Modeling the sustainability of lake trout fisheries in eastern Wisconsin waters of Lake Superior

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1. Introduction

Lake trout Salvelinus namaycush were historically important in the Great Lakes as top predators in the fish community and as a predominant species to the fishing industry. Native Americans first harvested lake trout for subsistence and trade, and Europeans developed commercial and recreational fisheries as they settled the Great Lakes basin in the late 1700s and early 1800s (Lawrie and Rahrer, 1972; Goodier, 1989; Hansen, 1999). Commercial fisheries expanded and effort shifted to previously unexploited grounds as stocks were depleted (Lawrie and Rahrer, 1972; Goodier, 1989; Hansen et al., 1995). Beginning in the late 1800s, advances in technology, including steam tugs, motor boats, hydraulic gill-net lifters, and nylon gill nets, made harvest more efficient. Lake trout abundance was already reduced in the lower Great Lakes, Ontario and Erie by 1900, rebounded slightly in the 1920s, only to collapse in the 1930s and 1940s (Christie, 1973; Cornelius et al., 1995; Elrod et al., 1995). Lake trout abundance was also declining in the upper Great Lakes, but yield was sustained through increased fishing effort (Hile et al., 1951; Pycha and King, 1975) until 1935 in Lake Huron, 1943 in Lake Michigan, and 1950 in Lake Superior (Baldwin et al., 1979). The invasion of sea lampreys Petromyzon marinus put even more strain on the already declining lake trout stocks. The combination of overfishing and sea lamprey predation drove lake trout to extirpation by 1962 in all of the Great Lakes except remote areas in Lake Huron and Lake Superior (Berst and Spangler, 1973; Lawrie, 1978; Pycha, 1980).

Fishery managers took steps to preserve and revive remaining lake trout stocks. Although several morphotypes of lake trout...
once occurred in the Great Lakes, rehabilitation efforts focused on the lean lake trout because commercial and recreational lake trout fisheries targeted this morphotype (Eschmeyer and Phillips, 1965; Lawrie and Rahner, 1973; Pycha and King, 1975). Several lake trout populations remained in Lake Superior. Therefore, a rehabilitation plan was developed first for that lake to restore recruitment, reduce total mortality, and sustain reproducing lake trout stocks capable of supporting annual yields of 2 million kg (LSLTTC, 1986; Hansen, 1996). The strategy was to increase recruitment by stocking and to reduce mortality by controlling sea lamprey abundance and regulating fisheries. Rehabilitation in Lake Superior began in 1947 with the stocking of hatchery-reared juveniles (Lawrie and Rahner, 1972, 1973; Lawrie, 1978; Hansen et al., 1995). Chemical control of sea lamprey was implemented in 1958 and helped reduce sea lamprey abundance by 86% in 1962 (Smith et al., 1974). Fisheries for lake trout were closed in 1962 to give lake trout a reprieve from fish-abundance by 86% in 1962 (Smith et al., 1974). Fisheries for lake lamprey was implemented in 1958 and helped reduce sea lamprey abundance by 86% in 1962 (Smith et al., 1974). Management agencies later reopened restricted recreational and commercial fisheries as lake trout stocks began to recover (Hansen et al., 1995). In Wisconsin waters, two refugia were also designated to protect lake trout (Swanson and Swedberg, 1980; Hansen et al., 1995). The Lake Superior Technical Committee (LSSTC) set the sustainable limit of total annual mortality for lake trout at 42%, based on the work of Healey (1978) (LSLTTC, 1986), but how this limit was intended to apply to an age-structured population was not made explicit.

Results of rehabilitation efforts varied among jurisdictions and areas of the lake. Abundance of wild lake trout from unknown parentage generally increased during 1970–1992 (Hansen, 1990; Hansen et al., 1994a,b), but abundance of stocked lake trout decreased despite relatively consistent stocking rates (Hansen et al., 1994a,b). An early stock–recruitment analysis indicated that stocked lake trout contributed to recruitment more than wild lake trout (Hansen et al., 1995), but subsequent analyses indicated that wild and stocked lake trout contributed equally to recruitment in Michigan waters (Richards et al., 2004) and wild lake trout drove recruitment in Wisconsin and Minnesota waters (Corradin et al., 2008). Survival of the 1963–1986 year-classes of stocked lake trout was limited by large-mesh gill-net fishing in Michigan and Wisconsin waters and by wild lake trout predation in Minnesota waters (Hansen et al., 1996). In contrast, survival of wild lake trout during 1970–1998 was not substantially limited by large-mesh gill-net fishing effort in Michigan waters (Richards et al., 2004). Survival of wild and stocked lake trout is likely regulated by different forces because catchability of stocked and wild lake trout differs, possibly due to differences in bathymetric distribution (Krueger et al., 1986). Further analysis of historical and modern lake trout abundance in Michigan waters indicated that wild lake trout stocks were more abundant during 1984–1998 than during 1929–1943 (Wilberg et al., 2003).

