POPULATION DYNAMICS OF A RECOVERING LAKE TROUT POPULATION
IN WISCONSIN WATERS OF LAKE SUPERIOR, 1980-2001

by

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ABSTRACT

Lake trout *Salvelinus namaycush* were historically important in Lake Superior due to their economic and ecological value. Lake trout populations collapsed in the early 1950s due to overexploitation by the commercial fishery and predation by sea lamprey *Petromyzon marinus*. Efforts to rehabilitate a naturally reproducing lake trout population included stocking of hatchery-reared lake trout, control of sea lamprey populations, and closure of the lake trout fishery. To understand the population dynamics of the recovering lake trout population in Wisconsin waters of Lake Superior between 1980 and 2001, I used statistical catch-at-age analysis to estimate abundance, recruitment, mortality, gear selectivity, catchability, and fishery harvest of lake trout. I found that estimated wild lake trout abundance increased, whereas estimated stocked lake trout abundance decreased. Estimated wild lake trout recruitment was erratic, whereas estimated stocked lake trout recruitment decreased until stocking was discontinued in 1996. Trends in estimated wild lake trout mortality were influenced by sea lamprey mortality, whereas trends in estimated stocked lake trout mortality were influenced by commercial fishing mortality. Estimated wild lake trout commercial fishery harvest declined, whereas estimated wild lake trout recreational harvest increased. Estimated stocked lake trout commercial fishery harvest declined, whereas estimated stocked lake trout recreational fishery harvest remained constant. Wild lake trout abundance should continue to increase and stocked lake trout abundance to decrease within Wisconsin waters of Lake Superior, if survival and recruitment of wild and stocked lake trout remains the same in the future as at present.
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INTRODUCTION

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

Recruitment is the process by which individuals are added to a population, primarily through reproduction. Our understanding of recruitment is based on the assumption that a fish population is limited by density dependent factors such as competition for food, habitat, and spawning grounds (Ricker 1954, 1975). However, recruitment also can be affected by density independent factors such as weather and temperature, which makes recruitment a difficult process to quantify (Ricker 1975). Over-exploitation of adult spawning stocks, known as recruitment overfishing, has led to the collapse of many fisheries (Gulland 1983).

Mortality is the process by which individuals are removed from the population. Mortality often is partitioned into fishing mortality, or deaths due to human removal, and natural mortality, or deaths due to natural causes (Ricker 1975). Fishing mortality often is calculated using the descending limb of a catch curve (Ricker 1975). Data needed to directly estimate natural mortality are difficult to obtain. Therefore, natural mortality is
assumed to be constant or is indirectly estimated by subtracting fishing mortality from total mortality (Ricker 1975).

**Historic Fishery**

Lake trout *Salvelinus namaycush* is a species of great interest to Lake Superior fisheries managers due to the importance of the historic fishery. Lake trout fisheries developed in Lake Superior throughout the 1800s and 1900s as commercial fishermen spread into new fishing grounds (Goodier 1989). The annual harvest of lake trout grew from 0.75 million kg in 1879 to an average annual harvest of 2 million kg from 1913 to 1950, with a maximum harvest of 3 million kg in 1903 (Baldwin et al. 1979). This long term, average harvest suggested that the fishery was sustainable. Yield was actually maintained by increased fishing intensity (Hile et al. 1951) and the adoption of nylon gill nets, which doubled efficiency, while lake trout abundance declined by 50% during the 1940s (Pycha and King 1975).

The appearance of sea lamprey *Petromyzon marinus* further exacerbated the lake trout decline in Lake Superior. The sea lamprey was first recorded in the lake preying upon lake trout in 1953 and reached peak abundance in early 1961 (Pycha and King 1975, Swanson and Swedberg 1980, Pycha 1980). Lake trout stocks soon collapsed due to a loss of older, spawning individuals (Lawrie and Rahrer 1973). Sea lamprey were implicated in the collapse because they preferred to prey on larger, older lake trout (Fry 1953, Fry and Budd 1958, Budd and Fry 1960). Lake trout abundance already was declining by the time sea lamprey invaded Lake Superior (Hile et al. 1951, Pycha and King 1975, Jensen 1978), so the collapse was caused by the combined effects of fishery
exploitation and sea lamprey predation (Pycha and King 1975, Swanson and Swedberg 1980, Pycha 1980). The commercial fishery for lake trout was closed in 1962 as a result of the collapse (Pycha and King 1975).

**Physiology and Behavior**


The three lake trout forms are differentiated by morphological characteristics and habitat distribution. Lean lake trout are slender bodied with pointed snouts, have the lowest body fat content, and inhabit depths less than 70 m (Eschmeyer and Phillips 1965, Pycha and King 1975, Miller and Schram 2000). Siscowets are fat bodied with blunt snouts, have the highest body fat content, and inhabit depths between 50 and 150 m (Eschmeyer and Phillips 1965, Pycha and King 1975, Miller and Schram 2000). Humpers have large eyes, thin abdominal walls, intermediate body fat content, and inhabit isolated reefs surrounded by basins greater than 100 m in depth (Rahrer 1965).

