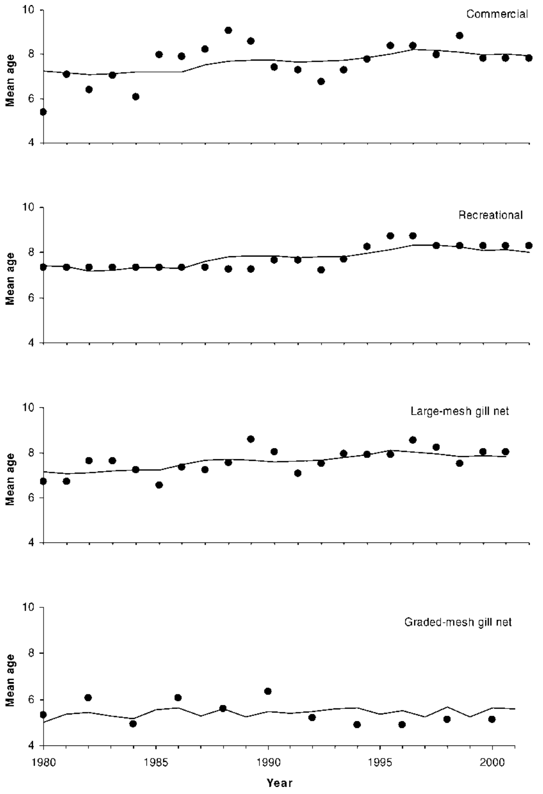

FIGURE 4.—Mean age (observed = solid circles; predicted = solid line) of wild lake trout caught in the commercial and recreational fisheries and large-mesh and graded-mesh gill-net surveys within Wisconsin management unit 2 of Lake Superior between 1980 and 2001.

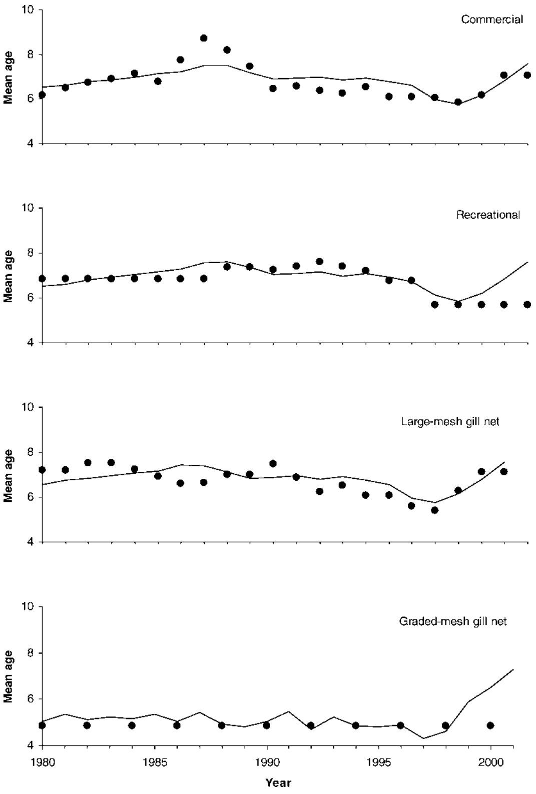

FIGURE 5.—Mean age (observed = solid circles; predicted = solid line) of stocked lake trout caught in the commercial and recreational fisheries and large-mesh and graded-mesh gill-net surveys within Wisconsin management unit 2 of Lake Superior between 1980 and 2001.

Estimated abundance of age-4+ wild lake trout more than doubled between 1980 and 2001, while estimated abundance of stocked lake trout decreased steadily from 1980 to 2001 (Figure 6). Estimated abundance of age-4+ wild lake trout increased from 670,358 fish in 1980 to 1,589,600 fish in 2001; the maximum of 1,797,000 fish occurred in 1999. Estimated abundance of age-4+ stocked lake trout decreased from a maximum of 630,897 fish in 1980 to 126,928 fish in 2001; a peak in abundance was observed in 1998 (301,345 fish).