Studies suggested that lake trout rehabilitation goals had been met, and stocking was halted in most areas of Lake Superior by March 1996 (Hansen, 1996). However, fisheries must be carefully regulated because lake trout are still in high demand in commercial and recreational fisheries and stock abundance must be accurately estimated to set harvest quotas, which are divided among state agencies and several Lake Superior Bands of Chippewa Indians. Agencies currently set quotas without knowing if the currently accepted 42% total annual mortality rate is sustainable. Our objective was to estimate the maximum sustainable fishing and total annual mortality rates (defined as those rates which will likely not cause extirpation) for lake trout in eastern Wisconsin waters of Lake Superior to address this issue. We developed an age-structured, density-dependent model to simulate long-term effects of various commercial and recreational harvest allocations. The model focused on the wild lean lake trout morphotype because this morphotype is the most highly sought by commercial and recreational fisheries, and because stocking was discontinued in our study area in 1996 and wild lake trout drive recruitment (Corradin et al., 2008).

2. Methods

2.1. Study area

The U.S. and Canadian waters of Lake Superior are divided into lake trout management units (Fig. 1). Our study focused on the eastern Wisconsin management unit known as W12, which has a surface area of 4474 km² and includes the 22 Apostle Islands. This management unit contains two fish refugia: the Gull Island Shoal refuge has a surface area of 336 km², and the Devils Island Shoal refuge has a surface area of 283 km². No commercial or recreational fishing is permitted in the refugia.

2.2. Overview of simulations and basic population model structure

A stochastic simulation model was built to predict future lake trout abundance in the eastern Wisconsin waters of Lake Superior. The simulation model was parameterized using the estimates of abundance-at-age, selectivity, natural mortality, total instantaneous mortality, and fully selected sea lamprey mortality (ages 4–15+²) during 1980–2004 from a statistical catch-at-age (SCAA) model for lake trout in non-refuge portions of the eastern Wisconsin waters of Lake Superior (Linton et al., 2007; Wisconsin State-Tribal Technical Committee, unpublished data).

The simulation model forecasted performance metrics (Section 2.6) for a range of commercial and recreational fishing mortality rates to identify the maximum sustainable fishing and total annual mortality rates. We evaluated (a) the same commercial and recreational fishing mortality rates, (b) a recreational mortality rate near recent levels (0.01), varying the commercial rate, and (c) a commercial mortality rate near recent levels (0.02), varying the recreational mortality rate (Table 1). The simulations included assessment and implementation error (Irwin et al., this issue; Punt et al., 2008), and the sensitivity of the results was evaluated to different values for each source of error. For each set of fishing mortality rates, assessment error, and implementation error, 1000 simulations were run for 200 years.

The initial abundances at age (i.e., in year zero) for each simulation were set based on the results from the SCAA model for 2004. Abundance \( N \) at age \( j \) in each subsequent year \( i \) was then predicted: \[ N_{i+1,j+1} = N_i e^{-Z_i}; \] where \( Z_i \) was the age and year specific total instantaneous mortality rate (the sum of instantaneous natural mortality rate \( M \), the instantaneous sea lamprey mortality rate \( L_{ij} \), the commercial instantaneous fishing mortality rate \( F_{Rij} \), and the recreational instantaneous fishing mortality rate \( F_{Rij} \)). \( M \) was estimated in the SCAA model as a constant for all ages (\( M = 0.1649 \text{yr}^{-1} \); Linton et al., 2007; Wisconsin State-Tribal Technical Committee, unpublished data). \( L_{ij}, F_{Rij}, \) and \( F_{Rij} \) are the product of fully selected mortality rates and selectivity, \( S_{ij} \), \( S_{ij} \), and \( S_{ij} \) (Fig. 2; Linton et al., 2007; Wisconsin State-Tribal Technical Committee, unpublished data), respectively:

\[ L_{ij} = S_{ij} L_{ij+1}, \quad F_{Rij} = S_{ij} F_{Rij}, \quad F_{Rij} = S_{ij} F_{Rij}; \]
Fig. 1. Lake trout management areas in Lake Superior. U.S. management areas are denoted by state: Michigan - MI, Minnesota - MN, and Wisconsin - WI. Canadian management areas are marked using only numbers.