Most research and management has focused on lean lake trout because lean lake trout were the target of the historic fishery and subsequent rehabilitation efforts. Lake trout as old as 42 years have been found in Lake Superior (Schram and Fabrizio 1998),
but individuals may live up to 50 years (Martin and Olver 1980). Lean lake trout mature around age 8 (Dryer and King 1968, Peck and Sitar 2000), and spawn from October to early November (Eschmeyer 1955, Peck 1986, Ebner 1990). Spawning occurs along the main shore and islands at depths of 2 to 40 m (Thibodeau and Kelso 1990). Lean lake trout also spawn on reefs separated from the shore by distances greater than 5 km or by depths greater than 75 m (Hansen et al. 1995a). Adult lake trout primarily eat fish, while juveniles eat invertebrates (Eschmeyer 1956; Dryer et al. 1965, Swedberg and Peck 1984, Conner et al. 1993). Adult lake trout usually are caught within 80 km of the site of marking or release (Eschmeyer et al. 1953, Buettner 1961, Rahrer 1968, Ebner 1990, Peck and Schorfhaar 1991).

**Rehabilitation Efforts**

Efforts to rehabilitate lake trout populations in Lake Superior began soon after stocks collapsed. Fishery managers on Lake Superior outlined the general management goal of developing self-sustaining fish communities, supplemented by stocking where necessary (GLFC 1980). Interagency management goals specific to lake trout were formulated by the Lake Superior Lake Trout Technical Committee (LSLTTC), and were based on the restoration of historic fishery yields (LSLTTC 1986, Hansen 1996). As a result, fish community objectives were developed for Lake Superior, which included goals for lake trout restoration (Busiahn 1990). Lake Superior fisheries managers attempted to meet these goals by stocking hatchery-reared lake trout to bolster natural recruitment, reducing sea lamprey mortality by controlling lamprey abundance, and reducing fishing mortality by regulating fisheries. Progress towards lake trout restoration objectives was reported in state of the lake reports (Hansen 1990, 1994).
Stocking of hatchery-reared lake trout was one of the first actions taken to rehabilitate lake trout populations. Experimental stocking began in 1950 with larger releases following in 1953 (Lawrie and Rahrer 1972, 1973). Ninety-four million lake trout had been stocked in Lake Superior by 1992, of which 88% were yearlings (Hansen et al. 1995a). Yearlings were preferred for stocking because their survival rates were 4-10 times greater than those of fingerling lake trout (Buettner 1961, Pycha and King 1967). Approximately 13.9 million lake trout were stocked in Wisconsin waters of Lake Superior between 1950 and 1992, of which 81% were yearlings (Hansen et al. 1995a).

The restoration plan recommended stocking levels based on historic yield and available habitat (LSLTTC 1986), but actual stocking levels only reached 61% of recommended levels in Wisconsin, which translates to 330,000 fish per year since 1951 (Hansen et al. 1995a). Lake-wide stocking levels in 1960 to 1992, which were between 1.1 and 3.7 million fish per year, were lower than historic, natural recruitment levels of 3.6 to 10.1 million fish per year (Sakagawa and Pycha 1971, Hansen et al. 1995a, Hansen 1996). Lake trout stocking levels in Wisconsin were reduced to 275,900 fish per year in 1989 because of declining survival of stocked yearlings and increased natural reproduction (Hansen 1988, 1989, Powell and Atkinson 1991). Large-scale stocking of lake trout in the WI-2 management unit was halted altogether in 1996.

Sea lamprey control evolved throughout the rehabilitation of Lake Superior lake trout. Electrical weirs were first employed in 1953 to block streams in which adult sea lamprey spawned (Smith et al. 1974), but sea lamprey control was not effective until chemical treatment methods were developed and used. Sea lamprey abundance was reduced by 87% in fall of 1961, due to the treatment of lamprey spawning streams from
1958 to 1960 with the lampricide 3-trifluoromethyl-4-nitrophenol (TFM) (Smith et al. 1974). Sea lamprey abundance averaged 296,000 individuals between 1958 and 1961, and was reduced to an average of 44,000 individuals after control from 1962 to 1992 (Klar and Weise 1994). Sterilization and release of male sea lampreys also is used as an alternative or supplemental form of control (Hanson and Manion 1978, 1980).

Fishery managers have used fishery regulations to reduce lake trout fishing mortality, especially to reduce lake trout by-catch in fisheries for other species. Wisconsin commercial licenses were reduced from 60 to 20 licenses to reduce fishing effort in the 1960s (Blust et al. 1988). The state assessment fishery was limited to a quota of 18,182 kg dressed weight from 1962 to 1970 (Hansen et al. 1995a). Individual gill nets were limited to less than 3,049 m in length and greater than 70 mm stretched mesh, but no limit was set on the total length of net set during a season (Hansen et al. 1995a). Two refuges were established to protect lake trout spawning habitat, one in 1976 at Gull Island Shoal (Swanson and Swedberg 1980), and another in 1981 at Devils Island Shoal (Hansen et al. 1995a). Tribal fishing rights in Wisconsin under the 1842 treaty were affirmed, in State of Wisconsin versus Gurnoe in 1972 (Blust et al. 1988). The state reached an agreement to limit lake trout harvest with the Red Cliff Band of Lake Superior Chippewas in 1981, and with the Bad River Band of Lake Superior Chippewas in 1985 (Hansen et al. 1995a). Quotas for lake trout harvest were 64,300 fish in 1981, 60,000 fish in 1986, 82,000 fish from 1987 to 1990, and 81,200 fish from 1991 to 1995 with the tribal quota split between the two bands (Hansen et al. 1995a). Lake trout by-catch in other fisheries made the 1986-1990 quotas ineffective (Hansen et al. 1995a). As a result, the total length of gill net fished in a year was limited, based on observed catches and