Recruitment of age-4 wild lake trout was erratic from 1980 to 2001, while recruitment of age-4 stocked lake trout declined through time except for a brief, sharp increase in 1998 (Figure 6). Recruitment of wild lake trout was lowest in 1982 (212,055 fish) and highest in 1999 (603,887 fish). Recruitment of stocked lake trout decreased from 200,487 fish in 1980 to no fish by 1999; a peak of 182,389 fish was apparent in 1998.

Instantaneous total mortality of age-7 (i.e., fully selected in the commercial and recreational fisheries) wild lake trout declined from 0.58 in 1980 to 0.28 in 2001 (Figure 7). Instantaneous natural mortality was estimated as a constant (0.18) and made up the largest component of total mortality in every year except 1980 and 1981 (when it was surpassed by commercial fishing mortality) and 1987 (when it was surpassed by sea lamprey-based mortality). Instantaneous sea lamprey-based mortality declined from 0.16 in 1980 to 0.04 in 2001; a peak of 0.19 occurred in 1987. Instantaneous commercial fishing mortality declined steadily from 0.22 in 1980 to 0.04 in 2001. Instantaneous recreational fishing mortality was the only mortality source to increase (from 0.009 in 1980 to 0.022 in 2001), but it still made up the smallest proportion of total mortality except in 1999, when it surpassed sea lamprey-based mortality.

Instantaneous total mortality of age-7 stocked lake trout was relatively constant from 1980 to 1996 and then declined from 0.69 in 1996 to 0.31 in 2001 (Figure 7). Instantaneous natural mortality was esti-

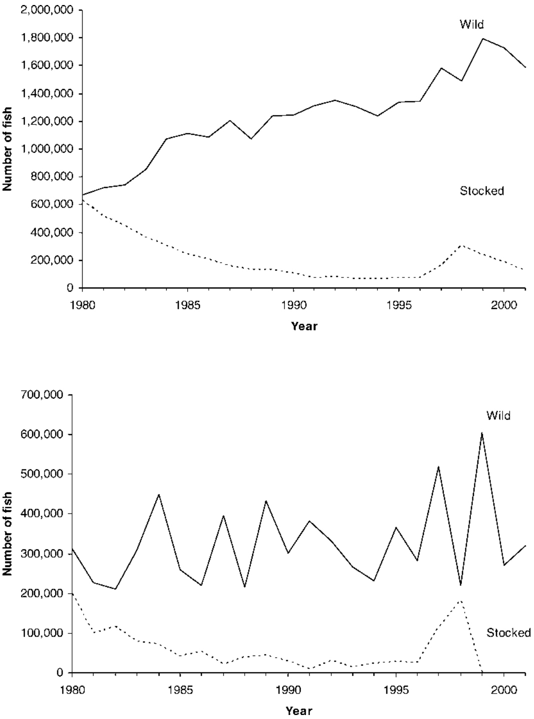

FIGURE 6.—Predicted age-4+ abundance (upper panel) and age-4 recruitment (lower panel) of wild (solid line) and stocked (dashed line) lake trout in Wisconsin management unit 2 of Lake Superior between 1980 and 2001.