2.3. Sea lamprey mortality sub-model

$L_{Li}$ was modeled as a density-dependent function of lake trout abundance, but at low lake trout densities sea lamprey mortality was held constant:

\[
L_{Li,15+} = \begin{cases} 
\lambda N_{Li,4+}^{-1} e^{\epsilon t} & \text{if } N_{Li,4+} \geq 100,000 \\
0.45 & \text{otherwise}
\end{cases}
\]

(3)

where $\lambda$ was the instantaneous sea lamprey mortality rate when lake trout abundance is zero, $N_{Li,4+}$ was the mean lake trout abundance across all ages weighted by sea lamprey selectivity:

\[
N_{Li,4+} = \sum_{j=4}^{15+} S_j N_{ij} (1 - e^{-Z_j}) / Z_j
\]

(4)

$\epsilon_{Li}$ was temporally autocorrelated process error:

\[
\epsilon_{Li+1} = \rho_i \epsilon_{Li} + \gamma_i; \quad \gamma_i \sim N(0; \sigma^2_i),
\]

(5)

and $\rho_i$ was the level of autocorrelation. The value for $\epsilon_{Li}$ for 2005 was drawn from the stationary distribution:

\[
N \left( 0; \frac{\sigma^2_i}{1 - \rho^2_i} \right).
\]

(6)

The instantaneous sea lamprey mortality rate on age-15+ lake trout was used to calculate the fully selected sea lamprey mortality rate because sea lampreys have been shown to select larger, older fish (Swink, 1991, 2003). The exponent in Eq. (3) was fixed at $-1$ because preliminary attempts to estimate it simultaneously with other parameters resulted in values less than $-1$, which are implausible for a Type-II functional response (Gotelli, 2001). The assumption that the sea lamprey mortality rate was (on average) inversely related to lake trout abundance reflects the biological assumption that individual sea lamprey are saturated and feed at the same maximal rate over the range of lake trout densities, and that sea lamprey abundance will be held relatively constant by population control. This assumption is consistent with available information, but the sea lamprey feeding rate would be expected to decline below some lake trout abundance as they will become encounter rate limited. Consequently, sea lamprey mortality was set to a constant value when lake trout abundance fell below 100,000 (approximately the lowest observed value for $N_{Li,4+}$). This corresponds to an assumption that the number of attacks by individual sea lamprey on lake trout was directly proportional to lake trout abundance at these lower lake trout abundances, similar to a Type-II functional response (Gotelli, 2001). The parameters determining sea lamprey predation ($\lambda$, $\rho_i$, $\sigma_i$) were estimated using a Bayesian approach applied to data from the SCAA for 1983–2004, with uniform priors imposed on all parameters (Appendix A).

Fig. 2. Age-specific selectivity for sea lamprey, the commercial gill-net fisheries, and the recreational angling fisheries for lake trout in eastern Wisconsin waters of Lake Superior during 1980–2004.

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3 The initial values in the first year for other autocorrelated error terms, described below, were defined similarly.
2.4. Stock–recruitment sub-model

Recruitment $N_{i=5,4}$ was modeled using the Ricker stock–recruitment relationship (Ricker, 1975):

$$N_{i=5,4} = \alpha N_{i,8.8} e^{-\beta N_{i,8.8}} e^{\varepsilon_i N}$$

(7)

where $\alpha$ was the number of recruits produced by each spawning adult lake trout at low population abundance, $N_{i,8.8}$ was the abundance of age-8+ lake trout, $\beta$ was the instantaneous decline in recruitment as parental abundance increased, and $\varepsilon_i N$ was temporal autocorrelated process error:

$$\varepsilon_{i+1} = \rho_i \varepsilon_i + \xi_i; \quad \xi_i \sim N(0; \sigma_i^2);$$

(8)

and $\rho_i$ was the level of autocorrelation. Our index of parental abundance assumed knife-edge maturity at age-8. Age-4 lake trout were used to index recruitment because age-4 was the first age-class when lake trout are recruited to large-mesh gill nets, and data were not available to estimate abundance at ages younger than age-4. Recruitment was lagged by five years to account for the time between when age-8+ lake trout spawned and when age-4 lake trout recruited to the gill-net fishery. The parameters ($\alpha$, $\beta$, $\rho_i$, $\sigma_i$) of the stock–recruitment relationship were estimated using a Bayesian approach with uniform priors for all parameters except $\varepsilon_i$ which was assigned a lognormal prior (Appendix A).

2.5. Assessment and implementation error

The simulation model included assessment and implementation error in a manner similar to that of Irwin et al. (this issue) and Punt et al. (this issue). Assessment error was modeled as a year-specific autocorrelation:

$$\tilde{N}_i = N_i e^{\varepsilon_i - \sigma_i^2/2};$$

(9)

where $\tilde{N}_i$ was the assessed abundance with error and $\varepsilon_i$ was the autocorrelated error:

$$\varepsilon_i = \rho_i \varepsilon_{i-1} + \omega_i; \quad \omega_i \sim N(0; \sigma_i^2);$$

(10)

and $\rho_i$ was the level of autocorrelation. Assessment error also affected the target catch that managers set for each fishery because target catches, $\tilde{C}_{Ki}$ for commercial and $\tilde{C}_{RI}$ for recreational fisheries, were set by applying the desired level of fully selected fishing mortality, $\tilde{F}_{Ki}$ and $\tilde{F}_{RI}$, to assessed abundance (i.e., $\tilde{N}_i$) rather than actual abundance. For the commercial fishery:

$$\tilde{C}_{Ki} = \frac{\sum_{j=1}^{15} \tilde{F}_{Kij} \tilde{N}_j (1 - e^{-2 \omega_j})}{\tilde{Z}_{ij}};$$