Results from lake trout rehabilitation efforts were mixed. Initial reports showed an increase in wild lake trout abundance, though parentage of the wild fish was unknown (Hansen 1990, Hansen et al. 1994b). Reports also revealed a decline in stocked lake trout abundance despite consistent stocking rates (Hansen et al. 1994a, 1994b). The validity of using historic fishery yield as a goal for restoration was questioned, because historic yield did not account for losses due to sea lamprey and unreported losses by commercial fishermen (Bronte et al. 1995, Hansen 1996). Early stock-recruitment analysis showed that stocked fish had fueled recovery while wild fish had contributed little (Hansen et al. 1995a, 1997a). This finding concerned managers because wild lake trout were expected to support a self-sustaining population as recovery progressed. Hansen et al. (1996) found that lake trout survival was still limited by large-mesh gill net effort in Wisconsin and Michigan waters of Lake Superior. Recent studies in Michigan have shown that wild and stocked lake trout both contributed to recruitment, wild lake trout were twice as reproductively effective as stocked fish, and large-mesh gill net effort no longer limits lake trout survival in Michigan waters of Lake Superior (Doemel 2000). Early studies also revealed that wild lake trout stocks in Michigan waters were less dense and more variable from 1979 to 1993 than they had been historically from 1929 to 1943 (Hansen et al. 1995b). Wilberg (2000) later found that lake trout restoration goals had been met in five of eight Michigan management units, where lake trout catch per unit effort (CPE) from 1984 to 1998 was equal to or higher than 1929 to 1943 CPE. Unfortunately, lake trout were recruitment overfished in six of eight Michigan management units before
1943, which means historic abundance indices do not provide appropriate restoration goals for these areas (Wilberg 2000).

**Research Objective**

My objective was to understand the population dynamics of the recovering lake trout population in Wisconsin waters of Lake Superior between 1980 and 2001 by addressing three questions. First, how has abundance of lake trout changed through time? Second, how has recruitment of lake trout changed through time? Third, how has mortality of lake trout changed through time? To achieve this objective, I used statistical catch-at-age analysis (SCAA) to estimate abundance, recruitment, mortality, gear selectivity, catchability, and fishery harvest of lake trout.
METHODS

Study Site

Lake Superior has a surface area of 82,414 km² and a mean depth of 148 m (Lawrie and Rahrer 1973). The lake has a mean temperature of 6°C (Bennett 1978), approximately 60 mg/L of dissolved solids (Weiler 1978), a mean monthly primary production of 1.6-5.6 mg C/m³/hr (Munawat and Munawar 1978), and an average annual fish yield of only 0.8 kg/ha (Smith 1972). These factors combine to classify Lake Superior as highly oligotrophic.

Wisconsin waters of Lake Superior are divided into two management units (Figure 1). Most fishing activity, stocking, and assessment surveys occur within WI-2. The WI-2 management unit has a surface area of 4,474 km² and includes the 22 Apostle Islands. Shallow, rocky reefs, 3-30 m deep, along the shoreline of both the mainland and islands serve as spawning grounds for lake trout (Coberly and Horrall 1980). 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, and both are closed to commercial and recreational fishing.

Data Collection

Harvest, effort, and age distribution data for recreational, commercial, and assessment lake trout fisheries in the WI-2 management unit of Lake Superior were compiled from records maintained by the Wisconsin Department of Natural Resources (WDNR), and the Red Cliff and Bad River Bands of Lake Superior Chippewas for use in SCAA analysis (Fournier and Archibald 1982; Deriso et al. 1985). Age distribution and
CPE data from two assessment fisheries provided independent estimates of the relative abundance of lake trout in each management area as auxiliary data for use in SCAA analysis (Deriso et al. 1985).

In Wisconsin waters of Lake Superior, the angling fishery was surveyed annually to estimate effort and harvest, whereas state and tribal commercial gill net fisheries were required to report their harvest and effort as part of their license requirements. The WDNR and the Red Cliff Band also randomly monitored state and tribal commercial fisheries. The percentage of wild fish caught in the large-mesh gill net survey was used to estimate separate harvests of wild and stocked lake trout. Age-length keys from the large-mesh gill net survey were applied 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).

