This is to certify that the

thesis entitled

Dynamics of Lake Trout (Salvelinus namaycush)
Size and Age Structure in Michigan Waters
of Lake Superior, 1971-1995

presented by

Christopher T. Weeks

has been accepted towards fulfillment
of the requirements for

Master of Science degree in Fish. & Wildl.

James R. Bence
Major professor

Date 12/11/97

O-7639

DYNAMICS OF LAKE TROUT (*Salvelinus namaycush*) SIZE AND AGE STRUCTURE IN MICHIGAN WATERS OF LAKE SUPERIOR, 1971-1995

By

Christopher Todd Weeks

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Fisheries and Wildlife

1997

ABSTRACT

DYNAMICS OF LAKE TROUT (*Salvelinus namaycush*) SIZE AND AGE STRUCTURE IN MICHIGAN WATERS OF LAKE SUPERIOR, 1971-1995

By

Christopher Todd Weeks

Lake trout (*Salvelinus namaycush*) were a native predator species in the upper Great Lakes but were nearly driven to extinction through combined effects of fishery exploitation and predation from sea lamprey (*Petromyzon marinus*). The Great Lakes Fishery Commission was established in 1956 between Canada and the United States to develop coordinated programs of research in the Great Lakes for lake trout restoration and sea lamprey control. Rehabilitation efforts, including stocking, reduced harvest rates, and sea lamprey control, have had some success in Lake Superior, where presently, wild lake trout outnumber stocked lake trout in annual harvest. In addition, survival of stocked lake trout in the lake appears to have been drastically reduced over time. These events, among others, have led to discussions by some fishery managers and researchers on whether lake trout in Lake Superior should now be considered rehabilitated.

To explore the dynamics of wild and stocked lake trout during the recovery period, I developed a statistical catch-at-age model for lake trout in Michigan waters of Lake Superior over 1971-1995, and fit the model to age-length composition data obtained from fisheries and non-fishery based sources, survey catch per unit effort (CPUE), and total harvest. My goal was to obtain a comprehensive assessment of growth, mortality, and abundance. I modeled wild and stocked lake trout independently and compared a

constant growth version of the model to a time-varying growth version. The time-varying growth version showed a significantly better fit to the data than the constant growth version ($P<0.005$) for both wild and stocked lake trout. Estimates of abundance of wild lake trout age-7 and older indicated a decline from 1988-1995. Estimates of total annual mortality of age-7 and older wild fish exceeded 45% each year except 1993 over the same time period. Mortality estimates indicate that fishing was the major source of mortality for lake trout age-5 and older. Based on results from stock assessment models for management unit MI4, if sea lamprey induced mortality is not reduced, and fishing intensity remains at 1990-1994 levels, wild lake trout stocks will continue to decline. These results suggest that lake trout populations in Michigan waters of Lake Superior cannot self-sustain themselves under the mortality rates they experienced from 1990-1994.

This work is dedicated to my dad, Richard,

who by taking a young boy fishing and hunting,

instilled in him the spirit of nature.

ACKNOWLEDGMENTS

I would like to thank the Red Cliff Band of Lake Superior Chippewas and the United States Fish and Wildlife Service (USFWS) Sport Fish Restoration Program for contributing financial support for this research. I would also like to thank members of the Lake Superior Technical Committee for their expertise and advice, particularly Richard Schorfhaar and Jim Peck (MIDNR), Bill Mattes (GLIFWC), and Mark Ebener (COTFMA).

I give my sincere thanks to the faculty of Michigan State University, Fisheries and Wildlife department, and my committee members, Dr. Dan Hayes and Dr. Don Hall, for their insights into biological sciences. I also thank my fellow graduate students, including Darren Benjamin, Kristi Klomp, Ann Krause, and Mike Rutter, for sharing their perceptions, knowledge, and camaraderie. I especially thank my mentors, Dr. Jim Bence and Harry Westers, for their wisdom and dedication to fisheries research, and for helping to point my soul toward a truly meaningful path.

Finally, I cannot nearly express the gratitude and love I have for my wife, Ianthe, and family, Jacob, Chad, and Kendra, for they're faith, love, and support.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Lake trout were dominant predators in Lake Superior but stocks were driven to extinction or extremely low levels in the 1950's through combined effects of fishing and predation by sea lamprey (Pycha and King 1975; Walters et al. 1980). Effective chemical control of sea lampreys, intensive stocking of hatchery-reared lake trout, and a cooperative lake trout rehabilitation plan between state, tribal, and international agencies, have helped restore naturally-reproducing populations of lake trout in most areas of Lake Superior in the 1990's. However, present abundances of inshore stocks are only 50-60% of historic abundances or the rehabilitation goal (Hansen et al. 1995).

Commercial fishing in Lake Superior is thought to have originated along the southern shores of Lake Superior in the 17th and 18th centuries by Native Americans (Nute 1944; Warren 1957). Lake trout harvest was less than 1 million kg in 1879, increased to a peak of 3 million kg in 1903, and averaged 2 million kg per year from 1913 to 1950 (Baldwin et al. 1979). Improvements in gear efficiency and increased fishing intensity in the 1940's and 1950's, combined with invasion of the sea lamprey beginning 1946, caused native lake trout populations to collapse (Pycha and King 1975; Walters et al. 1980; Hile et al. 1951). Management agencies initiated a sea lamprey control program beginning in 1953. Initially mechanical and electrical barriers were used to prevent upstream passage of spawn-run sea lampreys (Lawrie and Rahrer 1973). Sea lamprey abundance peaked between 1958-1961, but dropped 87% in 1962 when the chemical toxicant 3-trifluormethyl-4-nitrophenol (TFM) was proven to be an effective treatment to control sea lamprey abundance (Smith and Tibbles 1980).

Thousands of hatchery-reared lake trout were planted annually into Lake Superior starting 1947 in Ontario, in 1952 for Wisconsin and Michigan, and in 1962 for Minnesota. During the 1960's these fish increasingly dominated inshore lake trout catches, accounting for 95% of the trout taken in most areas (Lawrie and Rahrer 1973). Stocking of lake trout became intensive throughout the 1960's after methods to control sea lamprey became feasible. The commercial fishery for lake trout was closed lake-wide in 1962, and remained closed until the 1970's when abundances began to increase and tribal fishing rights were confirmed (Pycha and King 1975; Hansen et al 1995).

A *Joint Strategic Plan for Management of the Great Lakes Fisheries* (also known as SGLFMP), developed by fishery management agencies and the Great Lakes Fishery Commission (GLFC), called for fish communities based on self sustaining stocks, supplemented by stocking where necessary (GLFC 1980). Objectives for lake trout restoration in Lake Superior were established by an inter-agency plan in 1984-1986 by the Lake Superior Lake Trout Technical Committee (LSLTTC). The plan's long term goal is to achieve a sustainable lake trout yield of 2 million kg per year. The plan also defined management areas within Lake Superior (Figure 1), for reporting, lamprey control, assessment and research, and set protocols for stocking of lake trout and non-native salmonines (LSLTTC 1986).

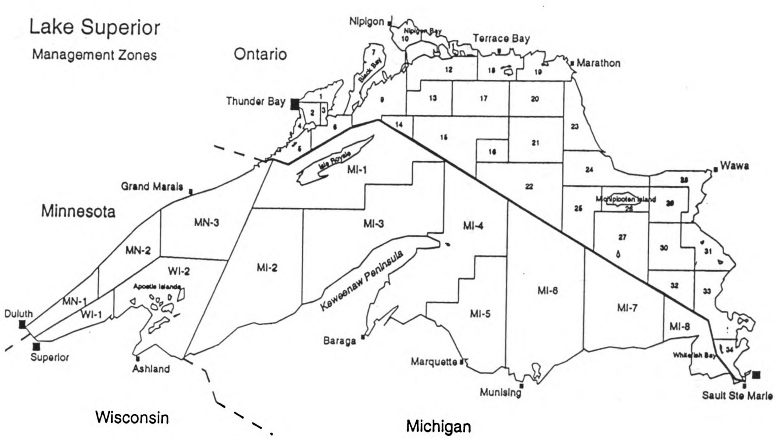


Figure 1. Lake trout management areas in Lake Superior. U.S. management areas are denoted by state: MI, Michigan; MN, Minnesota; WI, Wisconsin. Areas marked by numbers only are in Canadian waters.

Presently in Lake Superior three distinct morphological forms and/or behavioral variants exist; leans, fats (siscowets), and humpers, although increasing evidence suggests that cross-breeding takes place between variants (Burnham-Curtis and Smith 1994; Goodier 1981). Lean lake trout have slender bodies, low body fat, and are characteristic of inshore waters less than 73 meters (40 fathoms) in depth. Siscowets have stout bodies, a high fat content, and are usually found in water deeper than 90 meters (50 fathoms). Humpers have been described as deep bodied with a thin abdominal wall, an intermediate fat content, and have been found isolated above offshore shoals separated by deep water (Rahrer 1965). Lake trout rehabilitation in Lake Superior has emphasized recovery of lean lake trout, referred herein as "lake trout"; however, there are plans to develop fishery and assessment objectives for each of the three lake trout forms historically caught in Lake Superior (GLFC 1996).

Lake trout are slow growing fishes and can be long lived. In Lake Superior, lake trout have been reported to reach maturity between the ages of 6 and 11 (Peck 1979; Ebener 1990; Ferreri 1995). Spawning times and sites differ between variants, but leans normally spawn between late September and early November on gravel beaches and rocky shoals in waters 2-37 meters in depth (Eschmeyer 1955). Some populations of lake trout, possibly now extinct, migrated up tributaries as far as 2 miles to spawn (Loftus 1958). Long range migration of lake trout in Lake Superior is rare; tagging studies of wild and stocked lake trout indicate that most fish remain within a 81 km of release points or planting sites (Pycha et al. 1965; Rahrer 1968; Swansen 1973; Ebener 1990).

The Lake Superior Technical Committee (LSTC) has estimated that a target of

3.6-10.1 million recruits per year is required to achieve the rehabilitation goal of 2 million kg annual sustainable harvest (GLFC 1996). One strategy adopted by management agencies is to limit total mortality to 45% because model simulations of spawner abundance decreased when mortality exceeded 45% but increased when mortality was below that level (GLFC 1996; Technical Fisheries Review Committee 1992). Presently, "Total Allowable Catch" (TAC) models are used by commercial fishery management agencies to set annual harvest rates for individual management districts (Ebener et al. 1989). TAC models project yields of hatchery fish based on total mortality limits, the numbers of fish stocked, and estimated mortality rates. Similar calculations are done for wild lake trout, with wild recruitment estimated from the proportion of wild lake trout caught in assessment surveys.

Questions remain regarding the best management strategies for lake trout in Lake Superior. An important question is whether a total mortality rate of 45% is the optimal level for building and sustaining lake trout populations in Lake Superior. Even with an established target mortality rate, determination of TAC's following previously established procedures requires estimates of survival at young ages and an estimate of the ratio of marked hatchery fish to unmarked wild fish (Ebener et al. 1989). Estimates of early life survival are subject to potential error and are based on limited data. Furthermore, management agencies have decided to discontinue stocking throughout most U.S. waters of Lake Superior because recent analyses indicate that additional stocking of "lean" hatchery fish is doing little to promote restoration (Hansen et al. 1994; Roger Gordon, U.S. Fish and Wildlife, and M. Ebener, Chippewa/Ottawa Treaty Fishery Management

Authority, pers. comm.). Without information on the catch rate of hatchery fish of "known" abundance to calibrate catch rates of native fish, the current method of estimating absolute recruitment of naturalized fish will no longer be feasible. Thus, there is a need to develop estimates of absolute recruitment that are independent of known hatchery releases and estimates of their survival.

The goal of this research was to assess recent population dynamics of lake trout in Michigan waters of Lake Superior in order to provide guidance for managing lake trout populations. The objectives of this project were to:

1. Develop an age/size structured stock assessment model for lake trout in an example area of Lake Superior, designed to be fitted to age and length composition data from the fisheries and other sources, estimates of total fishery removals, and relative indices of abundance (e.g., catch per unit effort from assessment fisheries).
2. Estimate abundance, recruitment, growth, and mortality rates by fitting the model.
3. Estimate the relationship between recruitment and lake trout spawning stock size based on the stock assessment results described under objective two, and use this relationship to evaluate management strategies.

METHODS

Study area

Under the inter-agency lake trout restoration plan, Lake Superior is divided into specific geographic areas for reporting, assessment, and research (Figure 1), which are modified from the statistical districts established by Hile (1962). I examined assessment and creel data from the Michigan Department of Natural Resources (MIDNR), in addition to harvest and biological sampling data from the Great Lakes Indian Fish and Wildlife Commission (GLIFWC) and the Chippewa/Ottawa Treaty Fishery Management Authority (COTFMA) for Michigan waters of Lake Superior, MI2 - MI8. The first step in the model building process was to identify a nominal stock of lake trout subjected to similar recruitment, growth, and mortality rates. Based on data collected from 1980 to the present, stocks within Lake Superior Management zones MI4, MI5, and MI6 were separately, or collectively, a good target population for this study (R. Schorfhaar, Michigan Department of Natural Resources, and W. Mattes, Great Lakes Indian Fish and Wildlife Commission, pers. comm.).

The decision to model MI4, separately, as the initial target population was based on a number of issues. TAC models have reported different estimates of lamprey induced mortality rates across all management areas MI2-MI6 (Ebener et al. 1989). In addition, commercial harvest quotas were established on a management unit basis, and total harvests have been noticeably different over time between management areas (Mattes et al. 1996; Peck and Schorfhaar 1994). Based on mark-recapture of spawning stocks around the Keweenaw Peninsula, Ebener (1990) reported that a greater number of the fish tagged in MI4 were recaptured in MI4 than trout tagged in other units. Finally, the geographic region of Keweenaw Bay suggests that stocks in MI4 are isolated from surrounding areas, and, thus, a likely candidate for being approximated by a closed population model.

Data sources

I compiled data from the Michigan DNR spring assessment 1971-1995, summer assessment 1985-1995, and creel survey 1985-1995, in addition to the commercial fishery harvest and sampling data 1983-1995, for MI4 of Lake Superior. Spring assessments targeting commercial-size (17 inches and greater) lake trout were performed by commercial contractors or state-owned operators in the spring (April-June), using nylon 114-mm (4.5-4.6 in) stretched-mesh gill nets, fished for approximately 3 nights at depths of 20-40 fathoms. From 1971-1987 scale samples were taken from a lake-wide subsample of lake trout with a target of 40 fish per inch group. Ages were determined from the scales and applied to an age-length key to estimate the age-length compositions. From 1988-1994 scales and/or otoliths were taken from all fish sampled for subsequent ageing.

The summer assessment was designed primarily as an assessment of pre-recruit (to fishery) lake trout. They were performed from July-August by Michigan DNR personnel using nylon graded-meshed gill nets (300-ft panels of 2.0-, 2.25-, 2.5-, 2.75-, 3.0-, and 3.5-in stretch-measure mesh), fished approximately 24 hours at depths of 15-40 fathoms. All lake trout caught in the assessments were measured to the nearest 0.1 inch and checked for fin clips and lamprey wounds or scars. Total dressed and round weights were recorded and individual round weights were obtained periodically to evaluate length-weight relationships (Peck and Schorfhaar 1994; Peck and Schorfhaar 1991).

Commercial catch and effort data were obtained from catch reports submitted by commercial fisherman 1983-1995. Fisherman were required to record date of lift, total feet of gill net lifted, material of net, mesh size, location of lift, and pounds of each species caught (in round or dressed weights). Age-length compositions and length-weight relationships were derived from biological monitoring of catches, several times a month by the Bad River, Keweenaw, and Red Cliff Fisheries Departments, and the Great Lakes Indian Fish and Wildlife Commission (Ebener 1986; Mattes et al. 1996). Numbers of lake trout were obtained by dividing the commercial harvest dressed weight by the mean dressed weight per lake trout from commercial samples. Michigan DNR creel survey data 1987-1994 provided the observed recreational harvest. The catch from 1983-1986 was based on the mean recreational harvest from 1987-1989. The mean recreational harvest was approximately 16% of the total harvest and similar size ranges of fish appeared in both fisheries. I concluded that little would be gained from modeling both fisheries independently, and combined recreational harvest with commercial harvest to obtain the observed total harvest.

Data summarization

Catch per unit effort, as an index of relative abundance, and age composition were determined for each year in each data-set. Catch-per-unit-effort (CPUE) was defined as the number of lake trout caught in 1.0 km of gill net. Because net sets varied in duration, CPUE was standardized to net-nights using corrections derived from controlled fishing in 1970. A set of one night duration was the equivalent of 1.00 net-night, two nights duration - 1.52 net-nights, three or more nights duration - 1.80 net-nights (Curtis et al., unpublished manuscript). Hatchery reared lake trout were all fin clipped prior to stocking so distinctions between stocked and wild lake trout were made on the presence or absence of a fin clip. Age compositions and CPUE were determined separately for stocked and wild lake trout. I assumed variation in CPUE was constant for individual lifts; hence year to year variation in CPUE was caused by the number of lifts per year. Observed CPUE and corresponding coefficient of variation (C.V.) of mean CPUE are listed in tables (4 and 5) for the spring and summer assessments. To reduce model complexity, I also assumed that assessment data came from simple random samples. I realize, however, that assessments may be more systematic than random because they may target areas where fish tend to be caught. Also, weather conditions often dictate when assessments can be conducted. Treating individual gill net sets from spring and summer assessments as random samples, however, may lead to biased estimates of variances for CPUE, and the CPUE index itself, depending on the extent and nature of spatial correlation (see Discussion: *Suggestions for future research*).

Both the spring assessment and commercial sampling were inconsistent in reporting undersized lake trout (less than 17 inches). According to W. Mattes (pers.comm.), fish less than 17 inches are not included in total harvest reports. Where applicable, I subtracted the CPUE of fish less than 17 inches from the total survey CPUE to include only larger fish in observed CPUE.

Age-length compositions were calculated in two ways depending on data sources. For the spring assessment and the commercial fishery, length-classes started with a length of 17 inches (43.2 cm), and spanned over 2 inch length bins. Since all fish caught in both the commercial fishery and the spring assessment were age-3 or older, proportions of lake trout less than age-3 were set to zero. For summer assessments catches of fish less than 9 inches were combined as were fish greater than 24 inches; fish between 9-24 inches were grouped in one inch intervals.

Population assessment model

The lake trout population assessment model for MI4 was similar to the "stage 2" stock synthesis model developed by Methot (1990), although I developed my own model application using *Excel* version *5.0* software. This model is an implementation of the statistical catch-at-age analysis (SCAA) and incorporates auxiliary information from different sources. This approach models the age structure of the population but defines fishery selectivity patterns as explicit functions of length. In essence, this model simulates the population dynamics, fishery and data collection processes, and estimates a suite of parameter values so that the model produces the best possible match with observed quantities. Advantages of this modeling approach for lake trout in Lake Superior are:

- SCAA models integrate fishery assessment age composition data to estimate patterns of removals of the population and provide information on year-to-year recruitment (Fournier and Archibald 1982; Deriso et al. 1985; Methot 1990).
- Modeling selectivity as a function of length rather than age has the potential to reduce bias associated with time varying growth rates.
- Wild and stocked lake trout populations can be modeled independently of one another by estimating recruitment of both wild and stocked fish during model fitting.