(11)

where $\tilde{F}_{Kij}$ and $\tilde{F}_{Rij}$ were the product of the desired fully selected fishing mortality rates and $S_{Kj}$ and $S_{Rj}$, respectively, and:

$$\tilde{Z}_{ij} = M + L_j + \tilde{F}_{Kij} + \tilde{F}_{Rij}.$$  

(12)

The fully selected fishing mortality rates that would result in the target catch being removed when applied to actual abundance, $\tilde{F}_{Kij}$ and $\tilde{F}_{Rij}$, were found numerically using Newton–Raphson iterations. We set a maximum on $\tilde{F}_{Kij}$ and $\tilde{F}_{Rij}$ of 3.0 because $\tilde{C}_{Ki}$ and $\tilde{C}_{RI}$ were sometimes unachievable.

Implementation error was included in each fishery as an independent lognormal error:

$$F_{Kij} = S_{Kj} \tilde{F}_{Kij} e^{\varepsilon_i - \sigma_i^2/2}; \quad \tau_i \sim N(0; \sigma_i^2);$$

(13)

where $F_{Kij}$ was the actual commercial fishing mortality rate applied to the actual abundance. Equations and distributional assumptions for the recreational fishery were similar to those for the commercial fishery except that $K$ was replaced by $R$, and the variance defined as $\sigma_r^2$. Actual catch for each fishery, $C_{Ki}$ for commercial and $C_{RI}$ for recreational, was then calculated, e.g.:

$$C_{Ki} = \frac{\sum_{j=1}^{15} F_{Kij} N_j (1 - e^{-2 \omega_j})}{\tilde{Z}_{ij}}.$$  

(14)

For the baseline scenario, $\rho_i$, $\sigma_i$, $\sigma_r$, and $\sigma_{\tau}$ were set to values similar to those for another Great Lakes fishery (Irwin et al., 2008; Table 1). $\sigma_x$ was set to zero for the baseline scenario because we assumed that management actions could effectively limit commercial catch if the target catch ($\tilde{C}_{Ki}$) was reached, but in the actual fishery, catch is usually below the target catch, and so we have no data to support our assertion. The sensitivity of the results to the values chosen for assessment and implementation error was evaluated by running several other scenarios with different values for $\rho_i$, $\sigma_i$, $\sigma_r$, and $\sigma_{\tau}$ (Table 1).

### Table 1

Scenarios that define assessment error ($\rho_i$ and $\sigma_i$) and implementation error ($\sigma_r$ and $\sigma_{\tau}$), and commercial and recreational fishing mortality rates simulated for lake trout in the eastern Wisconsin waters of Lake Superior.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Parameters</th>
<th>Fishing mortality rates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\rho_i$</td>
<td>$\sigma_i$</td>
</tr>
<tr>
<td>Baseline</td>
<td>0.700</td>
<td>0.223</td>
</tr>
<tr>
<td>Scenario 1</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Scenario 2</td>
<td>0.700</td>
<td>0.536</td>
</tr>
<tr>
<td>Scenario 3</td>
<td>0.700</td>
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<tr>
<td>Scenario 4</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Scenario 5</td>
<td>0.700</td>
<td>0.223</td>
</tr>
<tr>
<td>Scenario 6</td>
<td>0.700</td>
<td>0.536</td>
</tr>
</tbody>
</table>

Each scenario of assessment and implementation error was simulated for each combination of fishing mortality rates.

2.6. Performance metrics

Mean abundance, mean catch for commercial and recreational fisheries, mean total annual mortality rate, and probability of decline were the performance metrics used to evaluate the sustainability of (desired) commercial and recreational fishing mortality rates, i.e., values for $F_K$ and $F_R$. Mean abundance $\bar{N}_{4+}$ was the average abundance of age-4+ lake trout over the last 150 years $i$ and simulations $v$:

$$\bar{N}_{4+} = \frac{1}{1000} \times \sum_{i=1}^{1000} \left( \frac{1}{150} \times \sum_{a=4}^{200} \sum_{i=51}^{15} N_{ij} \right)_{v}.$$  \hspace{1cm} (15)

Mean abundance of age-8+ lake trout $\bar{N}_{8+}$, and mean commercial and recreational catch, $C_K$ and $C_R$, respectively, were calculated in the same way over ages, years, and simulations. Total annual mortality rate $A_i$ was calculated using the fully selected sea lamprey and fishing mortality rates for each fishery:

$$A_i = 1 - e^{-(F_{K,i} + F_{R,i})}.$$ \hspace{1cm} (16)

This level of total annual mortality would only occur if fish were fully selected to all three sources of mortality at the same age, which they are not. Consequently, this method over-states the mortality experienced by any given age-group, but will also lead to conservative conclusions about what levels of mortality are sustainable. Mean total annual mortality rate $\bar{A}$ was the average (over simulations) total annual mortality rate over the last 150 years:

$$\bar{A} = \frac{1}{1000} \times \sum_{i=1}^{1000} \left( \frac{1}{150} \times \sum_{a=4}^{200} \sum_{i=51}^{15} A_i \right)_{v}.$$ \hspace{1cm} (17)