Relative abundance of lake trout was indexed with standardized large-mesh gill nets since 1959 in Wisconsin waters of Lake Superior (Hansen et al. 1995a). Fishing was carried out by either commercial contractors or state-owned operators using standardized gill nets of 114-mm stretched-mesh, 210/2 multifilament nylon twine, 18 meshes deep, hung on the 1/2 basis, and fished from late April through early June. Nets were not of uniform length, so CPE was defined as the number of fish caught per 304.8 m of net. Mean large-mesh survey CPE was calculated as a geometric mean. Ages were estimated from scales or otoliths removed from a sample of fish caught in gill nets and then expanded to the entire catch using age-length keys (Ricker 1975; Hansen et al. 1994a, 1995a). Prior to 1988, scales only were collected from all lake trout, whereas after 1988, scales were collected from lake trout shorter than 58.4 cm and otoliths were collected
from lake trout longer than 58.4 cm. Stocked fish were identified by the absence of one or more fins, which were removed prior to stocking. Separate CPE and age distributions were calculated for wild and stocked lake trout.

Relative abundance of lake trout also was indexed with standardized graded-mesh gill nets since 1970 in Wisconsin waters of Lake Superior. The graded-mesh survey was conducted using nets with a mesh range from 38-mm to 178-mm stretched-mesh in 12.7-mm increments, hung on the 1/2 basis, set for 24 hours, and fished from July through August. Multifilament nylon nets were used from 1970 through 1990, and monofilament nylon nets were used from 1991 through the present. The graded-mesh survey was conducted in WI-2 in alternate years beginning in 1980. The CPE was defined as the number of fish caught per 304.8 m of net. Mean graded-mesh survey CPE was calculated as a geometric mean. Lake trout ages were estimated and age-length keys were created as in the large-mesh survey. Separate CPE and age distributions were calculated for wild and stocked lake trout.

**Statistical Catch-at-Age Models**

Separate SCAA models were built for wild and stocked lake trout in the WI-2 management unit of Lake Superior using AD Model Builder (ADMB 2000). The models were used to estimate fishery harvest, abundance, recruitment, mortality, gear selectivity, catchability, and assessment CPE from 1980 to 2001 for lake trout of ages 4 to 15 and older. Parameters were estimated for the non-refuge portion of WI-2. Net lake trout movement between the refuges and the rest of the management unit and between the WI-
management unit and adjacent management units was assumed to be nil (i.e. immigration and emigration were assumed to be similar).

The heart of SCAA analysis is the simultaneous estimation of age-specific fishery harvest and the abundance required to produce that harvest. Commercial fishery harvest was estimated using Baranov’s catch equation (Ricker 1975, Quinn and Deriso 1999):

\[
C_{Cy,a} = \frac{F_{Cy,a}}{Z_{y,a}} N_{y,a} \left(1 - e^{-Z_{y,a}}\right)
\]

Where \(C_c\) is the commercial harvest of age class \(a\) in year \(y\), \(F_c\) was instantaneous commercial fishing mortality of age class \(a\) in year \(y\), \(Z\) was instantaneous total mortality of age class \(a\) in year \(y\), and \(N\) was abundance of age class \(a\) in year \(y\). Age distribution of commercial harvest was estimated as a proportion-at-age by dividing the catch-at-age by the total harvest for the year. Recreational harvest and age distribution were estimated in the same manner. Abundance was estimated using the equation (Ricker 1975, Quinn and Deriso 1999):

\[
N_{y+1,a+1} = N_{y,a} e^{-Z_{y,a}}
\]

Where the parameters are as defined above. To estimate recruitment of the first age class in each year and initial abundance of each age class in the first year, deviations around a mean of zero were estimated for recruitment of the first age class in each year and for each age class in the first year of the model. A population scaling parameter was estimated to scale the deviations to an appropriate population size. In the stocked lake trout model, numbers of age-4 fish were based on the number of yearlings stocked three
years before and the number of fingerlings stocked four years before. Fingerling over-winter survival was assumed to be 40% (Elrod et al. 1988). Survival from age-1 to age-4 was estimated as a yearly deviation around a mean survival, which scaled the number of yearlings stocked to account for age-4 predicted abundance.

Total mortality was partitioned into natural mortality, sea lamprey mortality and fishing mortality:

$$Z_{v,a} = M + M_L + F$$

Where $M$ was instantaneous natural mortality (i.e. assumed constant over all ages and years), $M_L$ was instantaneous sea lamprey mortality of age class $a$ in year $y$, and $F$ was instantaneous fishing mortality of age class $a$ in year $y$. Natural mortality was estimated using Pauly’s equation (Pauly 1980, Quinn and Deriso 1999):

$$\log_e M = -0.0152 - 0.279 \log_e L_\infty + 0.6543 \log_e K + 0.4634 \log_e T$$

Where $L_\infty$ was the maximum length from the von Bertalanffy growth equation (cm), $K$ was the Brody growth coefficient (1/year), and $T$ was the average annual temperature (°C). Sea lamprey mortality was separated from natural mortality due to the impact that sea lamprey had on lake trout abundance (Pycha and King 1975, Swanson and Swedberg 1980, Pycha 1980). Sea lamprey wounding rates were estimated externally to the model using a logistic function (Rutter in press):

$$W_{y,a} = \frac{\theta_y}{1 + e^{-\alpha(1-\beta)}}$$
Where $W$ was the estimated average wounding rate of a lake trout of length $l$ in year $y$, $\theta$ was the average number of observed wounds on large fish in year $y$, and $\alpha$ and $\beta$ describe the rate at which observed wounds reach the asymptote. The logistic model was used to estimate wounding rates because of small sample sizes of large lake trout from which observed wounding rates would be estimated. The wounding rates were then used to estimate sea lamprey mortality externally to the model:

$$M_{l,w} = W \left( \frac{1 - P_l}{P_l} \right)$$

Where $P$ was the probability of surviving a sea lamprey attack as summarized in Greig et al. (1992) from a laboratory study conducted by Swink (1990). Length-specific sea lamprey mortality was converted to age-specific sea lamprey mortality using large-mesh survey age-length keys. Fishing mortality was separated into two components:

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

Where $F_C$ was instantaneous commercial fishing mortality of age class $a$ in year $y$ and $F_R$ was instantaneous recreational fishing mortality of age class $a$ in year $y$. Commercial fishing mortality was estimated using:

$$F_{Cy,a} = S_{Ca} q_c E_C$$

Where $S_C$ was selectivity of commercial gill nets for age-class $a$, $q_C$ was overall catchability of the commercial fishery, and $E_C$ was commercial fishing effort in year $y$. Gear selectivity was estimated with a double logistic function:
$S_{Cz} = \frac{1}{1 + e^{-b_2(a-b_3)}} \left(1 - \frac{1}{1 + e^{-b_2(a-b_4)}}\right)$

Where $b_1$ was the first inflection point of the selectivity curve, $b_2$ was the first slope, $b_3$ was the second inflection point, $b_4$ was the second slope, and $a$ was the age class. The selectivity curve was standardized to the maximum estimated selectivity. Recreational fishing mortality, gear selectivity, and catchability were estimated in the same manner.

The CPE and age distribution for large-mesh and graded-mesh assessment surveys were estimated as:

$U_{L,y,a} = S_{La} q_L N_{L,y,a}$

Where $U_L$ was the large-mesh survey CPE for age class $a$ in year $y$, $S_L$ was the large-mesh survey gear selectivity for age class $a$, $q_L$ was overall large-mesh survey catchability, and $N_L$ was the population abundance at the time of year when the survey was conducted for age class $a$ in year $y$. Gear selectivity was estimated using the double logistic function described above. Large-mesh survey age distribution was calculated as a proportion-at-age, by dividing the age-specific CPE by the total CPE for the year. Graded-mesh survey CPE, gear selectivity, catchability, and age distribution were estimated in the same manner.

Errors in age estimation of lake trout, which affect the observed fishery catch-at-age and assessment age-specific CPE data, were accounted for in the SCAA analysis. An age estimation error matrix was constructed from a WDNR study where the ages of known-age lake trout were estimated. The age estimation error matrix converted the
predicted true age distribution of the fishery harvest and assessment CPE into predicted age distributions that would be seen in the presence of age estimation error.

Parameters and standard errors were estimated using a quasi-Newton iterative algorithm with maximum log-likelihood methods that fit model predictions to observed data. The log-likelihood function was formulated as:

\[ L = \sum_{i=1}^{I} \lambda_i L_i \]

Where \( L \) was the \( i \)th log-likelihood component, and \( \lambda \) was an emphasis factor for weighting the \( i \)th log-likelihood component. Eleven log-likelihood components were included for commercial and recreational fishing effort, harvest, and age distribution; large-mesh and graded-mesh gill net survey CPE and age distribution; and recruitment. The stocked lake trout model also included a log-likelihood component for post-stocking survival. Log-likelihood weighting factors for commercial and recreational fishing effort were set to 0.01 because fishing effort was not directed at lake trout. The log-likelihood weighting factor for large-mesh gill net survey CPE was set to 2.0 to emphasize the index of relative abundance. All other log-likelihood weighting factors were set to a default value of 1.0. Log-likelihood components for commercial and recreational fishing effort were of the form:

\[ L_i = n \log_e \sigma + \frac{0.5}{\sigma^2} \sum_{y=1}^{n} \sigma_y^2 \]

Where \( n \) was the number of years for which parameters were estimated, \( \sigma \) was observed variability in fishing effort, and \( \sigma' \) was the estimated variability in the relationship
between fishing mortality and fishing effort in year $y$. Log-likelihood components for fishery harvest and survey CPE were of the form:

$$L_i = \sum_{y=1}^{n} \left[ \log \sigma_y + 0.5 \left( \frac{0.5}{\sigma_y} \left( \log \frac{X_y}{X'_y} \right)^2 \right) \right]$$

Where $\sigma$ was variability in observed data for year $y$, $X$ was observed total fishery harvest or survey CPE, and $X'$ was predicted total fishery harvest or survey CPE for year $y$. Log-likelihood components for fishery and survey age distributions were of the form:

$$L_i = -\sum_{y=1}^{n} s_y \sum_{a=1}^{m} \left( P_{y,a} + \log_e P'_{y,a} \right)$$

Where $s$ was the sample size of fish that had ages estimated for the observed age distribution data, $m$ was the number of age classes included in the model, $P$ was the observed proportion-at-age of age class $a$ in year $y$, and $P'$ was the predicted proportion-at-age of age class $a$ in year $y$. Likelihood components for recruitment of the first age in each year and abundance of each age in the first year were of the form:

$$L_i = \sum_{x=1}^{Y} \sigma_x^2$$

Where $x$ was the year (for recruitment) or age class (for initial abundance), and $\sigma$ was the estimated deviation used to predict recruitment or initial abundance. In the stocked lake trout model, the likelihood component for post-stocking survival was of the same form as that for recruitment except that $\sigma$ represented yearly deviation around mean survival.
RESULTS

The SCAA models for wild and stocked lake trout converged on optimal solutions. Predictions of fishery harvest, fishery age distribution, survey CPE, and survey distribution for wild and stocked lake trout from the SCAA model were consistent with observed data.