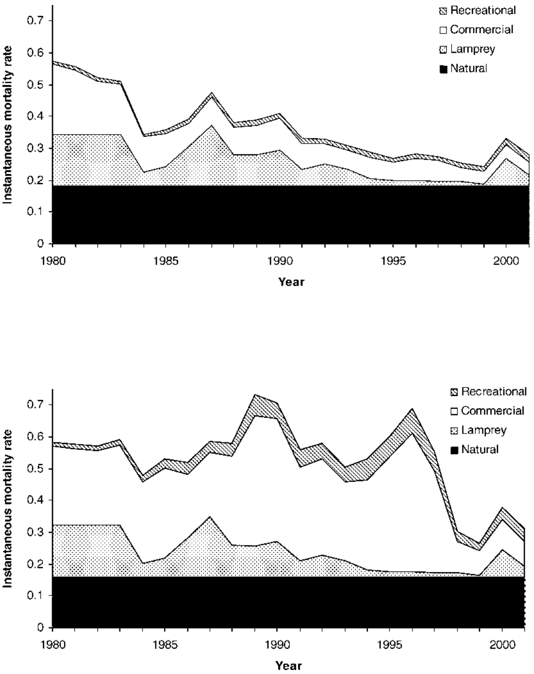

FIGURE 7.—Predicted instantaneous mortality rates (natural, sea lamprey-based, commercial fishery, and recreational fishery mortality) of age-7 wild (upper panel) and stocked (lower panel) lake trout in Wisconsin management unit 2 of Lake Superior between 1980 and 2001.

mated as a constant (0.16) from 1980 to 2001. Instantaneous sea lamprey-based mortality declined from 0.16 in 1980 to 0.04 in 2001; sea lamprey-based mortality peaked in 1987 at 0.19. Instantaneous commercial fishing mortality increased from 0.25 in 1980 to 0.44 in 1996 and then declined to 0.08 in 2001. Instantaneous recreational fishing mortality was 0.01 in 1980, attained a maximum of 0.08 in 1996, and then declined to 0.04 in 2001.

The commercial fishery, recreational fishery, and large-mesh gill-net survey exhibited similar trends in selectivity for wild lake trout (Figure 8). Predicted selectivity for commercial and recreational fisheries and the large-mesh gill-net survey was highest at age 7, whereas predicted selectivity for the graded-mesh gill-net survey was highest at age 5. Predicted selectivity decreased after the age of maximum selectivity for all four gears.

Fishery selectivity patterns for stocked lake trout were similar among the commercial fishery, recreational fishery, and large-mesh gill-net survey (Figure 9) but differed from those of wild lake trout (Figure 8). The graded-mesh gill-net survey selectivity pattern was similar between stocked and wild lake trout. For stocked fish, predicted selectivity was highest at age 5 for all four gears. Predicted selectivity was relatively constant from age 5 to 12 for the commercial fishery and to age 10 for the large-mesh gill-net survey; it declined sharply at older ages for both, declined slightly after age 5 for the recreational fishery, and declined sharply after age 5 for the graded-mesh gill-net survey.

For wild lake trout, large-mesh and graded-mesh gill-net survey CPUE increased from 1980 to 2001 (Figure 3). Large-mesh gill-net CPUE increased from 1.92 fish/305 m of net in 1981 to 6.86 fish/305 m of net in 2001. Graded-mesh gill-net CPUE increased from 0.38 fish/305 m of net in 1980 to 0.76 fish/305 m of net in 2001.

For stocked lake trout, large-mesh and graded-mesh gill-net survey CPUE decreased steadily from the early 1980s to the mid-1990s and peaked in the late 1990s (Figure 3). Large-mesh gill-net CPUE decreased from 16.0 fish/305 m of net in 1981 to 1.69 fish/305 m of net in 1994; the CPUE then increased to 9.41 fish/305 m of net in 1999. Graded-mesh gill-net CPUE decreased from 2.59 fish/305 m of net in 1980 to 0.23 fish/305 m of net in 1991; a subsequent increase to 1.65 fish/305 m of net was observed in 1998.