The probabilities of decline for age-4+ lake trout, $P_{\text{decl}4+}$, and age-8+ lake trout, $P_{\text{decl}8+}$, were the proportions of the 1000 simulations in which $\bar{N}_{4+}$ or $\bar{N}_{8+}$ was less than the average age-4+ or age-8+ abundance over the last three years included in the SCAA model; 2,747,633 and 1,132,485, respectively. We used these values because lake trout rehabilitation goals for Lake Superior have been met (Hansen, 1996), and we assumed that maintaining abundance near recent levels was desirable. The 95% probability intervals for mean abundance, mean catch for each fishery, and mean total annual mortality rate were calculated using the 2.5- and 97.5-percentiles for the 1000 simulations. A 95% confidence interval was calculated for the probability of decline using the exact upper and lower 95% confidence limits for a binomial proportion (Zar, 1999).

3. Results

Mean performance metrics and probability or confidence intervals were nearly identical to those for the baseline scenario when the parameter determining the extent of variability in implementation error was varied (scenarios 3 and 4; Figs. 3–9). Therefore, the results of scenarios 3 and 4 were not considered any further.

Mean abundance of age-4+ lake trout, $\bar{N}_{4+}$, depended on the scenario and desired fishing mortality rates for each fishery. In the baseline scenario, $\bar{N}_{4+}$ was insensitive to $F_R$ and $F_K$ until $F_K = F_R = 0.70$ yr$^{-1}$ (Fig. 3). For this scenario, $\bar{N}_{4+}$ remained insensitive to $F_K$ until it reached 0.40 yr$^{-1}$, after which $\bar{N}_{4+}$ declined when $F_K = 0.01$ yr$^{-1}$ (Fig. 3). The same result was evident as $F_K$ was varied and $F_R$ was set to 0.02 yr$^{-1}$, but $\bar{N}_{4+}$ only declined once $F_R$ reached 0.40 yr$^{-1}$ (Fig. 3). $\bar{N}_{4+}$ was generally lower when $F_K$ was varied and $F_R$ was set to 0.01 yr$^{-1}$ than when $F_K$ was varied and $F_R$ was 0.02 yr$^{-1}$.

Mean abundance of age-8+ lake trout, $\bar{N}_{8+}$, depended on the scenario and generally decreased as $F_R$ or $F_K$ increased. In the baseline scenario, $\bar{N}_{8+}$ decreased as $F_R = F_K$ was increased (Fig. 4). For this scenario, $\bar{N}_{8+}$ remained insensitive to $F_K$ until it reached 0.02 yr$^{-1}$, after which $\bar{N}_{8+}$ declined when $F_K = 0.01$ yr$^{-1}$. The same result was

![Fig. 3](image-url). Mean abundance of age-4+ lake trout in eastern Wisconsin waters of Lake Superior (with 95% probability interval) for a range of commercial and recreational fishing mortality rates ($F_K$ and $F_R$, respectively, in yr$^{-1}$) and different amounts of assessment and implementation error. Values for the baseline scenario and scenarios 1, 3, and 5 are represented by dashes. Values for scenarios 2, 4, and 6 are represented by dots.
Fig. 4. As for Fig. 3, except the results pertain to mean abundance of age-8+ lake trout.

Mean total annual mortality rate, $\tilde{A}$, depended on the scenario as well as on $\tilde{F}_R$ and $\tilde{F}_K$. $\tilde{A}$ increased to nearly 100% in the baseline scenario as $\tilde{F}_R = \tilde{F}_K$ was increased to 0.70 yr$^{-1}$ (Fig. 5). For this scenario, $\tilde{A}$ remained insensitive to $\tilde{F}_K$ until it reached 0.20 yr$^{-1}$ after which $\tilde{A}$ increased when $\tilde{F}_R = 0.01$ yr$^{-1}$ (Fig. 5). $\tilde{A}$ increased as $\tilde{F}_R$ increased when $\tilde{F}_K = 0.02$ yr$^{-1}$ (Fig. 5). Increases in $\tilde{A}$ were greater
when $\tilde{F}_R$ was set to 0.01 yr$^{-1}$ and $\tilde{F}_K$ was increased, than when $\tilde{F}_K$ was set to 0.02 yr$^{-1}$ and $\tilde{F}_R$ was increased (Fig. 5).