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 33,067 fish in 1980 to 23,860 fish in 2001, with a maximum harvest of 37,007 fish in 1983. Predicted recreational harvest of wild lake trout increased from 1,100 fish in 1980 to a maximum of 14,166 fish in 2001.

For stocked lake trout, commercial fishery harvest declined from 1980 to 2001 while recreational fishery harvest remained relatively constant over the same period (Figure 3). Predicted commercial harvest of stocked lake trout declined from 78,809 fish in 1980 to 7,825 fish in 2001. Predicted recreational harvest of stocked lake trout was highest in 2000 (6,036 fish) and lowest in 1993 (1,941 fish).

Estimated abundance of wild lake trout more than doubled between 1980 and 2001, while estimated abundance of stocked lake trout decreased steadily from 1980 to 2001 (Figure 4). Estimated abundance of age-4 and older wild lake trout increased from 870,568 in 1980 to 2,228,730 in 2001, with a maximum of 2,515,100 in 2000. Estimated abundance of age-4 and older stocked lake trout decreased from a maximum of 730,325 fish in 1980 to 267,639 fish in 2001, with a peak of 598,204 fish in 1998.
Recruitment of age-4 wild lake trout was erratic from 1980 to 2001, while recruitment of age-4 stocked lake trout declined through time with a brief, sharp increase in 1998 (Figure 5). Predicted recruitment of wild lake trout was lowest in 1981 (236,214 fish) and highest in 1999 (816,289 fish). Predicted recruitment of stocked lake trout decreased from 256,364 fish in 1980 to no fish by 1999, with a maximum of 376,585 fish in 1998.

Average annual instantaneous total mortality of wild lake trout declined from 0.4523 in 1980 to 0.2952 in 2001 (Figure 6). Instantaneous natural mortality was estimated as a constant, 0.1893, and made up the largest component of total mortality in every year except 1987 and 2000 when it was surpassed by sea lamprey mortality. Instantaneous sea lamprey mortality declined from a maximum of 0.2675 in 1987 to 0.0180 in 1999 before peaking again to 0.2090 in 2000. Instantaneous commercial fishing mortality declined steadily from 0.0791 in 1980 to 0.0122 in 2001. Instantaneous recreational fishing mortality was the only mortality source to increase from 0.0029 in 1980 to 0.0075 in 2001 but still made up the smallest proportion of total mortality.

Average age-specific instantaneous total mortality of wild lake trout increased with age to an asymptote around 0.37 at age 8 (Figure 7). Instantaneous natural mortality was estimated as a constant, 0.1893, and made up the largest proportion of total mortality across all ages. Instantaneous sea lamprey mortality increased from 0.0097 at age 4 to 0.1749 at age 15 and older. Instantaneous commercial fishing mortality reached a maximum of 0.0756 at age 7 and declined to 0.0141 at age 15 and older. Instantaneous recreational fishing mortality reached a maximum of 0.0105 at age 7 and declined to
0.0020 at age 15 and older. Recreational fishing mortality made up the smallest proportion of total mortality.

Average annual instantaneous total mortality of stocked lake trout was relatively constant from 1980 to 1996, and then declined from 0.5684 in 1996 to 0.3260 in 2001 (Figure 8). Instantaneous natural mortality was estimated as a constant of 0.1893 from 1980 to 2001. Instantaneous sea lamprey mortality declined from a maximum of 0.2675 in 1987 to 0.0180 in 1999 before peaking again to 0.2090 in 2000. Instantaneous commercial fishing mortality was relatively constant from 1980 to 1996, and then declined from 0.2763 in 1996 to 0.0316 in 2001. Instantaneous recreational fishing mortality increased from 0.0071 in 1980 to a maximum of 0.0617 in 1996, and then declined to 0.0190 in 2001.

Average age-specific instantaneous total mortality of stocked lake trout increased sharply from 0.2269 at age 4 to 0.4613 at age 5, and then increased more gradually to 0.6111 at age 15 and older (Figure 9). Instantaneous natural mortality was estimated as a constant 0.1893 from age 4 to age 15 and older. Instantaneous sea lamprey mortality increased from 0.0097 at age 4 to 0.1749 at age 15 and older. Instantaneous commercial fishing mortality increased from 0.0249 at age 4 to 0.2138 at age 5 and then remained relatively constant through age 15 and older. Instantaneous recreational fishing mortality increased from 0.0030 at age 4 to a maximum of 0.0403 at age 13 and then declined to 0.0262 at age 15 and older.

Gear selectivity of wild lake trout exhibited similar trends for the commercial fishery, recreational fishery, large-mesh gill net survey, and graded-mesh gill net survey
Predicted selectivity for commercial and recreational fisheries, and for 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.