Model description

The MI4 lake trout assessment model is a cohort survivorship model applied over a time series (1971-1995), based on data collected from assessment and fishery harvest information, and adapted to both wild and hatchery-reared stocks. Abundance estimates of age-1 fish to a cohort represent recruitment from either natural reproduction or numbers of "viable" stocked yearlings and are parameters directly estimated during the model fitting. The model predicts the numbers-at-age surviving to the following year and keeps track of each cohort throughout the time series. A growth submodel estimates mean total length and dynamically tracks changes in length over time. Auxiliary sources of data are modeled independently based on selectivity patterns as specific functions of length, rather than age, to assess time-varying growth affects. The model addresses bias associated with errors in ageing techniques by transforming true age compositions to what quantities. Advantages of this modeling approach for lake trout in Lake Superior are:

- SCAA models integrate fishery assessment age composition data to estimate patterns of removals of the population and provide information on year-to-year recruitment (Fournier and Archibald 1982; Deriso et al. 1985; Methot 1990).
- Modeling selectivity as a function of length rather than age has the potential to reduce bias associated with time varying growth rates.
- Wild and stocked lake trout populations can be modeled independently of one another by estimating recruitment of both wild and stocked fish during model fitting.

Model description

The MI4 lake trout assessment model is a cohort survivorship model applied over a time series (1971-1995), based on data collected from assessment and fishery harvest information, and adapted to both wild and hatchery-reared stocks. Abundance estimates of age-1 fish to a cohort represent recruitment from either natural reproduction or numbers of "viable" stocked yearlings and are parameters directly estimated during the model fitting. The model predicts the numbers-at-age surviving to the following year and keeps track of each cohort throughout the time series. A growth submodel estimates mean total length and dynamically tracks changes in length over time. Auxiliary sources of data are modeled independently based on selectivity patterns as specific functions of length, rather than age, to assess time-varying growth affects. The model addresses bias associated with errors in ageing techniques by transforming true age compositions to what we expect to see in the harvest or surveys. Harvest, effort, and age-length composition estimates are compared to observed quantities using a maximum likelihood approach. A numerical search is done for the set of parameter estimates that maximizes the likelihood.

Abundance

Numbers at age (*a*) and year (*y*) of the population were determined by the exponential mortality equation:

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

where Z was the instantaneous mortality rate equal to the sum of natural mortality (MO) plus lamprey mortality (ML) plus fishing mortality (F):

$$Z_{a,y} = MO_{a,y} + ML_{a,y} + F_{a,y} \tag{2}$$

Abundance at ages 2-15 in 1972-1995 were calculated from equation (1). Recruitment (the number of age-1 fish), and initial abundance at ages 2-7 for wild fish (ages 2-8 for stocked fish) in 1971 were parameters estimated during the model fitting. Abundance of wild lake trout older than age-7 and stocked lake trout older than age-8 in 1971 were set equal to zero, reducing the number of parameters required by the model, justified by the small percentages of older lake trout caught in spring assessments in the 1970's. Recruitment estimates of stocked fish were compared to the actual number stocked to assess survival of hatchery-reared lake trout.

Mortality 1983-1995

The model calculated age-specific total instantaneous mortality from equation (2), and also calculated age-length stratified values for mortality in 1983-1995 by:

$$Z_{a,y,l} = MO_{a,y} + ML_{a,y} + f_y S_l \quad (3)$$

where f_y was fishing intensity in year y and S_l was the length specific selectivity of the commercial fishery. Values for $Z_{a,y,l}$ were required to determine harvest age-length compositions comparable to observed values from commercial sampling data.

Natural mortality

I defined natural mortality (*MO)* as the mortality experienced by the population in absence of fishing and sea lampreys. I assumed natural mortality did not vary over the time period 1983-1995 for both wild and stocked fish, and I used the age-specific values of *MO* reported by Sitar (1996) , estimated from a SCAA model of lake trout in Lake Huron (Table 1).

Fishing mortality

Projections of abundance at age required age specific fishing mortality ($F_{a,y}$), while predictions of age-length compositions of the harvest required estimates of length specific mortality ($F_{y,l}$). Fishing mortality was calculated in terms of length categories and then converted to a function of age:

$$F_{y,l} = f_y S_l \quad (4)$$

Table 1. Age-specific natural mortality rates (MO) used in the population assessment model for MI4 of Lake Superior. Values were estimated by Sitar (1996) using an SCAA model for lake trout in Lake Huron.

Age	MO	Age	MO
1	0.6663	9	0.1001
2	0.3184	10	0.1000
3	0.1716	11	0.1000
4	0.1235	12	0.1000
5	0.1077	13	0.1000
6	0.1025	14	0.1000
7	0.1008	15	0.1000
8	0.1003		

$$F_{a,y} = \frac{\Sigma_l F_{l,y} N_{a,y,l}}{\Sigma_k \Sigma_l N_{k,y,l}} = f_y \Sigma_l S_l P_{a,y,l} \qquad (5)$$

where a was the target age in the range of age-classes (k), and $P_{a,y,l}$ was the proportion of fish in age class, a, length class, l, and year, y. The model calculated selectivity values for each source using a gamma-type function described by Deriso et al. (1985):

$$S_l = \frac{l^{\alpha} e^{\beta l}}{\max_j(j^{\alpha} e^{-\beta j})} \qquad (6)$$

where l was the midpoint of the length bin, α and β are selectivity coefficients estimated during the model fitting, and max_j (...) selects the length category (j) that maximizes the function and defines the length category with a selectivity equal to 1.0.

Lamprey mortality

I used spring assessment data on lamprey wounding rates to estimate instantaneous lamprey-induced mortality rates from a submodel in the Lake Superior lake trout TAC model (Ebener et al. 1989). Mean wounds per fish were calculated by:

$$\bar{W}_{i,y} = \frac{\Sigma W_{i,y}}{n_{i,y}} \tag{7}$$

where $W_{i,y}$ was the number of wounds recorded per fish of length-class (i) in year (y) and $n_{i,y}$ was the number of fish sampled. Lamprey-induced mortality rates were determined from Eshenroder and Koonce (1984):

$$ML_{i,y} = \bar{W}_{iy} \left[\frac{1 - P_{S\,i}}{P_{S\,i}} \right] \tag{8}$$

Probabilities of survival from a sea lamprey attack, $P_{S\,i}$, were reported by Grieg et al. (1992): 0.35 for 432-533 mm lake trout, 0.45 for 534-635 mm lake trout, and 0.55 for 636 mm or greater lake trout. Length specific mortality rates were converted to age specific mortality rates by:

$$ML_{a,y} = \sum_i \frac{n_{a,i,y}}{\sum_j n_{a,j,y}} ML_{i,y} \tag{9}$$

where *i* is the target length-class in the range of length-classes (*j*) (Ebener et al. 1989).

The lamprey submodel assumes that the wounds per fish from spring assessments were representative of attacks that occurred the previous year, and that lamprey-induced mortality was the same for both wild and hatchery-reared lake trout (Ebener et al. 1989).

Mortality 1971-1982

The period 1971-1982 differs from later years in that neither harvest, commercial sampling, nor summer assessment data were available. Over this time series the model relied entirely on spring assessment information. Simulation trials using the relationships described in equations (2) and (3) failed to predict mortality events required to match large fluctuations in observed abundance from spring assessments. I therefore combined the effects of *MO* and *F* together into a new parameter (Z_{MF}) for the fishable population, and allowed the model to estimate Z_{MF} over specified time intervals from 1971-1982 to best match the spring assessment CPUE:

$$Z_{a,y} = Z_{MF\,a,y} + Zl_{a,y} \tag{10}$$

Values of Z_{MF} for ages 1-4 were constant and equal to the natural mortality values used in the later years because these fish were too small to be caught in significant numbers by the fishery. Z_{MF} estimates for ages 5-15 were grouped into periods of equivalent mortality rates during simulation trials based on two objectives: (1) annual mortality rates were combined for as many years as possible in attempt to reduce the number of parameters required by the model, and (2) spring assessment CPUE estimates fitted by the model peaked in close approximation to observed values.

Growth

Mean length at age for age-1 fish in 1971-1995 and ages 2-15 fish in 1971 was determined by the von Bertalanffy equation:

$$\bar{L}_{1,y} = L_{\infty y-1} \; (1-e^{-k(1-t_0)}) \tag{11}$$

Mean length for ages 2-15 in 1972-1995 were calculated by adding growth predicted by the von Bertalanffy equation in incremental form to the mean length of that cohort:

$$\bar{L}_{a,y} = \bar{L}_{a-1,y-1} + (L_{\infty y-1} - \bar{L}_{a-1,y-1}) \; (1-e^{-kt}) \tag{12}$$

k and t_0 were growth parameters estimated by the model, and t was set at 1 year. Values of L_∞, theoretical maximum length, represented yearly growing conditions and were estimated during the model fitting process. Thus, a large estimated L_∞ represented favorable growing conditions and a larger incremental growth rate than a smaller L_∞. If predicted growth increments from equation (12) were less than zero, an increment of zero was used. I also modeled growth using time-varying values of k rather than L_∞, but this did not improve the model fit.

Age-length compositions

The proportion of the population ($P_{a,y,l}$) of age (a) in length class (l) and year (y) was based on a normal distribution about the mean length for that age. I assumed a constant coefficient of variation in lengths about their age specific mean (Ricker 1975), and the CV was estimated during the model fitting. Proportions falling in specific length categories (described in the section titled *Data summarization*) were then calculated from a normal cumulative distribution function.

Survey estimates

The model predicted abundance at age of the population at the beginning of each year (Equation 1) and followed the numbers surviving to the appropriate time interval of both spring and summer assessments by:

$$N_{a,y+t} = N_{a,y}\, e^{-(Z_{a,y})t} \tag{13}$$

Abundance at time $t = 0.3$ estimated the size of the population at approximately the midpoint of the spring survey (May 15th), and abundance at $t = 0.59$ represented the population at the midpoint of the summer survey (August 2nd). Numbers at age in a given length class were calculated as:

$$N_{a,y+t,l} = N_{a,y+t}\, P_{a,y,l} \tag{14}$$

$N_{a,y+t,l}$ values were multiplied by the appropriate selectivity function estimates (Equation 6) to predict the age-length compositions expected in the assessments:

$$n_{a,y+t,l} = N_{a,y+t,l}\, S_l \tag{15}$$

Where necessary, these values were transformed to coded age-length compositions to predict observed data (see later section titled *Aging error*). Proportions were then determined by:

$$p_{a,y+t,l} = \frac{n_{a,y+t,l}}{\sum_l \sum_k n_{k,y+t,l}} \tag{16}$$

Spring and summer assessment CPUE's were estimated by multiplying survey age-length compositions by catchability, q, and summing over all ages and lengths:

$$K_y = q \sum_l \sum_a n_{a,y+t,l} \tag{17}$$

<u>Harvest estimates</u>

Numbers at age in the beginning of the year (Equation 1) were multiplied by the age-length proportions in the population, $P_{a,y,l}$, using equation (14) to obtain age-length compositions, $N_{a,y,l}$, in the population. Harvest at age and length was determined by the Baranov catch equation:

$$C_{a,y,l} = \frac{F_{y,l}}{Z_{a,y,l}} \left(N_{a,y,l} - N_{a,y,l} e^{-Z_{a,y,l}} \right) \tag{18}$$

where $Z_{a,y,l}$ was determined from equation (3), $F_{y,l}$ from equation (4). Total harvest was obtained by summing the age-length composition of the harvest over all ages and lengths:

$$C_y = \sum_l \sum_a C_{a,y,l} \tag{19}$$

Fincodes were used to age hatchery-reared lake trout from 1984-1989; all remaining harvest estimates required ageing error transformations to coded ages of harvest.

Proportions of the harvest age-length compositions were determined after ageing error (if required):

$$p_{a,y,l} = \frac{c_{a,y,l}}{C_y} \tag{20}$$

Ageing error

Ageing techniques used by assessment and commercial fishery management personnel are listed in Table (2). Beginning in 1989 ageing methods changed from scales only, to scales for fish less than 23 inches and otoliths for fish 23 inches and greater, based on Johnson and MacCallum's (1987) results that lean lake trout older than age-8 were not growing sufficiently to form annuli on scales. I examined 1993-1995 assessment data collected across all Michigan management units and compared the recorded ages of lake trout aged independently by two or more different methods: scales, otoliths, and fincodes. From these data I constructed a combination of ageing error transition matrices used by the model, relating true ages (fincoded) to coded ages (recorded age by either scale or otolith method) in attempt to reduce bias associated with ageing error.

The first matrix was applied to wild lake trout over the period 1971-1988, prior to the use of otoliths (Appendix). The probability that a fish of true age ($P_{t\,a}$) was coded age c was based on a normal distribution described by the standard distribution about the mean coded age for ages 4-8. For example, for a fish with a true age of 4, the probability that it was correctly coded as age-4 was taken as the probability the fish was aged between 3.5 and 4.5, based on the distribution of recorded ages from scale readings of

Table 2. Methods used to age samples of lake trout from MI4 of Lake Superior by Michigan DNR assessments and commercial sampling from 1971-1995.

Sampling source	Period	Lake trout type	Ageing Method	Reference
Michigan DNR	1971 - 1995	Stocked	Fincodes + subsamples of scales and otoliths	Peck and Schorfhaar (1994)
	1971 - 1988	Wild	Scales	
	1989 - 1995	Wild < 23 in.	Scales	
		Wild 23+ in.	Otoliths	
Commercial	1984 - 1989	Stocked	Fincodes	M. Ebener (pers.comm.)
	1984 - 1989	Wild	Scales	
	1990 - 1995	Any < 23 in.	Scales	B. Mattes (pers. comm.)
		Any 23+ in.	Otoliths	

age-4 fincoded lake trout caught in spring assessments. Sample sizes for true ages above 8 were small or non existent, so probabilities were based on a normal distribution about the coded age obtained from a linear regression of mean coded ages to true ages (Figure 2) and a standard distribution of 1.25, the mean standard deviation for fincoded ages 9-15 for which data existed.

The second matrix transformed true ages to coded ages for wild lake trout and commercial samples of stocked lake trout in 1989-1995. This matrix was identical to the first matrix through age-8. For ages 9 and above, probabilities are based on a normal distribution about the coded age obtained from a linear regression of mean otolith age to fincode age and a standard distribution equal to that for an 8 year old fish (σ = 0.82) (Figure 3). The transition matrices converted estimates of numbers at true age to an expected coded age by:

$$n_{a,\,y+t,\,l}\, x\ T_a = c_{a,\,y,\,l} \tag{21}$$

where $n_{a,\,y+t,\,l}$ was the estimated true age-length composition in year (y) from assessments

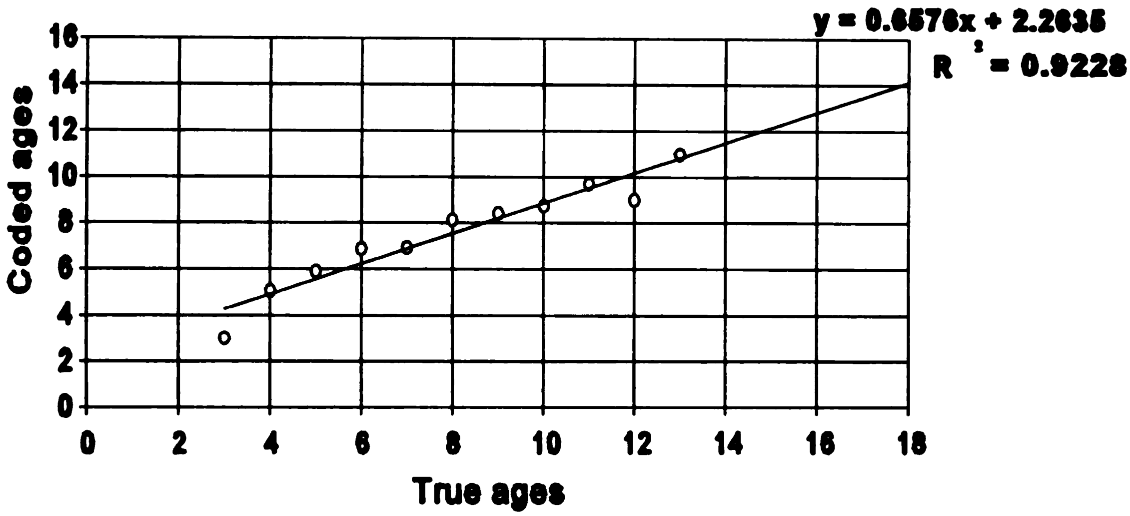


Figure 2. Linear regression of mean coded ages from scales to fincoded (true) ages of lean lake trout caught in the spring assessment in Michigan waters of Lake Superior from 1993-1995. Data from Michigan Department of Natural Resources.

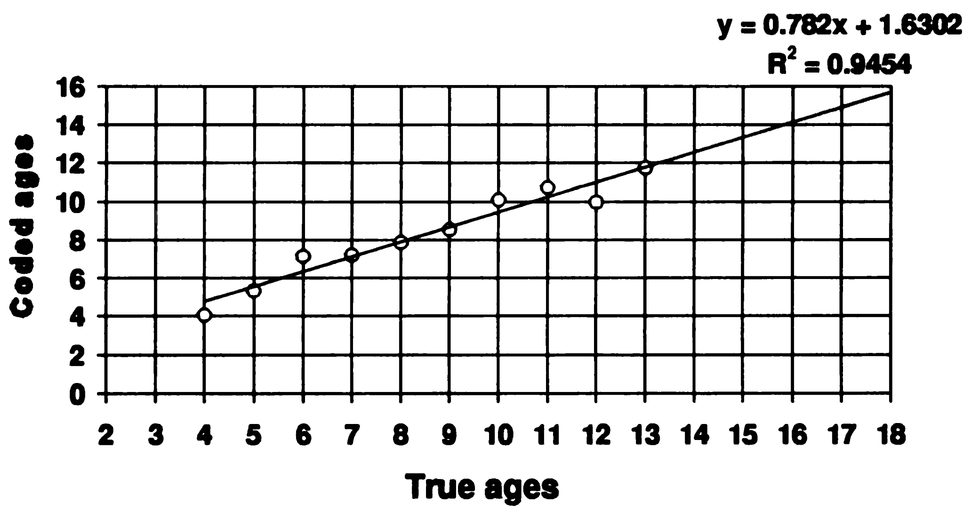


Figure 3. Linear regression of mean coded ages from otoliths to fincoded (true) ages of lean lake trout caught in the spring assessment in Michigan waters of Lake Superior from 1993-1995. Data from Michigan Department of Natural Resources.

or harvest, T_a was the ageing error transition matrix containing individual P_{ta}'s, and $c_{a,y,l}$ was the coded age-length composition in year (y). For the commercial harvest age compositions, $C_{a,y,l}$ (Equation 18) can be substituted for $n_{a,y,l}$ in equation (21) to obtain observed coded age predictions in the harvest.