Mean commercial catch, $\bar{C}_K$, and recreational catch, $\bar{C}_R$, also depended on the scenario as well as on $\tilde{F}_R$ and $\tilde{F}_K$ (Figs. 6 and 7). For the baseline scenario, $\bar{C}_K$ increased gradually from zero to a peak when $\tilde{F}_R = \tilde{F}_K = 0.40$ yr$^{-1}$. When $\tilde{F}_K$ was set to 0.01 yr$^{-1}$, $\bar{C}_K$ increased with $\tilde{F}_R$ until $\tilde{F}_K = 0.40$ yr$^{-1}$, after which $\bar{C}_K$ declined. As expected, $\bar{C}_K$ was insensitive to $\tilde{F}_R$ when $\tilde{F}_K$ was set to 0.02 yr$^{-1}$. The lower 95% probability interval for $\bar{C}_K$ included zero for all scenarios and values of $\tilde{F}_R$ and $\tilde{F}_K$. The results for mean recreational catch, $\bar{C}_R$, behaved as expected given changes to $\tilde{F}_K$ (Fig. 7).

The results for the baseline scenario and those with no assessment error (1 and 5) were similar. In contrast, $\bar{A}$ was similar to or higher, and $\bar{N}_{4+}$ and $\bar{N}_{8+}$ were generally lower, than the base-
line values for the scenarios with high assessment error (2 and 6) for all combinations of $\tilde{F}_R$ and $\tilde{F}_K$ (Figs. 3–5). $\tilde{C}_K$ and $\tilde{C}_R$ were generally lower for the scenarios with high assessment error for all combinations of $\tilde{F}_R$ and $\tilde{F}_K$ (Figs. 6 and 7).

The probability of decline for age-4+ lake trout, $P_{\text{dec}4+}$, decreased as $\tilde{F}_R$ or $\tilde{F}_K$ increased, and the extent was scenario-dependent. In the baseline scenario, $P_{\text{dec}4+}$ decreased when $\tilde{F}_R = \tilde{F}_R$ increased to 0.40 yr$^{-1}$, but was higher and, at least 91%, for all other values of $\tilde{F}_R$ or $\tilde{F}_K$ (Fig. 8). When $\tilde{F}_R$ was set to 0.01 yr$^{-1}$, $P_{\text{dec}4+}$ decreased slightly as $\tilde{F}_K$ increased from 0.02 to 0.10 yr$^{-1}$ and increased for higher values of $\tilde{F}_K$. When $\tilde{F}_K$ was set to 0.02 yr$^{-1}$, $P_{\text{dec}4+}$ was insensitive to $\tilde{F}_K$. Results were similar for scenarios with no assessment error (1 and 5), except that $P_{\text{dec}4+}$ was generally less for all combinations of $\tilde{F}_R$ and $\tilde{F}_K$. For scenarios with high assessment error (2 and 6), $P_{\text{dec}4+}$

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**Fig. 8.** As for Fig. 3, except the results pertain to the probability of decline of age-4+ lake trout (with 95% confidence interval).

**Fig. 9.** As for Fig. 3, except the results pertain to the probability of decline of age-8+ lake trout (with 95% confidence interval).
was generally higher than the baseline values for all combinations of $F_R$ and $F_K$ (Fig. 8).

The probability of decline for age-8+ lake trout, $P_{\text{dec8+}}$, increased as $F_R$ or $F_K$ increased, and the extent of increase was slightly scenario-dependent. $P_{\text{dec8+}}$ increased to values equal to or near 100% for all combinations of $F_R$ and $F_K$ above zero for the baseline scenario (Fig. 9). Results were similar for scenarios with no assessment error (1 and 5), while for scenarios with high assessment error (2 and 6) $P_{\text{dec8+}}$ was generally similar to or slightly higher than the baseline values (Fig. 9).

4. Discussion

4.1. Uncertainty and sources of error

This simulation model included assessment and implementation error. Although this is not new (e.g., Eggers, 1993; Frederick and Peterman, 1995; Hilborn et al., 2002), these sources of error have often been ignored in studies evaluating the performance of management strategies (Deroba and Bence, 2008). Studies that searched for levels of fishing mortality (or other parameters required for other control rules, such as abundance thresholds) that perform “optimally” for given objectives while including assessment and implementation error are also rare (Deroba and Bence, 2008). More frequently, control rule parameters, such as levels of fishing mortality, that performed optimally without error are used in simulations with error (Deroba and Bence, 2008). In this analysis, we searched over a discrete range of combinations of desired commercial and recreational fishing mortality rates so that a near-optimal combination of rates could be identified for a given metric. This process should lead to the selection of maximum sustainable fishing and total annual mortality rates that are robust to sources of error and parameter uncertainty we included in our simulations.