Gear selectivity of stocked lake trout exhibited similar trends for the commercial fishery, recreational fishery, and large-mesh gill net survey, but was similar to that for wild lake trout for the graded-mesh gill net survey (Figure 11). Predicted selectivity was highest at age 14 for the commercial fishery, age 13 for the recreational fishery, and age 5 for the large-mesh and graded-mesh gill net surveys. Predicted selectivity was relatively constant after age 5 for the commercial, declined slightly at older ages for the recreational fishery and large-mesh gill net survey, and declined sharply after age 5 for the graded-mesh gill net survey.

Catchability of stocked lake trout was higher than that of wild lake trout for the commercial and recreational fisheries, and the large-mesh and graded-mesh gill net surveys (Table 1). Stocked lake trout catchability was an order of magnitude higher than wild lake trout catchability for the commercial and recreational fisheries and the graded-mesh gill net survey.

For wild lake trout, large-mesh and graded-mesh gill net survey CPE increased from 1980 to 2001 (Figure 12). Predicted large-mesh gill net CPE increased from 1.7542 fish/304.8 m of net in 1981 to 7.2442 fish/304.8 m of net in 2001. Predicted graded-mesh gill net CPE increased from 0.3612 fish/304.8 m of net in 1980 to 0.8521 fish/304.8 m of net in 2001.
For stocked lake trout, large-mesh and graded-mesh gill net survey CPE decreased steadily from the early 1980s to the mid 1990s and peaked in the late 1990s (Figure 13). Predicted large-mesh gill net CPE decreased from 13.5068 fish/304.8 m of net in 1981 to 2.6816 fish/304.8 m of net in 1997, and then increased to 13.7364 fish/304.8 m of net in 1999. Predicted graded-mesh gill net CPE decreased from 2.1036 fish/304.8 m of net in 1980 to 0.3073 fish/304.8 m of net in 1996, and then increased to 2.2703 fish/304.8 m of net in 1998.
DISCUSSION

Wild lake trout abundance increased and stocked lake trout abundance decreased from 1980 to 2001 in Wisconsin waters according to SCAA model predictions, as was found by earlier studies of lake trout population dynamics in Lake Superior. 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 by-catch 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. 1995a). Hansen et al. (1995a) predicted that lake trout abundance would increase in the late 1990s, as I found, due to effort limitations on the commercial fishery, which would decrease lake trout by-catch and thereby 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 noted a decline in the survival of stocked lake trout as wild lake trout reproduction increased in the late 1980s (Powell and Atkins 1991; Hansen 1988, 1989), which corresponded to my findings. 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.

Total mortality of wild lake trout declined from 1980 to 2001, with an increase in 2000 caused by increased sea lamprey mortality. Total mortality of stocked lake trout
was higher than that of wild lake trout because of higher commercial fishing mortality on stocked lake trout. 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 the commercial fishery is less active, and thereby experience lower fishing mortality (Krueger et al. 1986). Second, less abundant stocks, like stocked lake trout, within a mixed fishery composed of stocked and wild fish, experience higher fishing mortality and can be driven to extinction as a consequence (Ricker 1958. Paulik et al. 1967). In support of the second reason, I found that stocked lake trout had higher estimates of catchability than wild lake trout in the commercial and recreational fisheries, which means that a greater proportion of the stocked lake trout population was removed by one unit of fishing effort compared to wild lake trout.

Selectivity for wild and stocked lake trout by commercial and recreational fisheries, and for wild lake trout by large-mesh and graded-mesh gill net surveys all exhibited skew-normal selectivity curves, whereas selectivity for stocked lake trout by commercial and recreational fisheries exhibited logistic curves. Gill net selectivity curves generally follow a normal distribution skewed towards older ages, where old fish are too large to become wedged in the net but are still able to entangle themselves by their teeth or mouth parts (Hamley 1975). For example, Hansen et al. (1997b) found gill net selectivity curves for lake trout in Lake Superior followed a skew-normal pattern. The skew-normal recreational fishery selectivity curve for wild lake trout may represent the actual gear selectivity or it may be an artifact of the large-mesh gill net survey age-length keys used to estimate the recreational fishery age distribution. Differences in
commercial and recreational fishery selectivity curves for stocked lake trout may be caused by changes in age distribution through time. Early ages of stocked lake trout no longer appear in the age distribution data after the cessation of stocking in 1996, thereby making gear selectivity difficult to estimate.

Wild lake trout abundance should continue to increase and stocked lake trout abundance should continue to decrease if survival and recruitment of wild and stocked lake trout remains the same in the future as at present within the Wisconsin waters of Lake Superior. The increase in sea lamprey mortality in 2000 should have no long-term effects on lake trout abundance if sea lamprey mortality continues to decrease in the future. Stocked lake trout will soon disappear from WI-2, though a small population may persist through immigration of stocked lake trout from other jurisdictions. For example, Kapuscinski (2002) found that lake trout immigrate to WI-2 from Michigan and Minnesota management units, perhaps searching for food or spawning habitat. Wild lake trout abundance will continue to increase because commercial fishing effort was limited in 1991 (Hansen et al. 1995a), until the population grows to the point that density dependent factors take effect.