Objective function

The MI4 lake trout model estimated a suite of parameter values describing the population dynamics and compared observed values to the model's expected values using a log-likelihood approach similar to that of Methot (1990). The objective function was sum of the log-likelihoods from each of the model's components:

$$L_{max} = L_1 + L_2 + L_3 + L_4 + L_5 + L_6 \tag{22}$$

where L_1 and L_2 were the likelihood functions for the spring and fall assessment CPUE, respectfully, L_3 was the total harvest, L_4 and L_5 were the age-length compositions of the spring and summer assessments, and L_6 was the age-length composition of the harvest. This objective function was maximized by forward differencing of parameters in log-space using a quasi-Newton algorithm.

The model assumed log-normal distributions for assessment CPUE and total harvest. Log-likelihood components L_1 , L_2, and L_3 were calculated from:

$$L = -0.5 \sum_y \frac{\left[\ln\left(\frac{\lambda_y}{\lambda_y'}\right)\right]^2}{\sigma_y^2} + \ln\left(\frac{1}{\sigma_y\sqrt{2\pi}}\right)^N \tag{23}$$

where λ_y was the predicted assessment CPUE and total harvest in year y (K_y and C_y respectively), λ'_y was observed assessment CPUE and total harvest in year y, and σ_y was the assessment CPUE and total harvest standard error on a log-normal scale in year y. Values for σ were calculated from the coefficient of variation from each data source (Law and Kelton 1982) using:

$$\sigma = \sqrt{\ln[(C.V.)^2 + 1]} \tag{24}$$

The model assumed that the C.V. of the total harvest was constant and based on a 1% error in the reporting of true harvest (C.V. = 0.01).

Likelihood functions for assessment and harvest age-length compositions, L_4, L_5, and L_6, were calculated from a multinomial error structure:

$$L = \Sigma_y J_y \Sigma_a \Sigma_l p'_{a,y,l} \ln(p_{a,y,l}) + \Sigma_y \ln\left(\frac{J_y!}{n_{a,y,l}!\, n_{a+1,y,l}! \ldots n_{j,y,l}!\, n_{a,y,l+1,}! \ldots n_{a,y,k}!}\right) \tag{25}$$

where $p_{a,y,l}$ was the estimated proportions of age-length compositions in assessments and harvest and $p'_{a,y,l}$ was observed proportions. Also in equation (25): J was the effective sample size, n was the age-length composition, j was the number of age classes, and k was the number of length classes, all observed in the assessments and commercial biological sampling. Effective sample sizes were set to a maximum of 100 individuals so that large sample sizes would not dominate the model's fit (Fournier and Archibald 1982).

Model simulation

The MI4 model was adapted to assess wild and hatchery-reared lake trout independently and compare constant growth to time-varying growth. Simulation one, the reduced model, assumed a constant growth rate described by a single estimate of L_∞ over the entire time series. The constant growth (CG) model required 24 less parameters (yearly L_∞ values) than the second simulation, the time-varying growth (TVG) model. I used the likelihood ratio test statistic: $2[L(\hat{\theta}) - L(\theta_0)]$, to compare the fit of both models to observed data (Seber and Wild 1989). In this test, $L(\hat{\theta})$ and $L(\theta_0)$ were the total log-likelihood values (L_{max}) from the time-varying growth and constant growth models, respectfully.

RESULTS

The time-varying growth versions of both wild and stocked lake trout models fit data significantly better than the constant growth versions ($P<0.005$ for both). Temporal patterns in mortality and recruitment were similar between the TVG and CG versions, except for larger peaks in recruitment in the late 1970's and in mortality between 1981-1982 for the CG versions of both wild and stocked lake trout models. I conclude that the driving force behind the differences between the CG and TVG models were responses to peaks in observed CPUE. First, I present the contrasts between the TVG and CG versions of both wild and stocked lake trout models. For the time-varying growth models, I then compare estimates to observed data and present population level patterns for wild and stocked lake trout. Estimated parameters for all versions of the MI4 lake trout model are in the appendix.

Comparison of TVG and CG models

Both wild and stocked lake trout constant growth models estimated periods of much higher recruitment followed by higher mortality rates than the time-varying growth models. This general pattern appears to be a differential response by the two models to spikes in observed spring assessment CPUE, which was the only data source available during the period that major differences between the CG and TVG models occurred. Both CG and TVG model predictions matched observed harvest closely. This result is not surprising given the large weight errors in predicted harvest were given during model fitting. Summer assessment CPUE predictions fit well with observed values from both CG and TVG models, but were modeled only over the short time series of available data (1985-1995).

Wild lake trout CG and TVG model comparison

For wild lake trout, recruitment estimates in 1975-1977 (Figure 4) were substantially higher for the CG model than the TVG model. Age-1 fish in 1975-1977 were 4-6 year-olds in 1980, and 5-7 year-olds in 1981, which were peak years in spring assessment CPUE. Thus, the CG model required much higher rates of recruitment in order to match the large spike in observed CPUE than the TVG model (Figure 5).

Observed wild CPUE in the spring assessment dropped dramatically in 1982 to approximately 50% of the 1981 peak value (Figure 5). This resulted in high estimates of total instantaneous mortality (Z) in 1981 and 1982 (Figure 6). The CG model required higher mortality rates than the TVG model over this period to reduce a larger population produced from higher recruitment estimates in 1975-1977. After 1983, mean total mortality rates from the two models followed similar trends, although mortality estimates were slightly greater for the time-varying growth model.

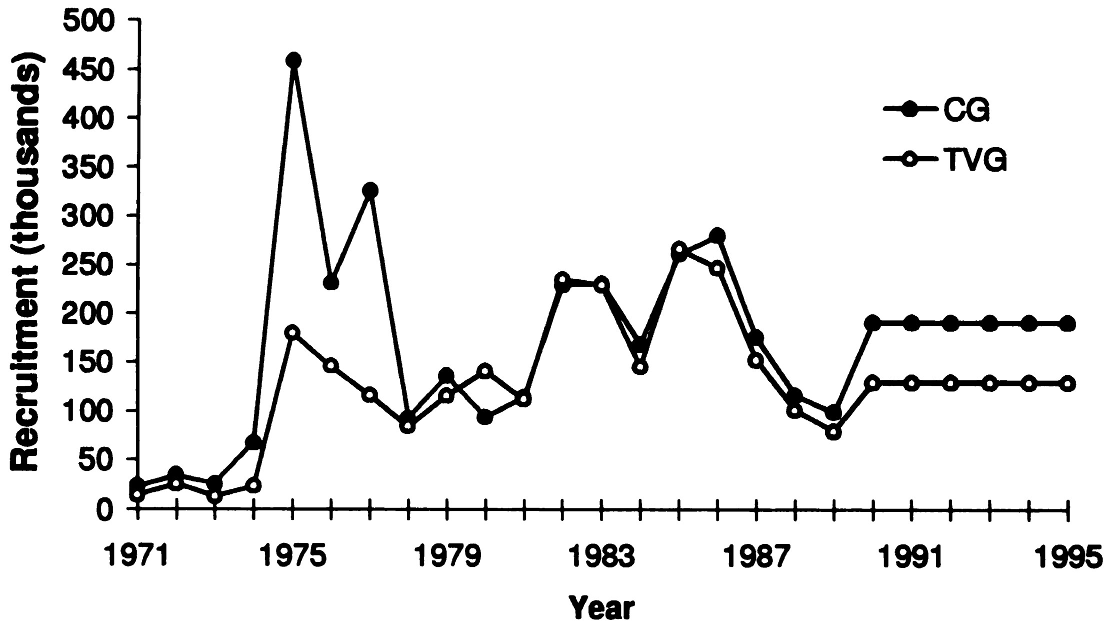


Figure 4. Recruitment estimates from constant growth (CG) and time-varying growth (TVG) models of wild lake trout in MI4 of Lake Superior, 1971-1995. Recruitment after 1990 was set equal to the estimate for 1990 because one year-olds after 1990 were never large enough to be adequately sampled.

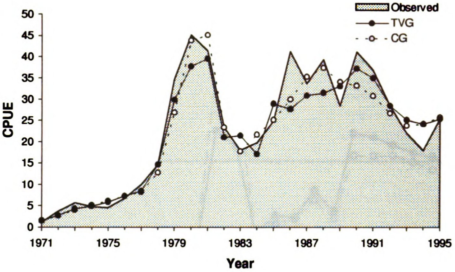


Figure 5. Observed and predicted catch per unit effort (CPUE) of wild lake trout in MI4 spring assessments of Lake Superior, 1971-1995. CPUE is defined as the number of lake trout caught in 1.0 km of gill net, standardized to net-nights. Predictions were made using constant growth (CG) and time-varying growth (TVG) population assessment models.

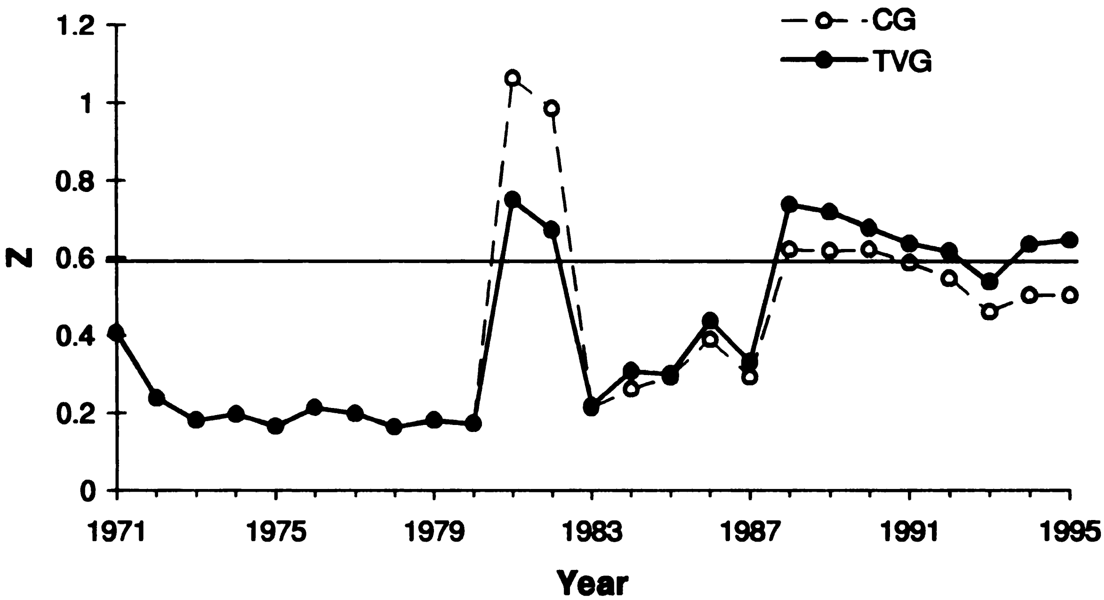


Figure 6. Mean instantaneous mortality rates of wild lake trout ages 5-10 in MI4 of Lake Superior, 1971-1995, from constant growth (CG) and time-varying growth (TVG) models. The horizontal line represents a total annual mortality rate of 45%.

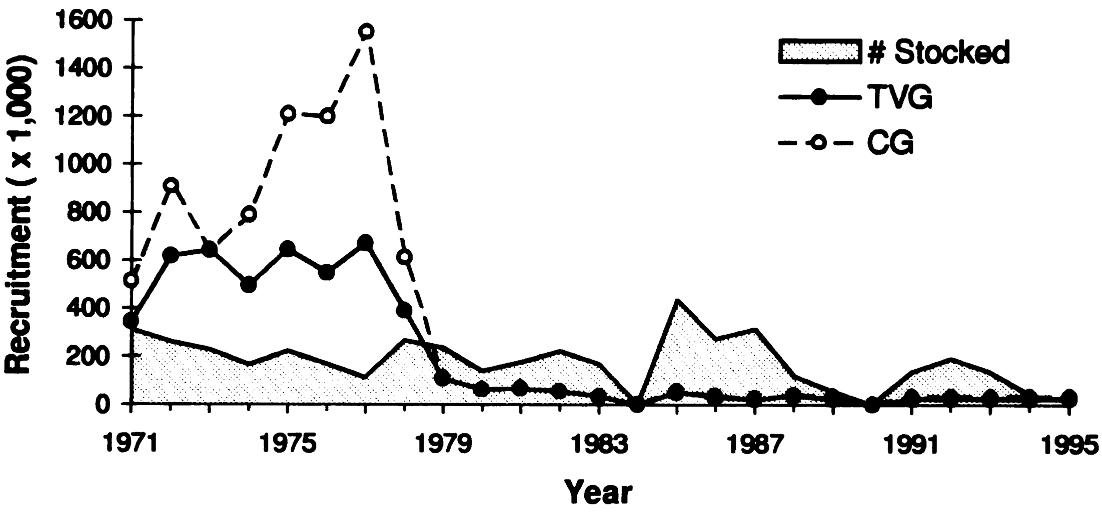


Figure 7. Actual numbers of hatchery-reared lake trout stocked and recruitment estimates of stocked lake trout from constant growth (CG) and time-varying growth (TVG) models for MI4 of Lake Superior.

Stocked lake trout CG and TVG model comparison

Recruitment (age-1) estimates for hatchery-reared fish (Figure 7) showed little resemblance to the actual number of yearling lake trout planted in MI4. My estimates of recruitment for both constant and time-varying growth models were well above planting levels prior to 1979. After 1979 this is reversed and recruitment estimates dropped to very low levels.

Total instantaneous mortality estimates (Z) of stocked lake trout, averaged over ages 5-10, peaked in 1981-1982, when once again the CG model's estimates were much higher than the TVG model's estimate (Figure 8). This scenario is similar to that seen for wild lake trout in that increased mortality was required to "kill off" excess fish left-over

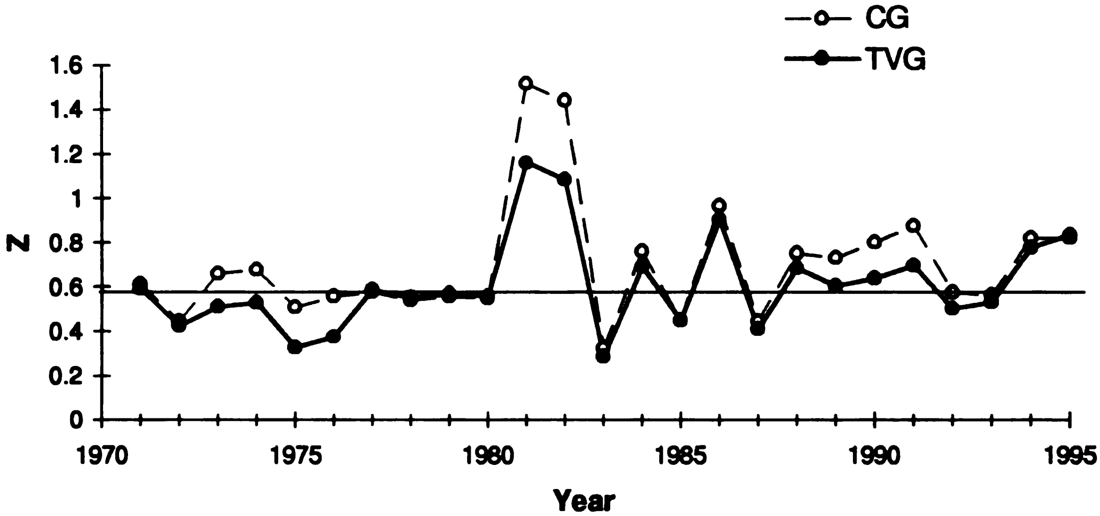


Figure 8. Mean instantaneous total mortality rate estimates of stocked lake trout ages 5-10 in MI4 of Lake Superior, 1971-1995. Estimates were made using constant growth (CG) and time-varying growth (TVG) assessment models. The horizontal line corresponds to a total annual mortality rate of 45%.

from high recruitment years. After 1983, total mortality estimates were similar between the TVG and CG versions of the model.

Model responses to peaks in observed CPUE

Parameter estimates of both wild and stocked lake trout models were strongly influenced by peaks in observed spring assessment CPUE. Rapid increases followed by rapid decreases in observed CPUE coincided with elevated recruitment estimates five to six years prior to a peak in observed CPUE and higher estimates of mortality rates during the years observed CPUE declined than in earlier years. For wild lake trout, the elevated recruitment value estimated for 1975 (Figure 4) preceded a large increase in observed CPUE values for 5, 6, and 7 year olds in 1979-1981 from the spring assessment (Figure 5). This was followed by elevated total mortality estimates (Figure 6) for wild fish in 1981-1982, as spring assessment observed CPUE rapidly declined. Similarly, for stocked lake trout, recruitment estimates were high in 1971-1977 (Figure 7) in order to match the 1976-1981 peak in observed CPUE (Figure 9), and estimated mortality rates rose in 1981-1982 (Figure 8), when observed CPUE of stocked lake trout fell.

My results indicate that the primary differences between the CG and TVG models for both wild and stocked lake trout were responses to peaks in observed spring assessment CPUE, mainly much higher recruitment leading to higher mortality rates for the CG model than the TVG model. Since selectivity was modeled as a constant function of length, either increased recruitment or increased growth rates could produce an increase in predicted CPUE. Parameters of the CG model could only respond so as to match large peaks in observed CPUE through changes in recruitment and mortality rates. The TVG model allowed fish to grow faster at some times than at others. This allowed a larger peak in CPUE for a given amount of recruitment because these fish could more rapidly enter into the most highly selected sizes, and suffer less mortality in the process. Another consequence of rapid growth occurs at older ages when size exceeds the length of maximum selectivity, and CPUE falls with time, not only because abundance is declining but also because selectivity is declining. Therefore, the TVG model required less recruitment and subsequently less mortality to match large peaks in observed CPUE.

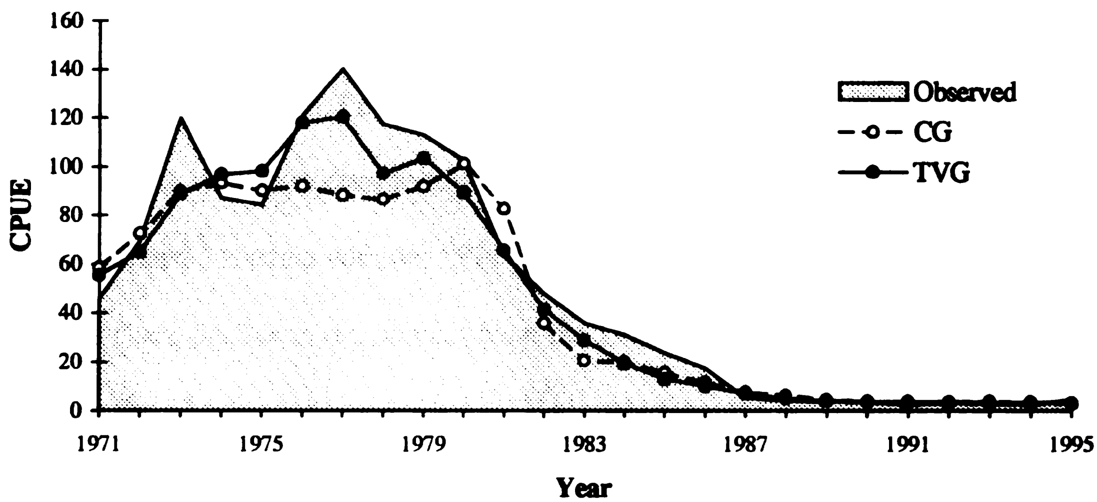


Figure 9. Observed and predicted catch per unit effort (CPUE) of stocked lake trout in MI4 spring assessments of Lake Superior, 1971-1995. CPUE is defined as the number of lake trout caught in 1.0 km of gill net, standardized to net-nights. Predictions were made using constant growth (CG) and time-varying growth (TVG) population assessment models.