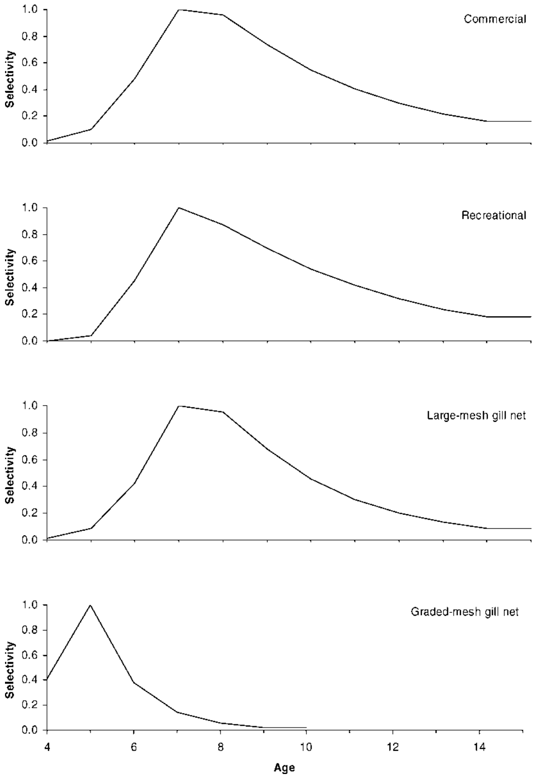

FIGURE 8.—Predicted selectivity of wild lake trout by commercial and recreational fisheries and large-mesh and graded-mesh gill-net surveys within Wisconsin management unit 2 of Lake Superior, 1980–2001.

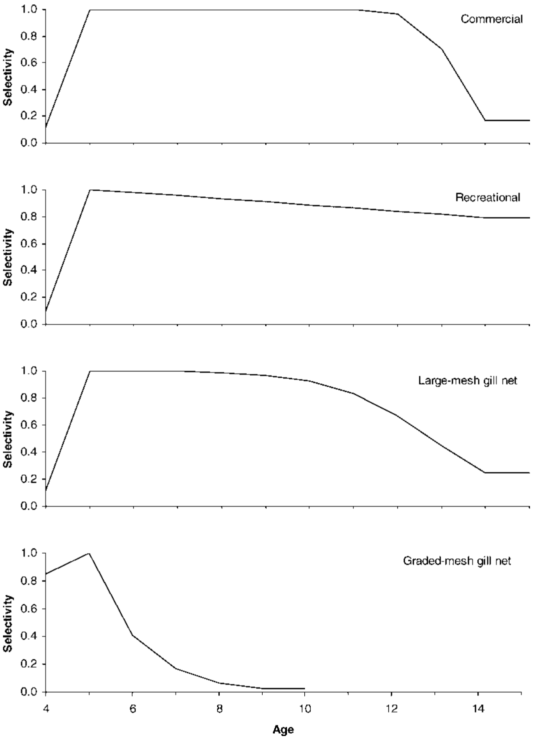

FIGURE 9.—Predicted selectivity of stocked lake trout by commercial and recreational fisheries and large-mesh and graded-mesh gill-net surveys within Wisconsin management unit 2 of Lake Superior, 1980–2001.

Discussion

The stocked lake trout model was not as stable as the wild lake trout model. Lack of stability in the stocked lake trout model was demonstrated by a poor fit between predicted commercial catch and observed catch, which normally fit closely, and by the model's failure to converge when commercial fishery harvest and age distribution and graded-mesh gill-net survey age distribution likelihood emphasis factors were changed. The stocked lake trout model's poor stability is probably due to the relatively low fishery catch during the latter half of the time series. Statistical catch-at-age analysis requires sufficiently high levels of fishery catch to estimate parameters and fit observed data accurately. The lack of fit for the commercial catch data is due to our assumption of 40% fall fingerling overwinter survival. Fall fingerlings were stocked from 1976 to 1985 and recruited to age 4 between 1980 and 1989, which represents the period when commercial harvest was underestimated. The model's inability to estimate abundances that were high enough to support observed catches suggests that fall fingerling overwinter survival was actually higher than 40%. The Elrod et al. (1988) value for overwinter survival was based on stocked lake trout from Lake Ontario, but fall fingerling overwinter survival may be different in Lake Superior.