To improve understanding of lake trout population dynamics in the WI-2 management unit of Lake Superior, I recommend that data be collected to develop an age-length key for the angling fishery, a stock-recruitment relationship be developed for wild lake trout, and a probabilistic simulation model be developed for lake trout. The age distribution for the angling fishery would be better estimated if age data were collected from the angler creel survey. At present, the age distribution for the angling fishery may be misrepresented by using the age-length key from the large-mesh gill net survey, which
is based upon an entirely different sampling gear. Stock-recruitment models should be
developed for the WI-2 management unit, as they were for Michigan management units
(Doemel 2000). Stock-recruitment models would provide better estimates of recruitment,
as well as aiding in population projections for setting harvest quotas and evaluating
management strategies. Probabilistic population projection models should be developed,
for use in setting harvest quotas and evaluating management strategies. Stochastic
models are better suited to simulate future abundance, mortality, and recruitment; as
opposed to the deterministic SCAA model I used to estimate historic lake trout
population dynamics.
Table 1. Predicted catchability of commercial fishery, recreational fishery, large-mesh gill net survey, and graded-mesh gill net survey for wild and stocked lake trout in WI-2 management unit of Lake Superior between 1980 and 2001.

<table>
<thead>
<tr>
<th></th>
<th>Commercial</th>
<th>Recreational</th>
<th>Large-mesh</th>
<th>Graded-mesh</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wild</td>
<td>9.79x10^-9</td>
<td>4.58x10^-8</td>
<td>1.00x10^-5</td>
<td>4.00x10^-6</td>
</tr>
<tr>
<td>Stocked</td>
<td>2.76x10^-8</td>
<td>1.48x10^-7</td>
<td>3.70x10^-5</td>
<td>1.30x10^-5</td>
</tr>
</tbody>
</table>
Figure 1. Lake Superior divided into management units. U.S. management units are marked by state: MI, Michigan; MN, Minnesota; WI, Wisconsin. Canadian management units are marked only by numbers.
Figure 2. Observed (solid circles) and predicted (solid line) commercial fishery harvest of wild lake trout, and observed (open circles) and predicted (dashed line) recreational fishery harvest of wild lake trout in WI-2 management unit of Lake Superior between 1980 and 2001.
Figure 3. Observed (solid circles) and predicted (solid line) commercial fishery harvest of stocked lake trout, and observed (open circles) and predicted (dashed line) recreational fishery harvest of stocked lake trout in WI-2 management unit of Lake Superior between 1980 and 2001.
Figure 4. Predicted abundance of age-4 and older wild and stocked lake trout in WI-2 management unit of Lake Superior between 1980 and 2001.
Figure 5. Predicted recruitment of wild lake trout and stocked lake trout represented as abundance of age-4 fish in WI-2 management unit of Lake Superior between 1980 and 2001.
Figure 6. Predicted average annual instantaneous mortality rates of wild lake trout in WI-2 management unit of Lake Superior between 1980 and 2001. Including total, natural, sea lamprey, commercial fishery, and recreational fishery instantaneous mortality. Annual instantaneous mortality rates are averages of age-specific mortality rates for age-4 and older fish.
Figure 7. Predicted average age-specific instantaneous mortality rates of wild lake trout in WI-2 management unit of Lake Superior between 1980 and 2001. Including total, natural, sea lamprey, commercial fishery, and recreational fishery instantaneous mortality. Age-specific instantaneous mortality rates are averages of annual mortality rates.
Figure 8. Predicted average annual instantaneous mortality rates of stocked lake trout in WI-2 management unit of Lake Superior between 1980 and 2001. Including total, natural, sea lamprey, commercial fishery, and recreational fishery instantaneous mortality. Annual instantaneous mortality rates are averages of age-specific mortality rates for age-4 and older fish.
Figure 9. Predicted average age-specific instantaneous mortality rates of stocked lake trout in WI-2 management unit of Lake Superior between 1980 and 2001. Including total, natural, sea lamprey, commercial fishery, and recreational fishery instantaneous mortality. Age-specific instantaneous mortality rates are averages of annual mortality rates.
Figure 10. Predicted gear selectivity of commercial fishery, recreational fishery, large-mesh gill net survey, and graded-mesh gill net survey for wild lake trout in WI-2 management unit of Lake Superior between 1980 and 2001.
Figure 11. Predicted gear selectivity of commercial fishery, recreational fishery, large-mesh gill net survey, and graded-mesh gill net survey for stocked lake trout in WI-2 management unit of Lake Superior between 1980 and 2001.
Figure 12. Observed (solid circles) and predicted (solid line) large-mesh gill net survey CPE of wild lake trout, and observed (open circles) and predicted (dashed line) graded-mesh gill net survey CPE of wild lake trout in WI-2 management unit of Lake Superior between 1980 and 2001.
Figure 13. Observed (solid circles) and predicted (solid line) large-mesh gill net survey CPE of stocked lake trout, and observed (open circles) and predicted (dashed line) graded-mesh gill net survey CPE of stocked lake trout in WI-2 management unit of Lake Superior between 1980 and 2001.


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