Stocking versus recruitment

In the stocked lake trout model I estimated recruitment (age-1) over time rather than using the actual numbers of yearlings stocked in the lake as known values. This was the same formulation I used for the wild lake trout model, for which I had no means of comparing recruitment estimates to the actual number of wild recruits. Since I assumed that natural mortality was fixed over all ages, and only natural mortality was operating at younger ages (1-3), changes in mortality for younger ages over time would show up as time-varying recruitment. Model estimates of recruitment can therefore be considered "viable recruitment", and discrepancies between estimated recruitment trends and trends in stocking imply a change in survival from yearling plantings to ages that were present in sampling (about age-4 and older).

Using the CG model, I estimated an increase in recruitment from the 1971 year class through the 1977 year class followed by a sharp decline to much lower recruitment levels that persisted starting with the 1979 year class. With the TVG model, I also estimated a sharp decline in recruitment from the 1977 to the 1979 year class and low recruitment for all subsequent year classes. Estimates from the two models differed in that the TVG model recruitment estimates were not increasing, but were relatively stable for 1971 through 1977 year classes. In contrast with the increasing trend in recruitment over the 1971-1977 year classes I estimated using the CG model, there was no such trend in actual numbers of yearlings stocked. Hence, if the trend I estimated using the CG model reflects reality it implies an increase in subsequent early life survival. I have found no independent reasons to suspect that early life survival should have increased over these year classes, and take this non-intuitive pattern as an additional reason to prefer the TVG model.

After 1979, my estimates of recruitment dropped well below the actual numbers of lake trout planted in MI4. Low values for CPUE from the summer assessment of stocked lake trout (Figure 10), and discrepancies between low recruitment estimates and the actual numbers of yearlings planted in MI4 after 1979, suggest that in the later years the actual

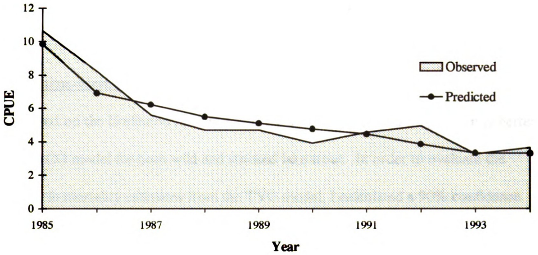


Figure 10. Observed and predicted values of catch per unit effort (CPUE) for stocked lake trout from the summer assessment in MI4 of Lake Superior, 1985-1994. CPUE is defined as the number of lake trout caught in 1.0 km of gill net, standardized to net-nights.

natural mortality rates suffered by young stocked lake trout were higher than those I used in the model.

The results from fitting the stocked lake trout model call into question the assumptions I made in both models concerning mortality rates of young lake trout, primarily ages 1-3. Over this age interval, I assumed constant and known natural mortality and that other mortality sources were trivial. For wild fish, I was unable to separate variations in recruitment at age-1 from variations in mortality between age-1 and age-3. Hence, variations in estimated recruitment, which nominally occurs at age-1, could be resulting from time-varying mortality after that age. Clearly for stocked fish such variation is occurring following planting as yearlings, as indicated by the mismatch between recruitment estimates and the actual numbers of stocked fish.

Lake trout time-varying growth model results

Based on the likelihood ratio test, the TVG model produced a significantly better fit than the CG model for both wild and stocked lake trout. In order to evaluate the uncertainty in mortality estimates from the TVG model, I calculated a 90% confidence interval for a single parameter, namely fishing intensity (f) from 1991. I fixed f in year 1991 at values both above and below the original estimate, and refit the model for each fixed value of f. I continued this procedure until I obtained values of f in year 1991 that resulted in total maximum likelihood values (L_{max}) approximately equal to the upper and lower bound of the 90% confidence interval. The upper and lower bounds were based on a Chi-square distribution using the likelihood ratio test statistic: $2[L(\hat{\theta}) - L(\theta_0)]$, where $L(\hat{\theta})$ was the total log-likelihood for the fixed values of f and $L(\theta_0)$ was the total log-likelihood for the original estimate (Seber and Wild 1989). The 1991 estimate of fishing intensity (f_{1991}) was equal to 0.675 and the 90% confidence interval for f_{1991} was 0.549 to 0.776.

In the following sections I present results from the wild and stocked lake trout TVG models for MI4. I compare model predictions of CPUE, mean length-at-age, and age-compositions to observed values obtained from spring assessment data because it spans a much longer time-series than fishery sampling or graded-mesh survey data. I also compare model predictions of harvest to observed harvest, present estimates of parameters describing growth, mortality, survey and fishery selectivity, and estimates of spawner abundance of wild and stocked lake trout in MI4.

Fit of wild lake trout TVG model predictions to observed data

Wild lake trout assessment CPUE

Predictions of assessment CPUE from the wild lake trout TVG model matched the general long term trends in observed CPUE, but did not match shorter-term variations. For the spring assessment, model predictions of CPUE (Figure 5) appeared to be responding to the 1979-1981 and 1986-1991 peaks in observed CPUE, but fell short of peak observed values. The model predictions matched the modest decline in summer assessment observed CPUE from the mid 1980's to the 1990's (Figure 11), but was not challenged greatly by the summer assessment data because large and rapid changes in CPUE did not occur.

No clear patterns were observed in log-scale residuals between TVG model predictions and observed spring assessment CPUE (Figure 12), suggesting the model fit observed data well. The only exception may be a short series of positive residuals for the period 1977-1982, which were probably an indication of how the model had difficulty matching the spike in observed CPUE.

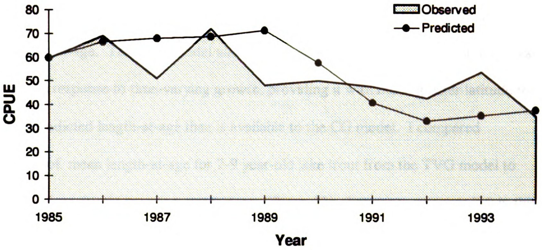


Figure 11. Observed and predicted values of catch per unit effort (CPUE) for wild lake trout from the summer assessment in MI4 of Lake Superior, 1985-1994. CPUE is defined as the number of lake trout caught in 1.0 km of gill net, standardized to net-nights.

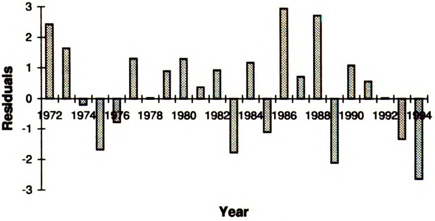


Figure 12. Log_e-based residuals from model predictions of spring assessment catch per unit effort (CPUE) of wild lake trout in MI4.

Wild lake trout mean length-at-age

One important area in which predictions from the TVG and CG models differ is in mean length-at-age. The TVG model allows mean length-at-age of the population to vary over time in response to time-varying growth, providing it with much greater latitude for changing predicted length-at-age than is available to the CG model. I compared predictions of mean length-at-age for 7-9 year-old lake trout from the TVG model to observed values caught in spring assessments (Figure 13). I chose to use ages 7-9 in this comparison because lake trout in Lake Superior reportedly become fully selected to the fishery and mature over these ages (Peck 1979; Ebener 1990), and the spring assessment was the selected data source because it provided the longest time series of available data. The model appeared to follow trends in observed mean length-at-age reasonably well, but did not match rapid changes in mean length-at-age well. This suggests either the model was constrained from matching large changes in size that really did occur, or the model successfully reduced excess variation, or "noise". Predictions of mean length-at-age for age-7 and possibly age-8 after 1984 tended to be higher than observed values. This was probably due to a complex interaction between model growth rates and predicted CPUE. The model needs to account for the large increase in observed spring assessment CPUE that began in 1984 and extended into the 1990's. Mean total lengths for age-7 and age-8 lake trout range between 19 and 23 inches. This size range also corresponded to the steeper part of the selectivity curve for wild lake trout (Figure 14). Increased growth rates in 1984 caused age-7 and age-8 fish to become more selected, and hence, increased CPUE. After 1984 trends in estimated mean length-at-age followed trends in observed

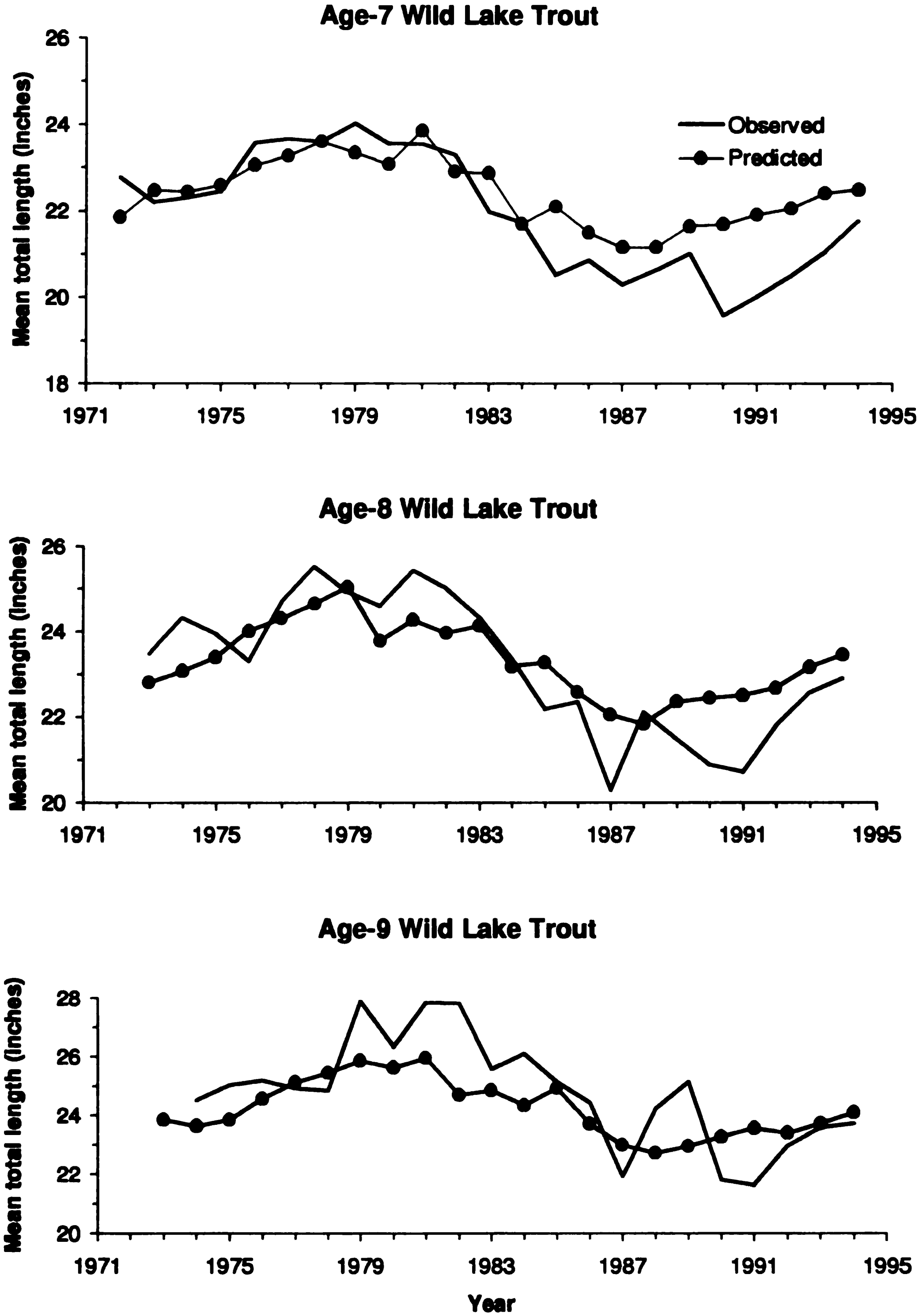
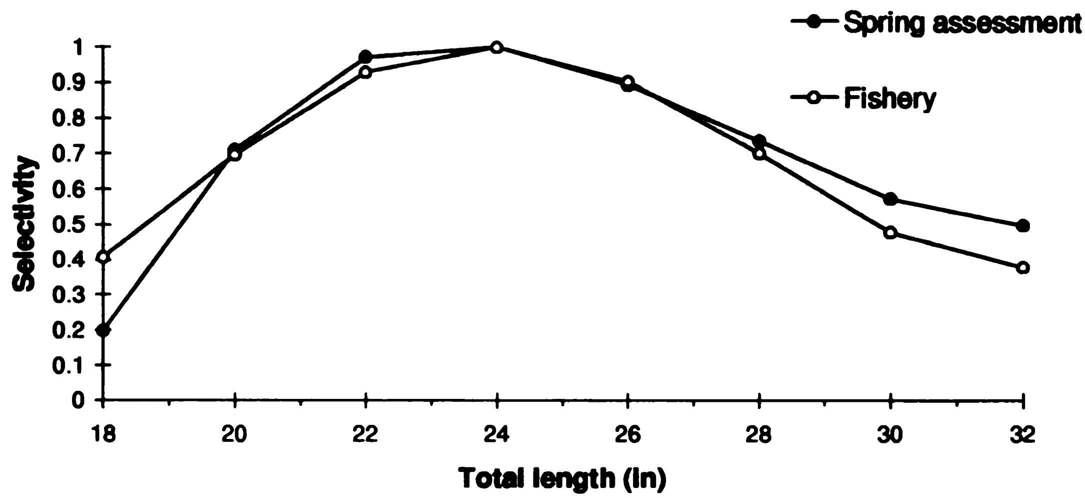


Figure 13. Observed and predicted mean total length for age 7-9 wild lake trout from spring assessments in MI4 of Lake Superior.



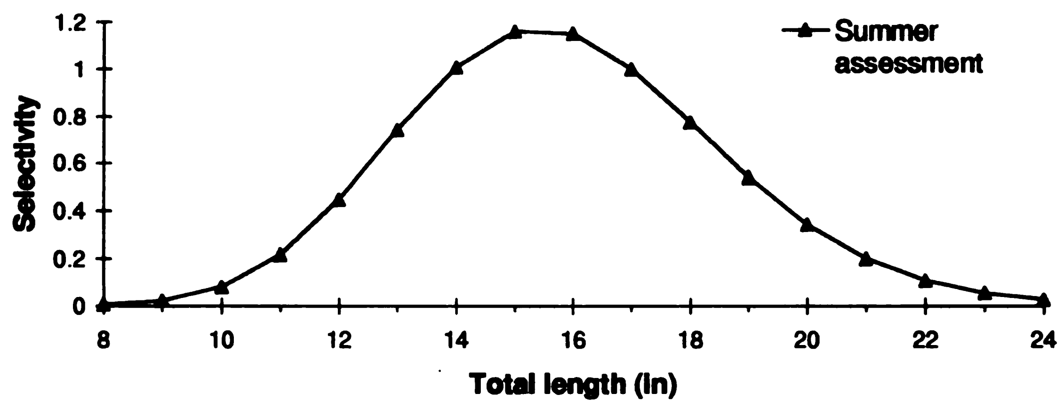


Figure 14. Length specific selectivity patterns estimated for spring and summer assessments and fishery harvest of wild lake trout.

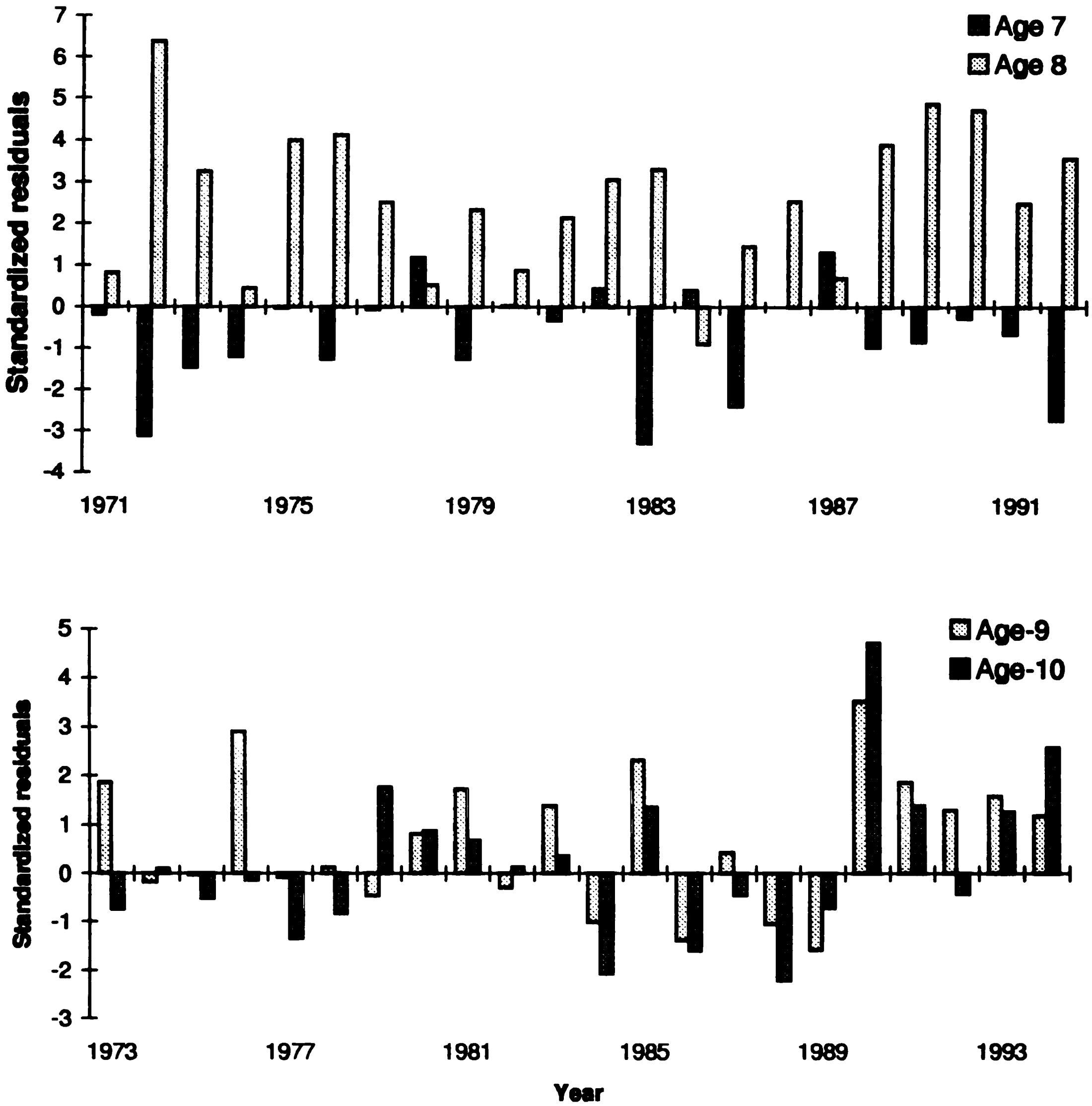


Figure 15. Standardized residuals for spring assessment age compositions of age 7-10 wild lake trout in MI4. Standardized residuals equals (observed) minus (predicted) proportions at age divided by estimated standard deviation.

mean length-at-age quite well but at a slightly higher level, which appears to be mainly due to the increase in growth that occurred between 1984 and 1985.