According to SCAA model predictions, wild lake trout abundance increased and stocked lake trout abundance decreased from 1980 to 2001 in eastern Wisconsin waters, as was found by earlier studies of lake trout population dynamics in Lake Superior. These results are similar to the earlier recovery of lake trout in Michigan waters of Lake Superior, where stocked fish abundance decreased while wild fish abundance increased to near-historic levels (Hansen et al. 1994b, 1995; Wilberg et al. 2003). In eastern Wisconsin waters, the decline in stocked lake trout abundance was temporarily reversed in the late 1990s. This increase was due to low poststocking mortality rates for yearlings stocked in 1994 and 1995 (the last two year-classes stocked). Earlier studies revealed that lake trout abundance increased in the 1960s after closure of the commercial fishery (Pycha and King 1975).

Abundance decreased from the 1970s to the early 1980s with the advent of tribal commercial fisheries and excessive lake trout bycatch in fisheries targeting other species (Hansen et al. 1994b). Stocked lake trout drove trends in abundance prior to 1970, whereas wild lake trout increased erratically from the 1970s to the 1990s (Hansen et al. 1995). Hansen et al. (1995) predicted that lake trout abundance would increase in the late 1990s, as we found, due to effort limitations on the commercial fishery, which would decrease lake trout bycatch and increase lake trout survival.

Wild lake trout recruitment fluctuated erratically from 1980 to 2001, whereas stocked lake trout recruitment declined to low levels before disappearing altogether with the cessation of stocking in 1996. Earlier studies also showed a decline in the survival of stocked lake trout as wild lake trout reproduction increased in the late 1980s (Hansen 1988, 1989; M. J. Powell and J. Atkinson, Ontario Ministry of Natural Resources, unpublished). Hansen et al. (1996) later attributed the decline in stocked lake trout survival in Wisconsin waters between 1963 and 1986 to increased mortality in the commercial fishery, which corresponds to our findings that stocked lake trout commercial fishing mortality increased from 1980 to 1996. The fluctuations without trend in wild lake trout recruitment are due to how we modeled recruitment (i.e., as a series of deviations around a mean value).

Total mortality of wild lake trout declined from 1980 to 2001; an increase in 2000 was caused by increased sea lamprey-based mortality. Pollock et al. (2007) found that stocked lake trout had higher mortality rates than wild lake trout spawning at nearby Gull Island Shoal. Our analysis confirmed that total mortality of stocked lake trout was higher than that of wild lake trout because of higher commercial fishing mortality on stocked fish. Stocked lake trout may have experienced higher fishing mortality than wild lake trout for two reasons. First, stocked lake trout may be distributed inshore, where the commercial fishery is more active, whereas wild lake trout may be distributed offshore, where they experience lower commercial fishing mortality (Krueger et al. 1986; Mattes 2004). Second, less-abundant stocks, like stocked lake trout, within a mixed fishery composed of stocked and wild fish will experience higher fishing mortality than the more abundant stocks (Ricker 1958; Paulik et al. 1967). Natural mortality estimates for wild and stocked lake trout in WI-2 were similar to natural mortality estimates (0.16–0.21) for lake trout in the Michigan management units of Lake Superior (MSC 2005), which suggests that our estimates of natural mortality are plausible.

Management Implications

Our study provides a quantitative description of wild and stocked lake trout populations in eastern Wisconsin waters of Lake Superior. Our results may be informative for managers that deal with similar sources of fishery exploitation and sea lamprey-based mortality in the lower Great Lakes, where lake trout are sustained by hatchery stocking. We found that stocked lake trout were disproportionately more vulnerable to commercial fisheries than wild lake trout, resulting in higher mortality rates on a broad range of age-classes. Great Lakes fisheries managers may want to be more restrictive with commercial fisheries that harvest stocked lake trout by use of large-mesh gill nets. Although the bottlenecks for lake trout recovery in the lower Great Lakes may include many factors besides fishing mortality (e.g., low early-life survival), maintaining sufficient spawning stock biomass of stocked lake trout is a prerequisite for the eventual transition to self-sustaining wild populations, as has occurred in Lake Superior.