We found that each performance metric moved toward an undesirable state (e.g., low mean abundance) for most combinations of fishing mortality rates with an increase in assessment error, implying the need for more conservative strategies, as in other studies (Frederick and Peterman, 1995; Katsukawa, 2004; Deroba and Bence, 2008). The negative effect of assessment error may have been caused by an asymmetric loss function, such that overestimates of abundance that lead to fishing mortality rates higher than desired are more costly than underestimates of abundance that lead to fishing mortality rates lower than desired (Frederick and Peterman, 1995; Deroba and Bence, 2008). Consequently, the decreased mean abundance, catch, and increased probability of decline when abundance is over-estimated and fishing mortality is higher than desired cannot be compensated for when abundance is under-estimated and fishing mortality is lower than desired. Similar to our results, the harvest rate that maximized expected present value (measured in dollars) for Atlantic menhaden Brevoortia tyrannus decreased as assessment error increased (Frederick and Peterman, 1995). Katsukawa (2004) found that control rules more like constant fishing mortality rate were favored and the optimal level of fishing mortality decreased as assessment error increased when the objective was to simultaneously maximize average yield and minimum biomass. Assessment error for the WI2 lake trout fishery has not been formally quantified, but inaccurate catch statistics and the relatively short assessed period on which the SCAA model is based could potentially lead to large amounts of assessment error. Consequently, setting fishing mortality rates at more conservative (i.e., lower) levels might lead to better performance in terms of mean abundance, catch, and probability of decline.

Our simulation model was not sensitive to the level of implementation error, which is consistent with other research on this subject (Sethi et al., 2005). For example, the optimal control rule for maximizing discounted yield was not affected by implementation error, although assessment error interacted with implementation error in the study by Sethi et al. (2005). Our results did not reveal an interaction between assessment and implementation error. One reason may be that Sethi et al. (2005) searched for an optimal control rule and its parameters, whereas we only searched for optimal parameters within a single control rule (i.e., an optimal level of fishing mortality for a constant fishing mortality rate control rule). Had we considered control rules other than constant fishing mortality rate, our results may have been more consistent with those of Sethi et al. (2005).

We attempted to incorporate parameter uncertainty and assessment and implementation error into our simulations, but fisheries are dynamic systems and models are not 100% accurate. Furthermore, our model did not consider all possible sources of uncertainty (e.g., in natural mortality), and the SCAA model on which our simulation was parameterized did not consider time-varying population parameters, such as catchability. Consequently, decisions based on our work may be optimistic, and our analyses should be updated as new information becomes available. Furthermore, our results should be interpreted cautiously because the lake trout fishery in WI2 may be supplemented by the highly productive spawning grounds provided by the refugia in this management unit.

4.2. Summary and management implications

Combinations of fishing mortality rates that resulted in total annual mortality rates near 42% generally reduced mean age-4+ abundance to about 50% of the unfished abundance. Maintaining spawner abundance in the range of 20–50% has been recommended as a way to ensure replacement and attain a large portion of maximum sustainable yield (Quinn et al., 1990; Clark, 1991; Fujikawa et al., 1997; Booth, 2004). So, we conclude that the current 42% total annual mortality rate limit is likely sustainable. To explicitly avoid reaching low spawner abundances, however, managers should also consider placing minimum thresholds on spawner abundance.

We also caution managers against using only age-4+ abundance as a measure of sustainability, because this metric only reflected changes in recruitment and not spawner numbers. For the baseline scenario, mean age-4+ abundances were relatively similar when there was no fishing mortality, when both recreational and commercial fishing mortality increased to 0.40 yr$^{-1}$, and when recreational mortality was held at recent levels and commercial mortality increased to 0.20 yr$^{-1}$. These combinations of fishing mortality rates correspond to total annual mortality rates similar to or greater than the current limit of 42%, which suggests that these rates may not cause a reduction in mean recruitment (Figs. 3 and 4). Mean age-8+ abundance, however, was reduced to 17% of the unfished abundance when both fishing mortality rates were set 0.40 yr$^{-1}$, and 42% of the unfished level when recreational mortality was held at recent levels and commercial mortality increased to 0.20 yr$^{-1}$. So, even though recruitment may remain high at the combination of fishing mortality rates described above, spawner numbers may decline, with the severity of decline dependent on the relative level of commercial and recreational fishing mortality rates. We recommend that management decisions about sustainable levels of total annual mortality rate and fishing mortality rates consider both age-4+ (recruit) and age-8+ (spawner) abundance, that threshold management strategies be considered as a way to avoid low spawner abundance, and that decisions also...
consider the relative level of fishing mortality rates. Furthermore, fishing mortality rates greater than the combinations described above would also generally result in less mean catch and mean total annual mortality rates greater than 74%, and so should be avoided.

Probability of decline from mean age-4+ abundance in the last three years of the SCAA model was 74% or higher for all scenarios and combinations of fishing mortality rates, and 88% or higher for mean age-8+ abundance. In some areas of Lake Superior, abundance in recent years is at or above levels before the fishery collapsed (Wilberg et al., 2003). Therefore, the high probability of decline, even when there is no fishing, may be driven by our selection of thresholds. Probability of decline for mean age-4+ abundance also decreased as fishing mortality rate in one or both fisheries was increased to a threshold where probability of decline then increased. This result occurred because age-4+ abundance reflected increases in recruitment as spawner numbers (age-8+ abundance) declined and moved recruitment toward the dome of the Ricker stock–recruitment relationship. Probability of decline for mean age-8+ abundance, however, increased as fishing mortality rates were increased. This result further supports our recommendation to consider both age-4+ and age-8+ abundance when making management decisions about sustainable mortality rates.