Wild lake trout age compositions from spring assessments

I examined standardized residuals of lake trout caught in spring assessments (Figure 15). Standardized residuals were defined by :

$$\frac{p_{a,y+t,l\ Observed} - p_{a,y+t,l\ Predicted}}{\hat{\sigma}}$$

where $p_{a,y+t,l}$ was the proportion at age and length in the assessments and the fishery (see Equation 16), $\hat{\sigma}=\sqrt{p_{a,y+t,l\ Predicted}\ (1-\ p_{a,y+t,l\ Predicted})\ /\ n_{eff}}$, and n_{eff} is the effective sample size. These residuals show that the time-varying growth model underestimated proportions of age-8 lake trout, as indicated by generally positive residuals, but residuals for older ages were randomly distributed with few outliers. Residuals for age-7 fish tended toward the negative side, but were much closer to zero. These results suggest that assumptions about ageing error of 7 and 8 year-old fish may require further attention. One possibility is that the model's values for ageing error result in an overlap, or "leaking", of age-8 fish into age-7 fish. I further explored this problem by combining age-7 and age-8 fish into a single age-class within the objective function of the model. Increases in the multinomial log likelihood functions L_4, L_5, and L_6 resulted in large increases in the overall log likelihood (Equation 26). Residuals for combined ages 7 and 8 still tended to be positive but were much closer to zero with fewer outliers than the residuals for the individual age-8 age-class. Parameter estimates from the combined age-7 and age-8 model, however, remained similar to those estimated when age-7 and age-8 were not combined in the objective function. Thus, combining ages 7 and 8 in the objective function improved patterns in the residuals of spring assessment but had very little affect on parameter estimates of the population.

Wild lake trout harvest

Model predictions of harvest matched observed harvest quite closely in all cases (Appendix). The low value assumed for error in reporting harvest (CV = 1 %) forced this close fit. In an ideal world reported harvest could be considered a known quantity since it is based on required reporting rather than sampling. In Lake Superior total commercial harvest is determined by transforming the total dressed weight of the reported harvest to numbers-at-age of wild or stocked lake trout based on sampling, and recreational harvest is determined through creel census. By-catch from commercial fisheries are likely to induce errors in reporting. Hence, the assumed CV of 1% is probably optimistic, but no hard data is available for fixing the CV at a higher level. I chose a low error rate since this is consistent with how harvest is treated in many catch-at-age models, where it is assumed known. It would be valuable to determine empirically the actual error rate in reported harvest.

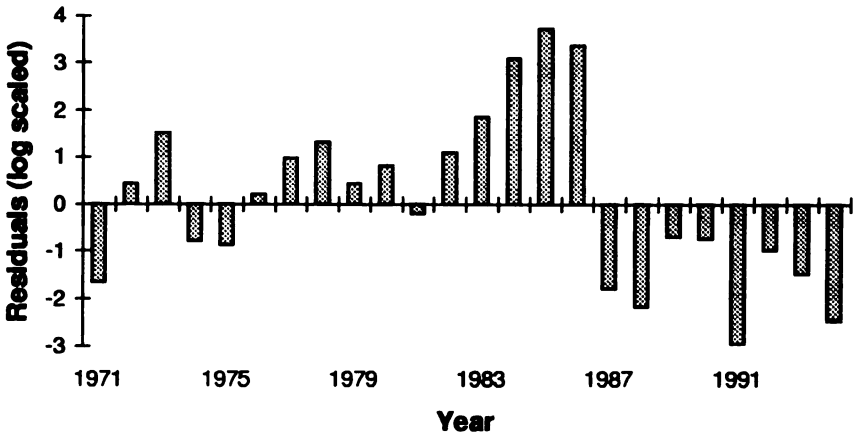


Figure 16. Log_e-based residuals from model predictions of spring assessment catch per unit effort (CPUE) of stocked lake trout in MI4.

<u>Fit of stocked lake trout TVG model predictions to observed data</u>

Stocked Lake trout assessment CPUE

Stocked lake trout made a significant contribution to the recovery of naturally reproducing wild stocks and lake trout rehabilitation in Lake Superior throughout the 1970's (Hansen et al. in press). In the 1980's, however, CPUE of the fish planted into the lake dropped significantly. The stocked lake trout TVG model followed general patterns in the observed trend in spring assessment CPUE (Figure 9). Closer examination indicates some lack of fit; residuals showed a prolonged period of positive residuals from 1976 to 1986 followed by a period of negative residuals (Figure 16). CPUE predictions were nearly always less than observed values from 1976-1986, and were greater than observed values from 1987-1994. The overall decline in observed CPUE from 1976-1994, then, was greater than the decline in predicted CPUE. This lack of fit occurs because estimates of mortality were not high enough to allow the model predictions to match the overall decline in observed CPUE. In the model, natural mortality was constant by assumption, and sea lamprey mortality rates varied only in response to observed wounding patterns. Only fishing mortality rates could be altered during the model fitting process in order to match the observed CPUE patterns, but this response was constrained by a need to match harvest levels. Hence, the pattern in residuals reflects a balancing of errors during 1976-1986 and 1987-1994 so that the residuals in neither time period is as large as they would be if the model had matched observed quantities during only one of the time periods.

Observed and predicted summer assessment CPUE values for stocked fish were much lower that those of wild lake trout and declined from 1985-1994 (Figure 10). The majority of the fish caught in the summer assessment range between ages 4-6 (13-18 inches length). When compared to the numbers of lake trout stocked in MI4, the low observed CPUE in summer assessments indicates low survival rates for fish less than 4 years of age, or 13 inches in length. This is dealt with by the model by low estimates of recruitment.

Stocked lake trout mean length-at-age

Mean length-at-age estimates of stocked lake trout were compared with observed values from spring assessment data (Figure 17). These results were similar to those of wild lake trout in that incremental changes in predicted mean length-at-age were nearly always less than changes in observed values. Modeled mean length-at-age estimates were almost always greater than observed values after 1982. The model therefore tended to grow fish faster to a larger size-at-age than what was actually observed through and after the rapid decline in CPUE. The reason for this lack of fit is unclear, but I believe it to be related to the lack of fit seen for spring assessment CPUE data. Without the changes in growth leading to the lack of fit in mean length-at-age, the pattern in residuals seen for CPUE might be even greater.

Stocked lake trout age compositions from spring assessment

The stocked lake trout model tended to underestimate the proportions of age-7 and age-8 fish caught in the spring assessment prior to 1983 (Figure 18). The model also appeared to overestimate proportions of age-5 fish prior to 1985 and age-6 fish after 1990. This lack of fit is probably related to the model not being able to mimic the decline in CPUE from the spring survey by increasing mortality rates. With natural and sea lamprey mortality rates fixed, and fishing mortality limited based on relationships with observed harvest, the model was forced to change other parameter (growth, selectivity, etc...) estimates, and this would have influenced the lack of fit between estimated and observed age compositions.

Stocked lake trout harvest

As in the case for wild lake trout, harvest estimates for stocked fish matched observed harvest closer than any other variable in the model (Appendix).

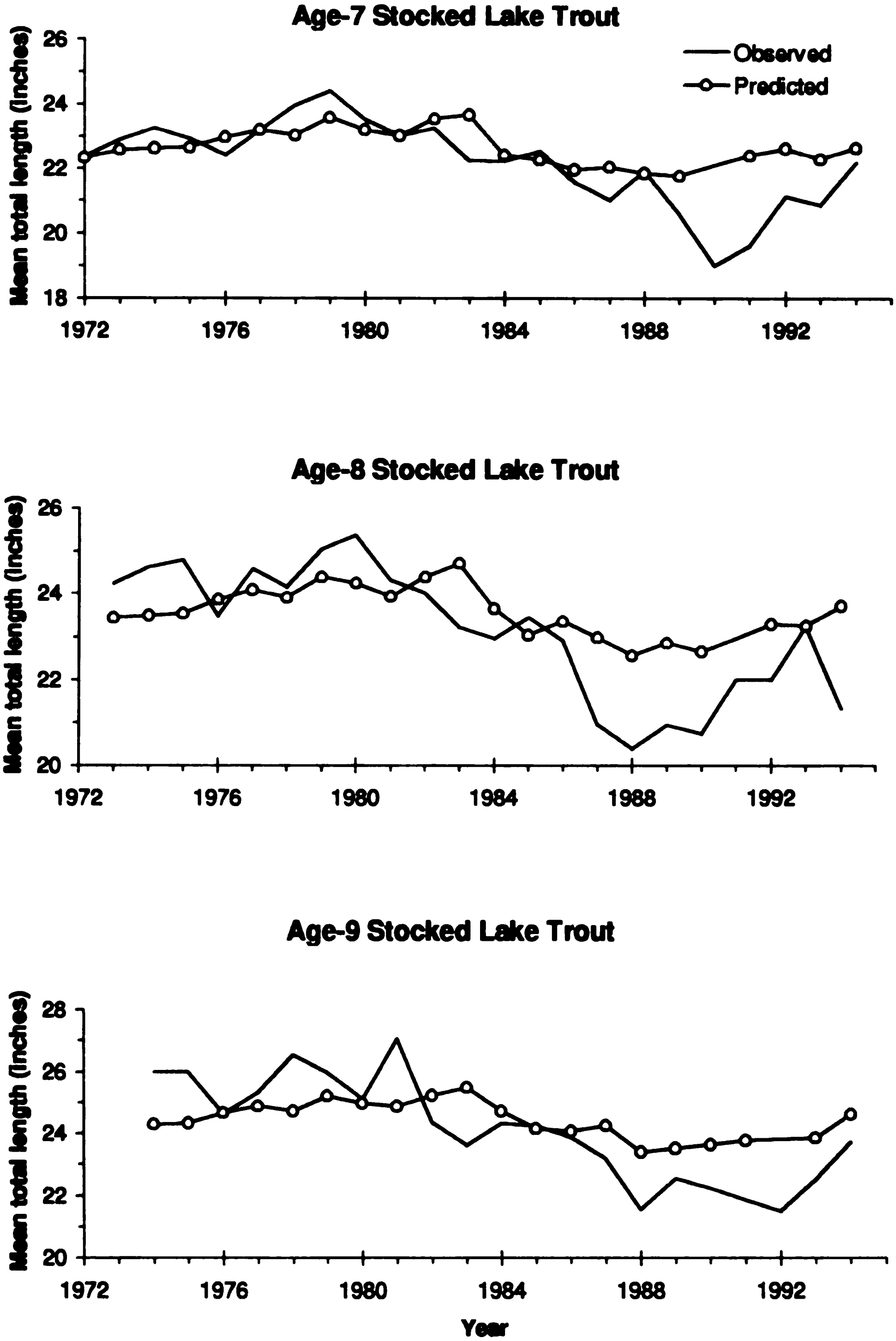


Figure 17. Observed and predicted mean total length for age 7-9 stocked lake trout from spring assessments in MI4 of Lake Superior.

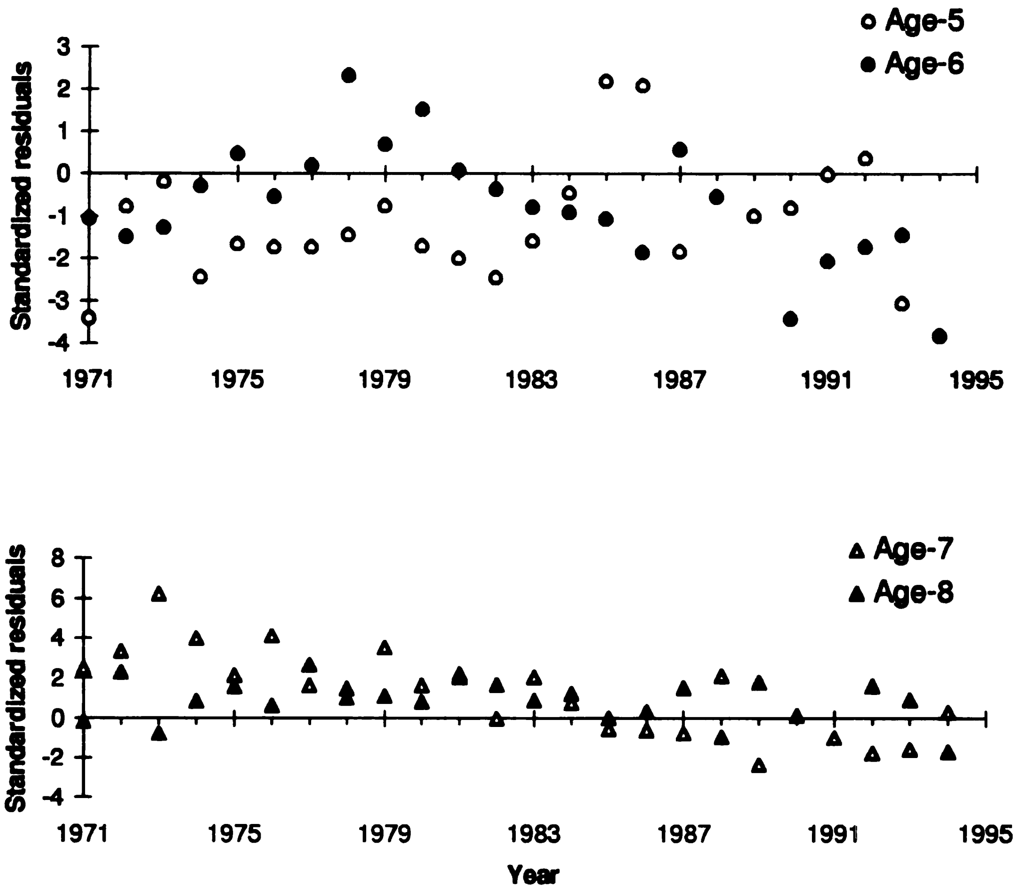


Figure 18. Standardized residuals for spring assessment age compositions of age 7-10 stocked lake trout in MI4. Standardized residuals equals (observed) minus (predicted) proportions at age divided by estimated standard deviation.

Growth, recruitment, mortality, selectivity, and abundance of lake trout in MI4

Wild lake trout growth

One of the unique features of this assessment model not present in previous lake trout models for the Great Lakes was that a growth submodel was used to explore the effects of time-varying growth on the population. The model estimated annual growth conditions by finding annual values of L-infinity (L_∞) using von Bertalanffy equations (11 and 12). Estimated growth conditions for wild lake trout were relatively constant during 1971-1980, varied greatly and appeared to decrease in the early 1980's, and have increased since 1985 (Figure 19). The period of large variations in L_∞ came right after the 1979-1981 spike in large-mesh CPUE of wild lake trout. This was also the period that observed spring assessment CPUE for stocked fish went from peak values into the large decline. The combination of these factors suggests that a density dependence effect may have triggered large changes in growth rates.

Wild lake trout recruitment

Historically, CPUE of age-7 lake trout has been used as a relative index for recruitment of a particular year-class. I compared the TVG model estimates of recruitment (age-1) to estimates of abundance at age-7 for the corresponding year-class. Figure (20) shows general correspondence between abundance at age-1 and age-7 for the same year class, but the relationships between age-1 and age-7 were not constant. This suggests that time-varying mortality between age-4 and age-7 influences recruitment to age-7. Since recruitment estimates are based on "seeing" those fish in the data, which

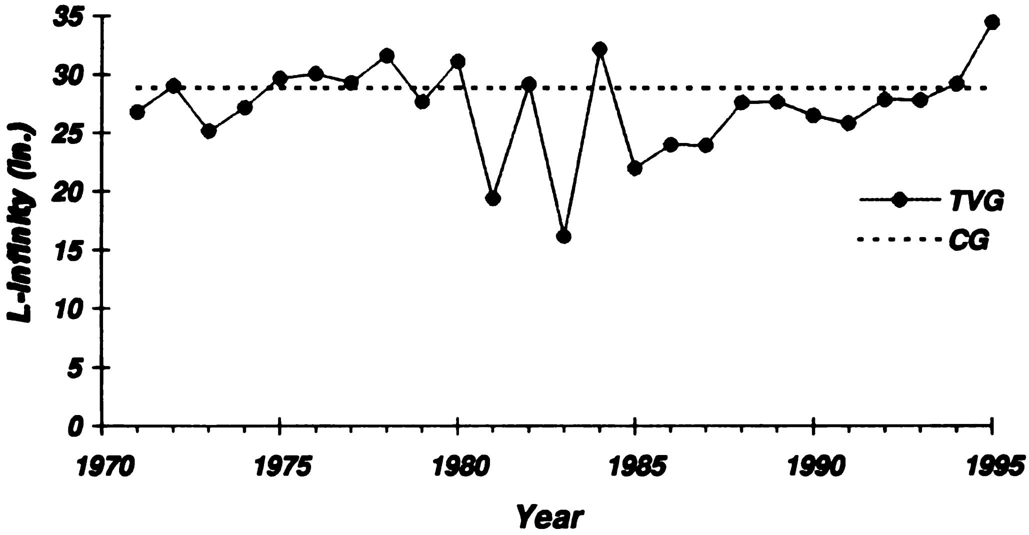


Figure 19. L-infinity estimates from constant growth (CG) and time-varying growth (TVG) models for wild lake trout in MI4.