By 2001, wild lake trout abundance for WI-2 was on par with precollapse abundance levels. The primary goal for lake trout rehabilitation in Lake Superior is to reestablish self-sustaining populations at precollapse abundance levels (Horns et al. 2003). Pycha and King (1975) used commercial fishery CPUE data from 1929 to 1943 for Michigan management unit 2 (MI-2), which is adjacent to WI-2 (Figure 1), as an index of historic lake trout abundance for Wisconsin waters of Lake Superior because no fishery effort data from Wisconsin are available for that period. Similarly, we compared our predicted large-mesh gill-net survey CPUE with the 1929–1943 average large-mesh gill-net CPUE for MI-2 (Wilberg et al. 2003) to evaluate current and historic abundance levels. We converted our predicted CPUE (fish/305 m of net) to fish per kilometer of net and standardized CPUE to 1.0 net-night using the gill-net saturation curve developed by Hansen et al. (1998) to facilitate comparison. We found that our predicted large-mesh gill-net CPUE for wild lake trout exceeded the historic average of 7.2 fish$\cdot$km$^{-1}\cdot$net-night^{-1} each year from 1999 to 2001.

Wild lake trout recruitment in WI-2 has yet to consistently reach the level thought necessary to sustain a recovering population. The number of recruits produced by the spawning stock is another measure of progress towards the goal of rehabilitating lake trout stocks to historic abundance levels. Hansen (1996) estimated numbers of wild yearling recruits needed to sustain the recovering lake trout population in WI-2. We used the natural mortality rate of 0.12 (Ebener et al. 1989; Hansen 1996), which was used in the recruitment estimate, to calculate the number of wild age-4 recruits needed for sustainability. Our estimated recruitment of age-4 wild lake trout only exceeded the target of 389,231 age-4 recruits in 1987, 1989, 1997, and 1999 but was within 150,000 fish of the target in most other years.

Wild lake trout in WI-2 experienced mortality rates consistent with the recovery of sustainable populations as of 2001. Excessive mortality due to either fishery exploitation or sea lamprey predation would be detrimental to lake trout recovery. Hansen (1996) recommended that total annual mortality for adult lake trout should be less than 45% to promote self-sustaining populations. We found that estimated total mortality for wild lake trout only exceeded this mortality limit in 1987 for age-8+ fish.

By 2001, wild lake trout in WI-2 had made considerable progress towards recovery. Wild lake trout abundance was above the historic average abundance and total mortality was below the recommended limit, but recruitment was still below the level thought necessary for sustainability. We recommend that a stock–recruitment model be developed for WI-2, as has been done for Michigan management units (Richards et al. 2004), to assess factors that are currently affecting wild lake trout recruitment. Such a study would help Wisconsin fisheries managers understand why recruitment is still below target levels and what might be done to improve wild lake trout recruitment.

We believe that improvement of our SCAA models will lead to a better understanding of population dynamics governing lake trout in WI-2 and will allow Wisconsin fisheries managers to better measure population recovery. Two areas of potential improvement are the recreational fishery age distributions in the wild and stocked lake trout models and selectivity functions in the stocked lake trout model. The recreational fishery age distributions would be better estimated if age data could be collected from the angler creel survey. At present, the age distribution for the recreational fishery may be misrepresented by using the age–length key from the large-mesh gill-net survey, which is based on a different sampling gear. The unusual selectivity patterns for the stocked lake trout commercial fishery, recreational fishery, and large-mesh gill-net survey (where a wide range of age-classes is highly vulnerable to the gears) suggest that selectivity might be misspecified. Selectivity may be better estimated using a different function or by allowing one or more of the selectivity function's parameters to vary over time.

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