Declines in mean age-4+ and age-8+ abundance and increases in total annual mortality rate were greater when recreational fishing mortality was held near recent levels and commercial fishing mortality was increased compared to when commercial fishing mortality was held near recent levels and recreational mortality was increased. This result suggests that the commercial fishery may have larger effects on the population than the recreational fishery, and ensuring that quotas for the commercial fishery are not exceeded may be crucial for sustainability. This result was likely a consequence of fish entering the commercial fishery at a younger age and remaining slightly more vulnerable at older ages than in the recreational fishery (Fig. 2).

We found that 95% probability intervals for mean age-4+ and age-8+ abundance overlapped with zero for nearly all scenarios and combinations of desired commercial and recreational fishing mortality rates, except when both fisheries were closed. This variability may have been driven by large uncertainty in the parameters of the stock–recruitment and sea lamprey mortality relationships, both of which were based on relatively few years of data over a limited range of lake trout abundances. Uncertainty in these relationships and future management decisions could be reduced through adaptive management techniques, such as passively continuing to collect more data through time, or active experimentation and manipulation of lake trout or sea lamprey abundance (Walters, 1986).

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Appendix A

A.1. Sea lamprey mortality sub-model

The parameters for the sea lamprey mortality sub-model were estimated assuming that residuals about the fit to the data were log-normally distributed:

\[
Q_i = \frac{n}{2} \log_e(\sigma_i^2) + \frac{1}{2\sigma_i^2} \left( \sum_{i=2}^{n} D_i \right); \tag{A1}
\]

where

\[
D_i = \left( \log_e \left( \frac{L_i, 15+}{\lambda N_{i,14+}} \right) - \rho_i \log_e \left( \frac{L_i-1, 15+}{\lambda N_{i-1,14+}} \right) \right)^2 + (1 - \rho_i^2) \left( \log_e \left( \frac{L_i-1, 15+}{\lambda N_{i-1,14+}} \right) \right)^2; \tag{A2}
\]

and \( n \) was the total number of observations (i.e., total number of years) and \( L_{i,15+} \) and \( N_{i,14+} \) were obtained from the SCAA model.

A different set of parameter values was used for each simulation by sampling from the joint posterior probability distribution obtained using Markov Chain Monte Carlo (MCMC) algorithm. One thousand sets of parameter values (i.e., one for each simulation) were generated by running the MCMC chain for 4 million cycles and sampling every 2000th cycle, discarding the first 1000 samples as a burn-in to reduce the effect of the starting values on the MCMC results (Gelman et al., 2004). Trace plots and chain autocorrelation functions were examined to identify any unusual structure in the posterior (Thiebaux and Zwiers, 1984). We also verified that the marginal posteriors for each parameter were not influenced by a long transient by also running a MCMC simulation of 6 million cycles sampled every 3000 cycles, with the first 1000 samples discarded as a burn-in. Lastly, we compared the means of the marginal posteriors with the maximum likelihood estimates (MLEs) to evaluate whether the posterior distributions were sensitive to the uniform priors, which they were not.

A.2. Stock–recruitment sub-model

The parameters of the stock–recruitment sub-model were estimated based on the following negative log-likelihood:

\[
Q_N = \frac{n}{2} \log_e(\sigma_N^2) + \frac{1}{2\sigma_N^2} \left( \sum_{i=2}^{n} D_N \right); \tag{A3}
\]

where

\[
D_N = \left( \log_e \left( \frac{N_{i,5,4}}{\alpha N_{i,8,4}} e^{-\beta N_{i,8,4}} \right) - \rho_N \log_e \left( \frac{N_{i-1,4,4}}{\alpha N_{i-1,8,4}} e^{-\beta N_{i-1,8,4}} \right) \right)^2 + (1 - \rho_N^2) \left( \log_e \left( \frac{N_{i-1,5,4}}{\alpha N_{i-1,8,4}} e^{-\beta N_{i-1,8,4}} \right) \right)^2; \tag{A4}
\]

and \( n \) was the total number of observations.

The prior assumed for the parameter \( \alpha \) was lognormal with mean 2.09 and variance 0.18. The values for the mean and variance of this prior were selected based on results of a stock–recruitment meta-analysis for Salmonidae (Myers et al., 1999).

A different set of parameters was used for each simulation by sampling from the joint posterior probability distribution obtained using the MCMC algorithm with the same characteristics (i.e., chain length, burn-in, etc.) as for sea lamprey mortality. The
same diagnostics (e.g., trace plots, comparison of means from the posteriors to MLEs, etc.) as for sea lamprey mortality were also examined. Recruitment was capped at 1,600,000, about twice that of the highest observed recruitment, to avoid unrealistic values. Although arbitrary, recruitment in excess of this amount occurred in less than 5% of samples from the posterior, so our results are likely robust to the cap.

References