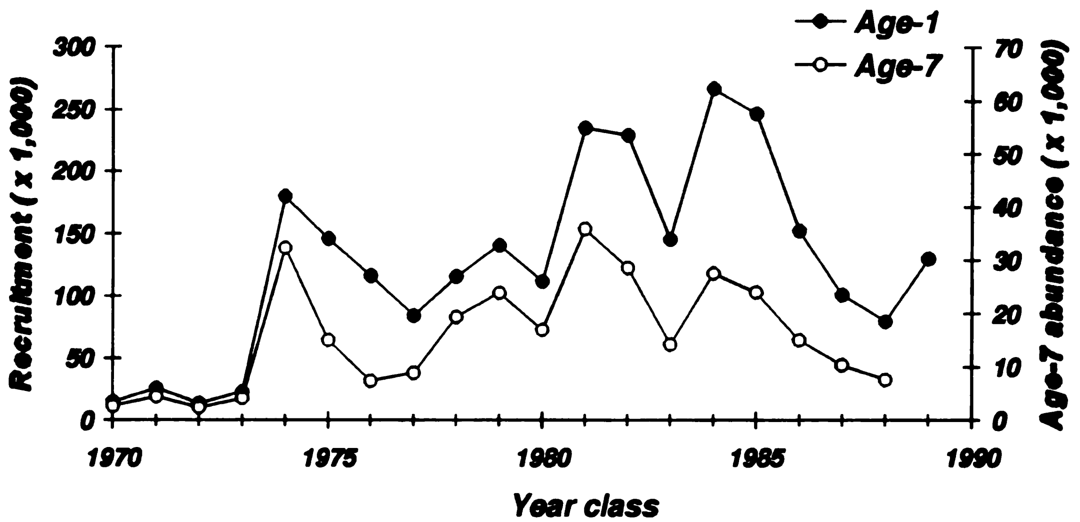


Figure 20. Recruitment (age-1) and abundance at age-7 estimates for 1970-1989 year classes of wild lake trout in MI4.

start at age-4, the lower bound of the age range for which I have evidence of time-varying mortality is age-4.

Wild lake trout mortality

Mortality of lake trout in Lake Superior varies in intensity over time and across ages. I estimated the various components of total mortality over time and ages, and fishing intensity over time, to assess the overall mortality suffered by lake trout in MI4. Age-specific mortality is presented based on mean 1990-1994 model estimates (Figure 21). Total mortality was broken down into components of natural, sea lamprey, and fishing mortality. Fishing was estimated to be the primary component of lake trout mortality in MI4.

I plotted sea lamprey, fishing, and total mortality estimates, averaged across ages 5-10, from 1983-1995 (Figure 22) to assess how mortality has changed over time. Estimates of sea lamprey mortality varied slightly but remained less than 0.11. Total mortality estimates increased from about 0.2 in 1983 to above 0.7 in 1988, primarily due to increased fishing mortality. Since 1990, mean instantaneous total mortality estimates have averaged 0.62 (total annual rate of 46.4%). Fishing intensity (f_y) estimates for wild lake trout (Figure 23) followed the same trend as the total mortality estimates, and fluctuated much less than those for stocked lake trout.

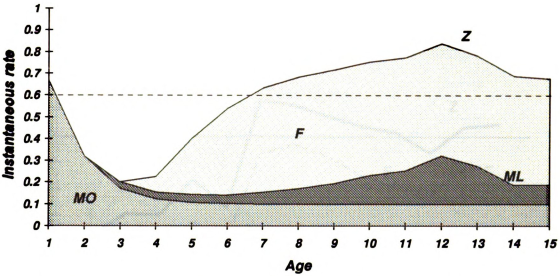


Figure 21. Instantaneous mortality rates based on mean 1990-1994 model estimates for wild lake trout, ages 1-15. Mortality components: MO = natural mortality, ML = sea lamprey induced mortality, F = fishing mortality, and Z = total mortality. The horizontal dashed line represents a total annual mortality rate of 45%.

Wild lake trout selectivity

Summer assessment selectivity had a dome shape relationship to length (Figure 14), starting and ending near zero and rising to a peak selectivity value at a total length of 15 inches (38.1 cm). In contrast, spring assessment and fishery selectivity patterns had a less pronounced dome and were nearly asymptotic functions of length. Similarities between selectivity patterns in the spring assessment and the fishery suggest that the assessment and fishery appear to be targeting similar size-classes of wild lake trout. This is expected because the gear used in the spring assessment is similar to that used in the fishery.

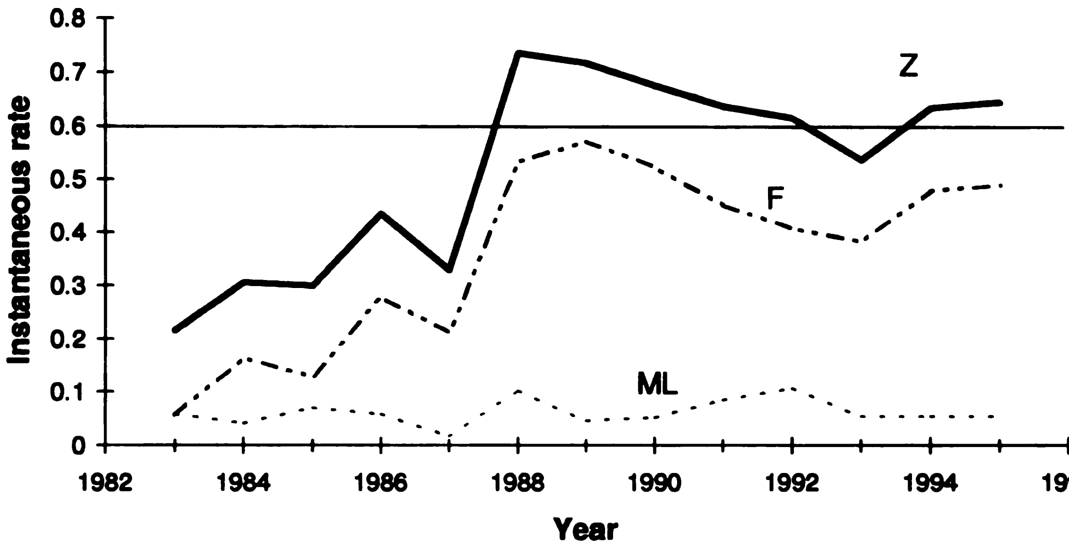


Figure 22. Instantaneous mortality rates averaged across ages 5-10 for wild lake trout in MI4, 1983-1995. Mortality components: ML = sea lamprey induced mortality, F = fishing mortality, and Z = total mortality. The horizontal line represents a total annual mortality rate of 45%.

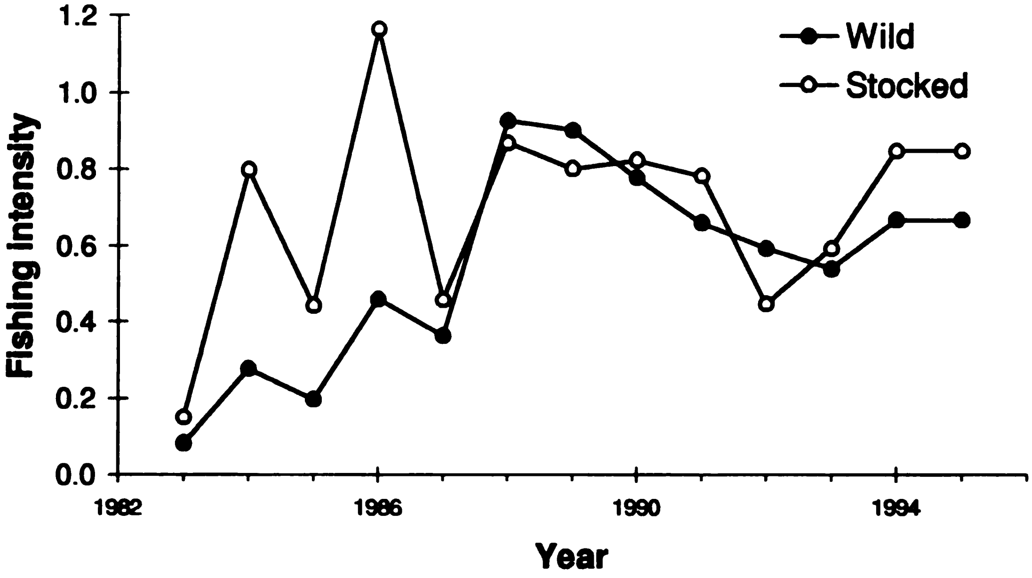


Figure 23. Fishing intensity estimates for wild and stocked lake trout in MI4 of Lake Superior, 1983-1995.

Lake trout spawner abundance

I multiplied estimates of lake trout abundance-at-age by the female maturity rates reported by Ebener et al. (1989), and summed these to obtain estimates of the available spawning stock of lake trout in MI4 over time (Figure 24). Available spawning stock increased to a peak of 130,000 spawners in 1977 and consisted primarily of stocked lake trout. Spawner abundance declined sharply until 1984, when it appeared to have leveled off at around 43,000 individuals (33% peak value), based on the 1984-1988 average. Since 1988, total spawner abundance estimates have been declining, and consists almost entirely of wild fish. Model estimates indicate that spawner abundance was dominated by stocked lake trout through the 1970's and into the early 1980's, but declined drastically beginning 1978 and has not recovered from the large decline. Estimates of wild lake trout spawner abundance increased from extremely low levels in the early 1970's to a peak value of 35,000 in 1988 and declined during the 1990's.

Stocked lake trout growth

In initial attempts at fitting the stocked lake trout model, L_∞ parameters were estimated to be many magnitudes greater than maximum lengths normally observed in surveys. Apparently, the model estimated unrealistic growth rates so that fish could become fully selected as quickly as possible by the fishery in order to match excessive mortality rates associated with stocked lake trout. I therefore constrained L_∞ values to a maximum of 40 inches (101.6 cm). Resulting L_∞ values are shown in figure (25). The CG

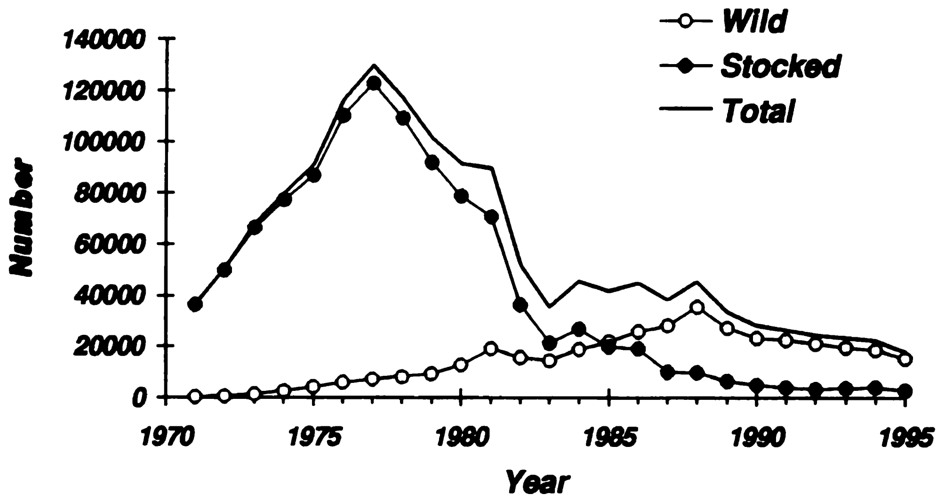


Figure 24. Wild, stocked, and total spawner abundance estimates of lake trout in MI4, 1971-1995.

model estimated an L_∞ value equal to the maximum constraint of 40 inches. The TVG

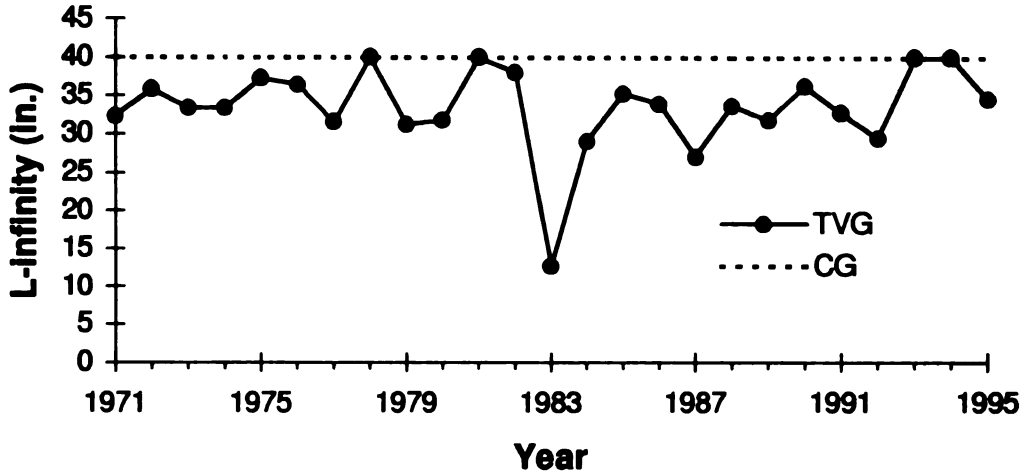


Figure 25. L-infinity estimates from constant growth (CG) and time-varying growth (TVG) models for stocked lake trout in MI4.

model showed improvement with L_∞ estimates "bound' at the 40 inch constraint in only 4 years out of the 25 year time series. The 1971-1995 mean L_∞ estimate for stocked lake trout was 33.5 inches, and the mean value for wild lake trout was 27.3 inches. If these model estimates actually reflect growing conditions, this would indicate overall better growth for stocked fish than wild fish. As discussed earlier, however, residual patterns in age compositions suggested that the stocked lake trout model tended to increase the growth rates and over select for younger lake trout than older fish to match the decline in CPUE (see section titled *Stocked lake trout age compositions*). For stocked lake trout the values estimated for L_∞ are influenced by assumptions about mortality rates, and as discussed above these assumptions may be incorrect. Hence the differences between L_∞

estimated for stocked and wild lake trout may not be truly indicative of differences in growth, because the estimates for L_∞ from the stocked model may be unreliable, especially in more recent years.

Stocked lake trout recruitment

Model estimates of recruitment and of age-7 abundance had markedly different trends for the 1970-1977 year-classes (Figure 26). Furthermore, neither recruitment nor age-7 abundance estimates followed the temporal pattern in the actual numbers of yearling fish that were planted. This suggests that mortality has varied over time for stocked lake trout between the ages of 1 and 7, and that survival from age-1 to age-7 decreased rather dramatically between the 1970 and 1976 year classes. This decline in survival experienced by stocked lake trout from 1971-1977 appears to have been caused by factors other than sea lamprey because estimates of sea lamprey induced mortality declined over that time period. Beginning with the 1978 year-class, estimates of recruitment at age-1 and abundance at age-7 tracked one-another closely but were at much lower levels than earlier years, and neither appear to follow the trend of the actual number of fish stocked in MI4. These results clearly suggest that natural mortality rates for stocked lake trout are time-varying and survival of young stocked fish have decreased considerably since 1971.

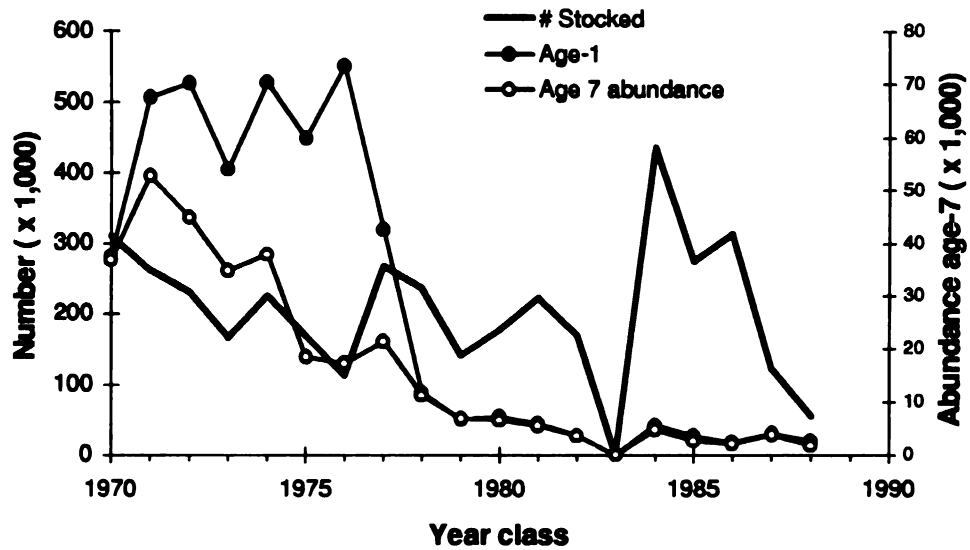


Figure 26. Estimates of recruitment (age-1) and abundance at age-7 of stocked lake trout and the actual number of lake trout planted in MI4 of Lake Superior for 1970-1988 year classes.

Stocked lake trout mortality

A target mortality rate for stocked lake trout was not specified within the lake trout rehabilitation goal for Lake Superior (GLFC 1996), but my estimates suggest that wild and stocked fish experience differential fishing mortality. Mean instantaneous mortality estimates for stocked fish, averaged from 1990-1994, were above 45% for fish age-8 and older (Figure 27). Both wild and stocked fish mean total mortality estimates for this time period peaked at age-12 but were higher for stocked lake trout ($Z = 1.0$) than for wild fish ($Z = 0.83$). Differences in total mortality estimates between wild and stocked fish were due to fishing since sea lamprey and natural mortality rates were equal for wild and stocked fish.

Mortality estimates of stocked lake trout, averaged across ages 5-10, were broken down into components of total mortality (Figure 28). Total annual mortality for these ages went above 45%, but to a much lesser degree than those of age-7 and older from 1990-1994. This figure indicates that time-varying mortality appears to be driven primarily by mortality due to fishing. Fishing intensity (f_y) rates estimated for stocked fish (Figure 23) were much higher than those for wild fish from 1983-1987, and during these years f_y estimates for stocked lake trout varied greatly. Variations in estimates of fishing intensity and fishing mortality rates suggest that the fishery fished harder for stocked lake trout than for wild fish during the mid 1980's.

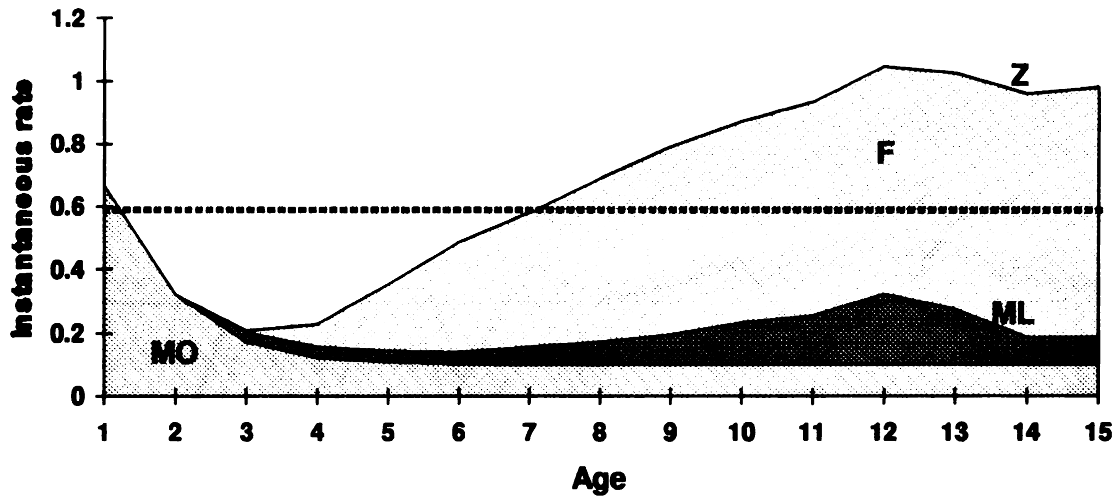


Figure 27. Instantaneous mortality rates based on mean 1990-1994 model estimates for stocked lake trout, ages 1-15. Mortality components: MO=Natural mortality, ML=sea lamprey mortality, F=fishing mortality, and Z=total mortality. The horizontal dashed line represents a total annual mortality rate of 45%.

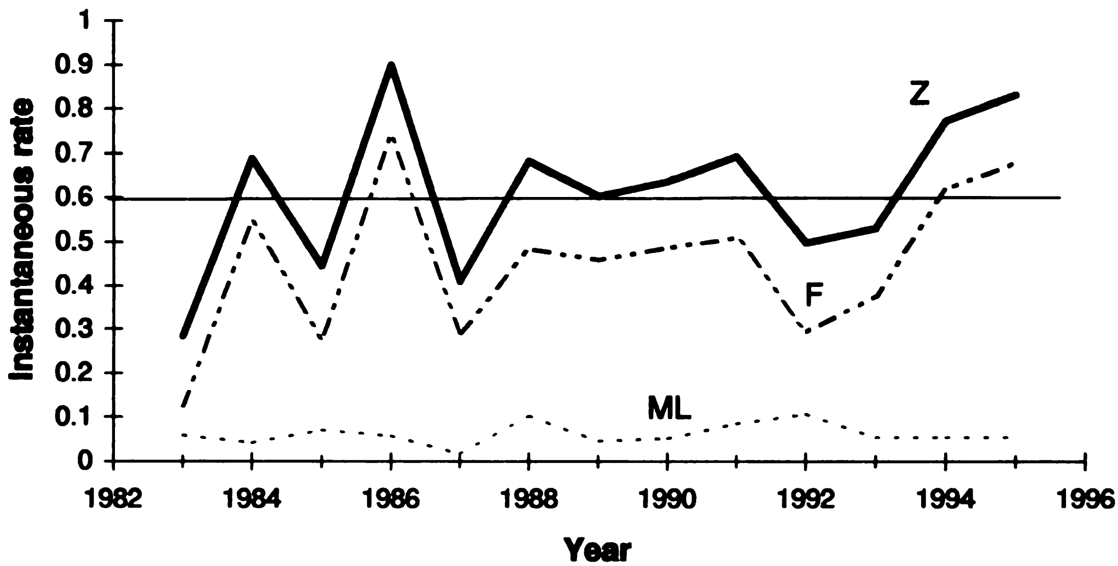
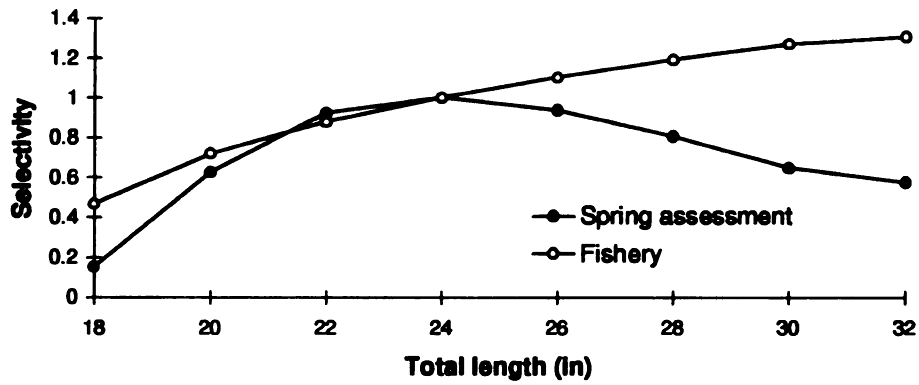


Figure 28. Instantaneous mortality rates of stocked lake trout averaged across ages 5-10. Mortality components: ML=sea lamprey induced mortality, F=fishing mortality, and Z=total mortality. The horizontal line represents a total annual mortality rate of 45%.

Stocked lake trout selectivity

Summer assessment selectivity patterns estimated for stocked lake trout (Figure 29) were similar to those estimated for wild fish but peaked at 16 rather than 15 inches. Estimated selectivity patterns for the spring survey and the fishery differed from one another. The selectivity pattern estimated for the spring survey for stocked lake trout was dome-shaped and similar to the pattern estimated for wild fish. In contrast, the selectivity pattern for the fishery increased asymptotically with increasing size. These results suggest that the spring survey and the fishery may be targeting different size-ranges of stocked lake trout. This pattern, however, may be confused by low levels in abundance of stocked lake trout and overall difficulties in fitting the stocked lake trout model.



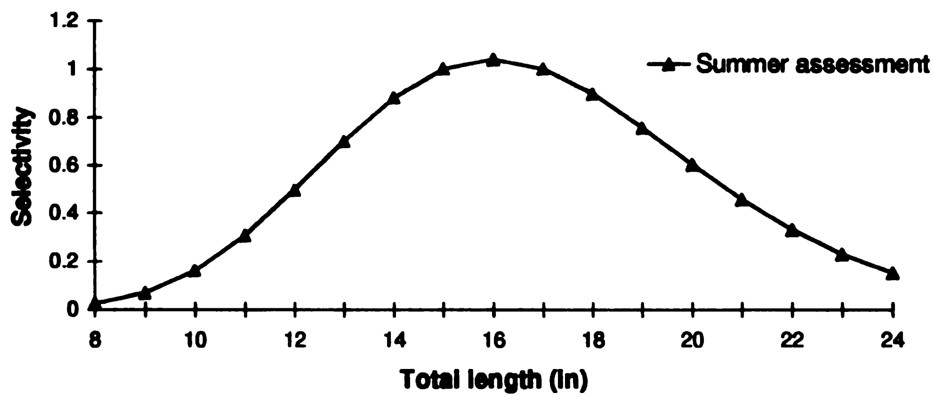


Figure 29. Length specific selectivity patterns for spring and summer assessments and fishery harvest of stocked lake trout.

DISCUSSION

Lake trout rehabilitation efforts in Lake Superior have led to considerable progress toward establishing naturally reproducing wild stocks, but, current harvest rates may be too high to allow stocks to sustain themselves. Based on results from a time-varying growth statistical catch-at-age (SCAA) model for lake trout in MI4, wild lake trout stocks are presently declining. Increased abundances of wild fish in the 1970's and 1980's, and reduced survival of stocked lake trout led to the decision by management agencies to eliminate stocking throughout most of Lake Superior. Observed CPUE values from 1985-1994 summer assessments in MI4 indicate that abundance of young wild fish was declining (Figure 11). Population assessment model estimates for MI4 indicated that spawner abundance has been declining since 1988 (Figure 24). Estimates also show that the 1990-1994 mean annual mortality rate of wild lake trout age-7 and older is above 45% (Figure 21). In the following sections I will discuss time-varying growth effects on lake trout, and how progress in lake trout restoration might be limited by fishing mortality and current stock recruitment relationships in the lake.

Time-varying growth effects on lake trout assessment

Assessment and commercial sampling data obtained for lake trout in Lake Superior have indicated that growth of lake trout has varied over time. Lake trout growth rates have been used as an indicator of fishery potential and ecosystem health, but variation in ageing and sampling of lake trout have precluded detailed assessment of the effects that time-varying growth has on the fitness of lake trout populations (Healey 1978; Marshall et al. 1987). I have developed a lake trout population assessment model that utilizes age and length composition data from assessment and commercial sampling to estimate abundance, recruitment, growth, and mortality. I then compared a time-varying growth version of the model to a constant growth version, and showed that the TVG model showed a significantly better fit than the CG model for both wild and stocked lake trout in MI4. The greatest discrepancy between the CG and TVG models appeared to be responses to peaks in observed spring assessment CPUE prior to 1983. Since commercial sampling and harvest information first became available beginning 1983, and prior to 1983 only spring assessment data was available, discrepancies between the CG and TVG model may have been a result of limited data before 1983. After 1983, the constant growth model appeared to perform as well as the time-varying growth model. While this does suggest that reasonable results can be obtained from less complicated constant growth SCAA models, changes in lake trout growth occurring since 1983 may not have been substantial enough to cause disparities between the CG and TVG models. I believe that the results from the MI4 model indicate that time-varying growth can be important, and the TVG model provides useful information about lake trout populations not provided by previous lake trout assessment models for Lake Superior. The time-varying growth model fit 24 additional parameters than the constant growth model. A drawback to the time-varying growth model is that the model fitting process took 36-72 hours to obtain a solution on a Gateway P5-150 (Pentium) computer, which was about twice the amount of time required by the constant growth model. Thus, when considering the use of constant versus time-varying growth models as management tools, managers should consider possible tradeoffs between model precision, model complexity, and computer processing time.

Wild lake trout mortality

One of the strategies developed by the LSTC was to limit harvest of spawning-sized lake trout (fish≥ 25 in.) so that total mortality is less than 45% per year (GLFC 1996). I used a stock recruitment model (Table 3) similar to Hansen et al. (in press) together with results from the wild lake trout model for MI4 to examine whether a target mortality rate of 45% would result in increased lake trout abundance. I estimated recruitment in 1995 and all subsequent years based on the relationship to spawning stock in January of the previous year, and projected estimates of abundance and yield out 100 years. Estimates of yield and spawner abundance dropped toward zero when fishing intensity (*f*) value is equal to the 1994 estimate (Figure 30). I then held selectivity constant and reduced *f* until total annual mortality (*A*) was lowered to 45% for age-ten fish (a 32% reduction in *f*), because present total allowable catch (TAC) models specify a female maturity of 100% beginning at age-10 (Ebener et al. 1989) (see Figure 30). For this scenario, yield and spawner abundance increased asymptotically. I repeated these

Table 3. Stock recruitment model with parameter estimates and asymptotic errors for lake trout in MI4. Variable definitions: W_i = estimated total number of wild lake trout eggs produced in year *i*, and S_i = estimated total number of stocked lake trout eggs produced in year *i*. Parameter estimates were obtained from unpublished results.

Equation	Description
$R_i = (\alpha_W W_i + \alpha_S S_i)\, e^{-\beta_W W_i - \beta_S S_i}$	"Multi-species" Ricker stock recruitment function

Parameter	Estimate	Asymptotic standard error
α_W	0.0118	0.005136
α_S	0.00204	0.000671
β_W	1.01×10^{-8}	2.05×10^{-8}
β_S	8.60×10^{-9}	3.35×10^{-9}

projections for reduced values of f (ranging 5-50% of the 1994 value) and estimated that a 30-40% reduction in fishing intensity from that estimated for 1994 would optimize the projected yield (Table 4, Figure 31).

The results from the stock recruitment projections clearly imply that wild lake trout stocks will decline if fishing pressure is not reduced below 1990-1994 average. These results agree with the findings of P. Ferreri (1995), who reported a finite rate of population growth (λ) for wild lake trout in Michigan waters of Lake Superior to be less than one (λ=0.930), indicating a decreasing population. If my estimates of mortality are realistic, then current management practices do not appear to have effective control over

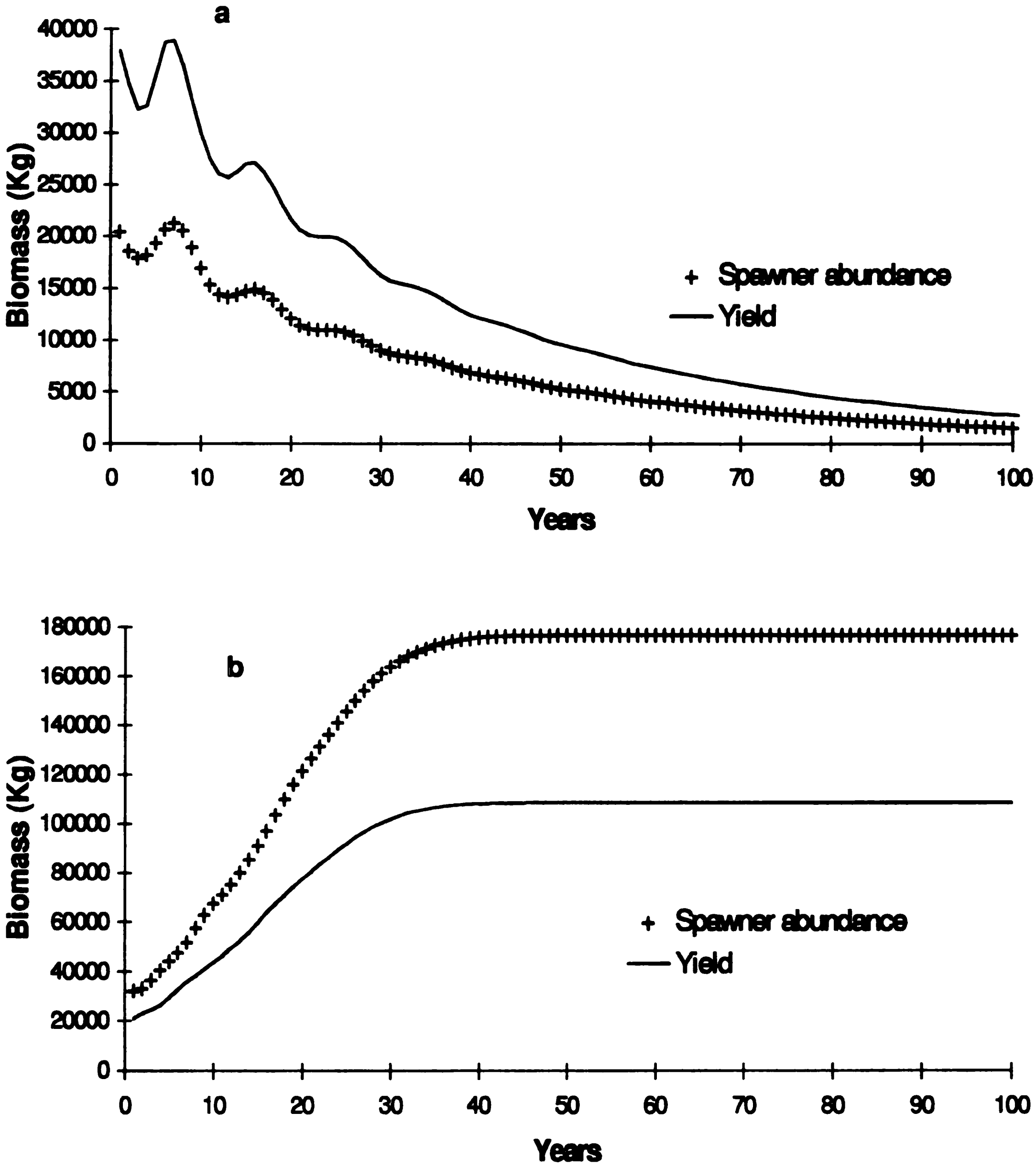


Figure 30. Yield and spawner abundance projections for lake trout in MI4 of Lake Superior based on (a) fishing intensity rate equal to that estimated for 1994 (f =0.67), and (b) fishing intensity rate reduced 32% (f =0.45) from the 1994 f estimate. Projections in year 0 correspond to the year 1995.

Table 4. One hundred year projected values of recruitment (number), spawner abundance, and total annual yield (both in Kg) of lake trout in MI4 of Lake Superior. The 1994 estimate of fishing intensity (*f*) was used as a baseline value.

Fishing intensity (*f*)	Reduction from *f* 1994 (%)	Recruits (number)	Spawner biomass (Kg)	Yield (Kg)	Note
0.67	0	9,150	1,510	2,659	SCAA estimate for 1994
0.65	3	17,190	2,851	4,791	SCAA estimated 1990-1994 average
0.60	10	65,796	11,264	16,836	
0.57	15	138,298	24,987	34,089	
0.53	20	232,066	45,601	56,370	Total mortality (*A*)=45% for age-7
0.50	25	318,988	69,348	77,223	
0.47	30	384,106	92,689	92,576	
0.45	32	407,162	103,127	97,769	Total mortality (*A*)=45% for age-10
0.43	35	428,748	114,780	102,385	
0.40	40	457,511	135,985	107,779	
0.37	45	473,600	156,596	109,605	
0.33	50	479,276	176,707	108,424	

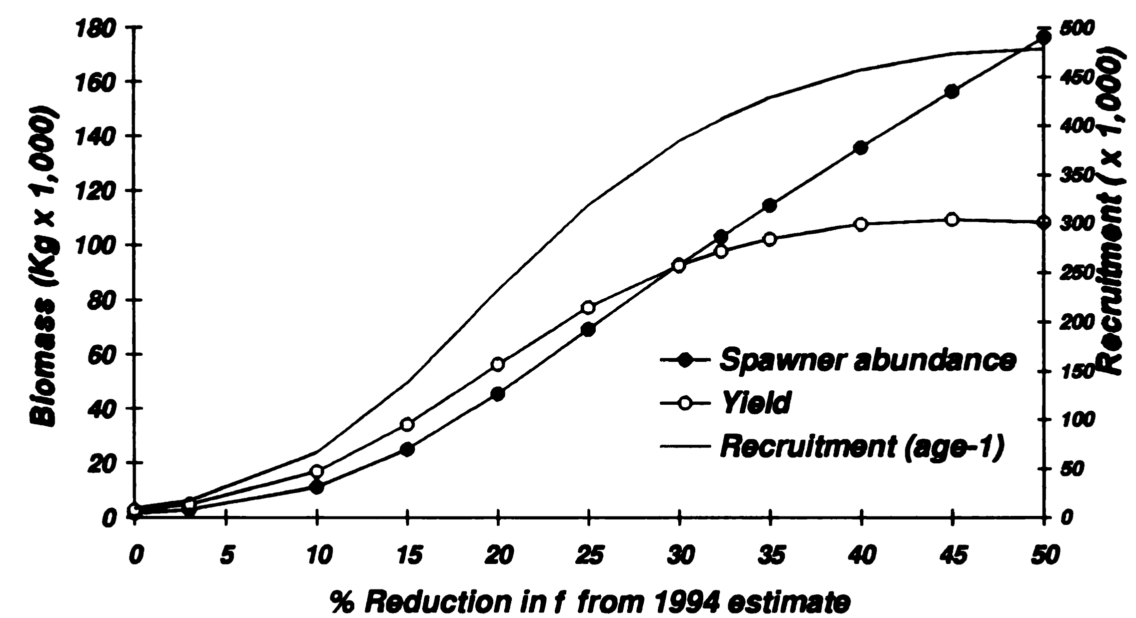


Figure 31. One hundred year projections of recruitment (numbers), spawner abundance, and total annual yield (both in Kg) of lake trout in MI4 using the 1994 estimate of fishing intensity (*f* = 0.67) as a baseline value.

compliance of the 45% mortality goal for spawning lake trout. Another concern is that small changes in fishing intensity (i.e. 20%) resulted in opposite trends of either increasing or deceasing yields. Establishing total mortality targets below 45% may actually provide higher long term yields.

Stocked lake trout mortality

Changes in survival of young stocked lake trout were probably the result of intensive fishing and environmental responses to over 30 years of stocking. When stocking was initiated in the 1960's, wild abundance was low, and stocked lake trout survived well because there was little competition and/or predation from wild fish. Early plants of stocked lake trout in Michigan waters of Lake Superior successfully spawned on inshore spawning reefs. Over-exploitation of lake herring appears to be responsible for a dramatic reduction in the forage base in the early 1980's (Selgeby 1992), and increasing numbers of wild fish competed for food and habitat with stocked lake trout. As a result, survival and growth for both wild and stocked fish began to decline in the early 1980's. Repeated years of stocking must have influenced the entire lake ecosystem. As forage base levels were reduced, wild lean stocks and siscowet populations may have preyed more heavily on young lake trout. Survival rates of young stocked lake trout may be less than those of wild fish simply because they are easier for predators to locate and capture. If supplemental stocking is required in the future, managers should examine different stocking approaches (timing and location of plants, size/age of fish at release, etc.).

Progress of lake trout restoration

The long term goal set by the Lake Superior Technical Committee (LSTC) is to achieve a sustainable lake trout yield of 2 million kg per year - the average annual yield in 1929-1943 (GLFC 1996). One way to assess progress toward the long term goal is to measure or estimate the number of recruits that are produced by the spawning stock in an individual management area (GLFC 1996). The LSTC has estimated that 3.6 million recruits per year lake-wide is required to produce the annual yield of 2 million kg, based on a natural mortality rate of 0.12. Using total surface area of lean lake trout habitat in Lake Superior, this breaks down to 305,444 recruits required for MI4 annually. I estimated the mean number of recruits from 1986-1990, the last 5 years that recruitment was estimated, and obtained a value of 141,788, or 46.4% of the objective estimated by the LSTC. Thus, if we were able to double our present levels of recruitment, we should be within 10% of the long-term restoration goal for MI4. Projections based on the stock recruitment relationship for MI4, however, indicate that a 45% reduction in fishing mortality would maximize both recruitment and yield (Table 7) at 437, 600 recruits and a yield of 109,600 Kg. The ratio of the area of MI4 (1,430 Km^2) to the area of the lake (16,856 Km^2) is approximately 8.5%. Using this as a scaling factor, I estimate the maximum lakewide sustainable yield as 1.3 million Kg.

According to the restoration plan, achievement of the target level of recruitment would suggest that the long-range goal for lake trout restoration in that area has been achieved (GLFC 1996). However, results from the SCAA and stock recruitment models for MI4 produced much less yield and spawners per recruit than those predicted using a constant natural mortality of 0.12. In my model I used age-specific mortality rates reported by Sitar (1996) ranging from 0.66 for age-1 fish to 0.10 for fish age-5 and older. Predictions from the wild lake trout model appeared to fit observed data well suggesting that the assumed mortality rates were reasonable. Results from my stocked lake trout model suggested that natural mortality may have changed over time. A wide range of natural mortality estimates (excluding sea lamprey induced mortality) have been previously reported for lake trout in Lake Superior: 0.26 by Pycha (1980), 0.10-0.25 by Sakagawa and Pycha (1971), and 0.31 for wild fish by Ebener (1990). Accurate estimates of natural mortality are essential for predicting allowable harvests, and establishing restoration targets based on a single natural mortality rate of 0.12 appears questionable.

Suggestions for future research

Results from the statistical catch-at-age models for lake trout in MI4 were based on a method similar to Methot's (1990) stock synthesis approach. This approach uses a maximum likelihood function to fit model estimates to observed data. CPUE and harvest variance estimates are internalized in the log-likelihood objective function, and act as weighting factors to the overall solution. In the MI4 model, I assumed spring and summer assessment data came from simple random samples. According to J. Peck, Michigan DNR (pers. com.), assessments targeted fixed locations spread out over the study area each year, with replicate samples at each location. Treating fixed stations, spread out in space, as random samples may result in an overestimation of the variance in CPUE. In addition, assessment data may also contain cluster (year and station) effects which could bias variance estimates for CPUE. It is also possible that use of fixed stations leads to biased trends in CPUE indices, if the fixed stations are not representative of the entire study area. Future research should examine possible temporal and spatial correlations caused by the sampling design.

A common assumption used in catch-at-age and VPA models is that catch is known (Hilborn and Walters 1992; Bence et al. 1993). In the MI4 model, I assumed that the coefficient of variation (CV) in reported harvest to be 1.0%. M. Ebener, COTFMA (pers. com.), suggested that the error rate in reported harvest was probably higher than the 1.0% CV that I used for the MI4 fishery. Model simulations based on a 15% error rate showed similar mortality estimates to the original model (1.0% error rate), but nearly doubled the width of the 90% confidence interval of the fishing intensity estimate in 1991. Accuracy of reported harvest appears to greatly affect the reliability of the model results. Fishery management agencies need to stress the importance of accurate catch reports and determine methods to reduce under reporting of harvest.

<u>Managing toward the long term goal</u>

The target yield called for by the restoration plan was based on the 1929-1943 average annual yield. Two critical biological events have taken place within the lake since that time period: (1) sea lampreys invaded the lake in the late 1940's (Pycha and King 1975), and (2) the forage base for adult lake trout has significantly changed over time (Bronte and Hoff 1996; Selgeby 1992; Dryer et al. 1965). Chemical treatments of TFM has proven to be an effective method for killing ammocoetes, but after 30 years of treatment sea lampreys remain a substantial mortality source of lake trout in the Great Lakes. Lake herring was historically the primary prey item of lake trout but was replaced by rainbow smelt, an exotic to the Great Lakes, as the major food of lake trout in the 1970's (Dreyer et al. 1965; Bronte 1992). Annual harvest of both lake herring and rainbow smelt in US waters have declined well below historic levels (Selgeby 1992).

Presently, lake trout management in Michigan waters of Lake Superior appears to be focused on maximizing harvest rates while maintaining total mortality rates of 45%. Uncertainties associated with estimating natural and lamprey mortality rates, stochastic environmental events, time varying growth and mortality, sampling and ageing error, etc. . . . , can distort estimates of mortality from true mortality rates experienced by the population. Management objectives have not resulted in increasing wild lake trout stocks in MI4 through 1990's. If total annual mortality of lake trout is to remain a rehabilitation objective, fishery managers need to carefully analyze two critical issues: (1) is the objective mortality rate currently being met, and if not, how can compliance be enforced; and (2) will the mortality rate objective lead to lake trout restoration. Projections for MI4 indicated that a total annual mortality rate equal to 45% for age-7 fish (greater than 45% for fish older than age-7) slightly increased yields. However, when mortality was reduced below 45% for age 7-9 fish (equal to 45% for age-10 fish) the projected yield was nearly double that produced when mortality was equal to 45% for age-7 (Table 7, Figure 31).

Finally, to achieve the long term goal of the restoration plan, conditions within Lake Superior must be similar, or better, to the conditions that existed before the invasion of sea lamprey and before major changes occurred in the forage base. Whether this goal is realistic or not is debatable, but the direction of the long term goal seems appropriate in that it implies that fishery management agencies should continue to conduct scientific research, control harvest, reduce sea lamprey induced mortality, and improve lake trout habitat. Total restoration of lake trout in Lake Superior may not be possible unless sea lamprey are eradicated and harvest of lake trout and forage fish is strictly controlled.

APPENDIX - ADDITIONAL TABLES

Table 5. Model ageing error matrix for 1971-1988 based on lake trout samples from Michigan waters of Lake Superior, 1993-1995. True ages determined from finclips of stocked lake trout. Coded ages determined by scale annuli. Data supplied by Michigan Department of Natural resources.

True	Coded Ages														
Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0.1016	0.7367	0.1608	0.0006	0	0	0	0	0	0	0	0
5	0	0	0	0.0003	0.158	0.7644	0.0773	0.0001	0	0	0	0	0	0	0
6	0	0	0	0	0.0107	0.2525	0.586	0.1473	0.0035	0	0	0	0	0	0
7	0	0	0	0	0.0007	0.1669	0.7285	0.1036	0.0002	0	0	0	0	0	0
8	0	0	0	0	0.0004	0.0186	0.1942	0.473	0.2751	0.0376	0.0012	0	0	0	0
9	0	0	0	0.0015	0.0143	0.0733	0.2035	0.3077	0.2537	0.114	0.0279	0.0037	0.0003	0	0
10	0	0	0	0.0002	0.0035	0.0269	0.1113	0.251	0.3084	0.2066	0.0754	0.0149	0.0016	0.0001	0
11	0	0	0	0	0.0007	0.0076	0.0468	0.1575	0.2884	0.2879	0.1566	0.0464	0.0075	0.0007	0
12	0	0	0	0	0.0001	0.0016	0.0151	0.0759	0.2074	0.3086	0.2503	0.1106	0.0266	0.0035	0.0003
13	0	0	0	0	0	0.0003	0.0037	0.0281	0.1147	0.2545	0.3075	0.2026	0.0727	0.0142	0.0016
14	0	0	0	0	0	0	0.0007	0.008	0.0488	0.1614	0.2907	0.2854	0.1528	0.0445	0.0077
15	0	0	0	0	0	0	0.0001	0.0017	0.0159	0.0787	0.2114	0.3093	0.2467	0.1073	0.0288

Table 6. Model ageing error matrix for 1989-1994 based on lake trout samples from Michigan waters of Lake Superior, 1993-1995. True ages determined from finclips of stocked lake trout. Coded ages determined by scale annuli up to age-8 and by otoliths age-9 and older. Data supplied by Michigan Department of Natural resources.

True	Coded Ages														
Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0.1016	0.7367	0.1608	0.0006	0	0	0	0	0	0	0	0
5	0	0	0	0.0003	0.158	0.7644	0.0773	0.0001	0	0	0	0	0	0	0
6	0	0	0	0	0.0107	0.2525	0.586	0.1473	0.0035	0	0	0	0	0	0
7	0	0	0	0	0.0007	0.1669	0.7285	0.1036	0.0002	0	0	0	0	0	0
8	0	0	0	0	0.0004	0.0186	0.1942	0.473	0.2751	0.0376	0.0012	0	0	0	0
9	0	0	0	0	0.0001	0.004	0.0729	0.3417	0.4263	0.1423	0.0124	0.0003	0	0	0
10	0	0	0	0	0	0.0002	0.0085	0.1144	0.4012	0.3757	0.0939	0.0061	0.0001	0	0
11	0	0	0	0	0	0	0.0004	0.0168	0.1685	0.4424	0.311	0.0581	0.0028	0	0
12	0	0	0	0	0	0	0	0.0011	0.0312	0.2328	0.4583	0.2417	0.0337	0.0012	0
13	0	0	0	0	0	0	0	0	0.0025	0.0543	0.302	0.446	0.1764	0.0183	0.0005
14	0	0	0	0	0	0	0	0	0.0001	0.0055	0.0885	0.3679	0.4077	0.1208	0.0095
15	0	0	0	0	0	0	0	0	0	0.0002	0.0113	0.1353	0.4209	0.3502	0.0821

Table 7. Fitted parameters from statistical catch-at-age constant growth (CG) and time-varying growth (TVG) models for wild and stocked lake trout in MI4.

Parameter	Description	Estimates			
		Wild CG	Wild TVG	Stocked CG	Stocked TVG
k	Von Bertalanffy	0.213	0.270	0.074	0.128
to	growth parameters	0.699	0.837	-1.940	-0.640
L-inf (71)	L-infinity	28.881	26.799	39.997	32.292
L-inf (72)		28.881	29.052	39.997	35.871
L-inf (73)		28.881	25.167	39.997	33.424
L-inf (74)		28.881	27.204	39.997	33.418
L-inf (75)		28.881	29.704	39.997	37.267
L-inf (76)		28.881	30.059	39.997	36.461
L-inf (77)		28.881	29.302	39.997	31.515
L-inf (78)		28.881	31.619	39.997	39.997
L-inf (79)		28.881	27.694	39.997	31.289
L-inf (80)		28.881	31.093	39.997	31.760
L-inf (81)		28.881	19.389	39.997	39.983
L-inf (82)		28.881	29.184	39.997	38.066
L-inf (83)		28.881	16.119	39.997	12.671
L-inf (84)		28.881	32.165	39.997	29.019
L-inf (85)		28.881	22.008	39.997	35.299
L-inf (86)		28.881	24.026	39.997	33.977
L-inf (87)		28.881	23.935	39.997	27.029
L-inf (88)		28.881	27.590	39.997	33.683
L-inf (89)		28.881	27.691	39.997	31.810
L-inf (90)		28.881	26.524	39.997	36.282
L-inf (91)		28.881	25.845	39.997	32.678
L-inf (92)		28.881	27.915	39.997	29.463
L-inf (93)		28.881	27.850	39.997	39.997
L-inf (94)		28.881	29.236	39.997	39.997
L-inf (95)		28.881	34.500	39.997	34.615
a	Variation in age-length composition CV = a + bx (b=0)	0.163	0.138	0.188	0.172

Table 8. Fitted parameters from statistical catch-at-age constant growth (CG) and time-varying growth (TVG) models for wild and stocked lake trout in MI4. Values with and asterix (*) were set at zero since no fish were stocked in that particular year.

Parameter	Description	Estimates			
		Wild CG	Wild TVG	Stocked CG	Stocked TVG
$N_{a=1}$ (71)	Age-1 abundance	23370	14694	513642	342321
$N_{a=1}$ (72)		34367	25682	906642	618452
$N_{a=1}$ (73)		25540	13428	641903	641903
$N_{a=1}$ (74)		66942	22984	789603	494094
$N_{a=1}$ (75)		458481	179581	1208935	643597
$N_{a=1}$ (76)		231380	145903	1196081	547982
$N_{a=1}$ (77)		325881	115978	1549875	672214
$N_{a=1}$ (78)		92265	83990	612599	389516
$N_{a=1}$ (79)		135443	115451	110593	107729
$N_{a=1}$ (80)		93479	140509	63443	62255
$N_{a=1}$ (81)		114549	111850	67304	65613
$N_{a=1}$ (82)		229045	235093	55292	54052
$N_{a=1}$ (83)		230276	229363	33267	33142
$N_{a=1}$ (84)		168126	145268	* 0	* 0
$N_{a=1}$ (85)		261182	266635	54677	50873
$N_{a=1}$ (86)		280070	246658	36301	32121
$N_{a=1}$ (87)		175500	152247	23785	21167
$N_{a=1}$ (88)		115894	101033	40590	36837
$N_{a=1}$ (89)		98653	79444	34130	24331
$N_{a=1}$ (90)		190928	129558	* 0	* 0
$N_{a=2}$ (71)	Abundance age-2	12192	8923	838589	561414
$N_{a=3}$ (71)	Abundance age-3	9868	6886	494764	337333
$N_{a=4}$ (71)	Abundance age-4	10813	8050	383528	292384
$N_{a=5}$ (71)	Abundance age-5	6316	4537	165399	134693
$N_{a=6}$ (71)	Abundance age-6	1300	1032	118237	104871
$N_{a=7}$ (71)	Abundance age-7	449	368	31527	31527
$N_{a=8}$ (71)	Abundance age-8			54322	54322
alpha $_{LM}$	Selectivity function	1.769	1.646	1.771	1.740
beta $_{LM}$	parameters	0.298	0.263	0.192	0.251
alpha $_{GM}$		37.509	35.523	20.129	21.303
beta $_{GM}$		2.337	2.230	1.197	1.293
alpha $_{F}$		27.486	25.387	0.775	0.390
beta $_{F}$		1.207	1.067	1.23E-47	1.23E-47
q_{LM}	Catchability	4.92E-04	5.70E-04	6.37E-04	5.02E-04
q_{GM}		4.79E-04	4.91E-04	1.84E-04	2.16E-04

Table 9. Fitted parameters from statistical catch-at-age constant growth (CG) and time-varying growth (TVG) models for wild and stocked lake trout in MI4.

Parameter	Description	Estimates			
		Wild CG	Wild TVG	Stocked CG	Stocked TVG
f (83)	Fishing intensity	0.078	0.081	0.300	0.149
f (84)		0.175	0.276	1.152	0.796
f (85)		0.182	0.195	0.521	0.441
f (86)		0.340	0.458	1.510	1.165
f (87)		0.261	0.363	0.608	0.458
f (88)		0.622	0.927	1.023	0.867
f (89)		0.700	0.902	1.094	0.800
f (90)		0.699	0.776	1.208	0.822
f (91)		0.596	0.657	1.286	0.782
f (92)		0.506	0.592	0.682	0.446
f (93)		0.453	0.539	0.760	0.591
f (94)		0.519	0.666	1.242	0.848
Z_{MF} (71-72)	Combined natural and fishing			0.306	0.285
Z_{MF} (71-80)	mortality (age-5 and older)	0.100	0.100		
Z_{MF} (73-74)				0.578	0.430
Z_{MF} (75-76)				0.443	0.262
Z_{MF} (77-80)				0.477	0.487
Z_{MF} (81-82)		0.942	0.628	1.395	1.039

Table 10. Commercial harvest, mean weight, recreational harvest, and total harvest of lean lake trout in MI4 of Lake Superior, 1983-1994. The 1990 commercial harvest was determined from the average mean weight from the two adjacent years. The recreational harvest prior to 1987 is estimated as the mean recreational harvest from 1987-1989. Data provided by Great Lakes Indian Fish and Wildlife Commission and Michigan Department of Natural Resources.

Year	Commercial Fishery				Recreational	Total
	Total Catch (dressed wt in lbs)	Mean Weight (lbs)	Total Catch (numbers)	Trap Net Incidental	Catch (numbers)	Harvest
1983	15900	4.03	3941		9166	13107
1984	91725	3.00	30601		9166	39767
1985	49132	3.70	13273	45	9166	22484
1986	135821	3.77	36028	38	9166	45232
1987	75346	3.34	22548	22	4675	27244
1988	130756	2.75	47501		8319	55820
1989	119283	2.89	41321		14504	55825
1990	144899		50459	11	3606	54076
1991	108305	2.86	37915	6	5866	43787
1992	86671	3.30	26239	1	4789	31029
1993	77152	3.55	21736	40	4898	26674
1994	76295	2.91	26211	40	6051	32303

Table 11. Observed (obs.) and predicted (pred.) harvest (in numbers) from time-varying growth models for wild and stocked lake trout in MI4. Observed data obtained from Michigan Department of Natural Resources and the Great Lakes Indian Fish and Wildlife Commission.

Year	Wild obs. harvest	Wild pred. harvest	Stocked obs. harvest	Stocked pred. harvest
1983	3130	3130	9977	9981
1984	8309	8308	31458	31579
1985	10113	10111	12372	12374
1986	22164	22166	23068	23120
1987	20228	20231	7017	7023
1988	46878	46931	8942	8926
1989	48847	48815	6978	6972
1990	47557	47517	6519	6507
1991	37521	37505	6266	6251
1992	27402	27404	3627	3625
1993	22399	22414	4275	4275
1994	26367	26367	5936	5932

Table 12. Number of gill net lifts, mean catch per unit effort (CPUE), coefficient of variation (CV) of CPUE from individual years, and variation of mean CPUE all years combined ($CV\ mean = \overline{CV}\ divided\ by\ \sqrt{lifts}$) for wild and stocked lake trout caught in spring assessments in MI4 of Lake Superior from 1971-1995. Data from Michigan Department of Natural Resources.

Year	# Lifts	Wild lake trout			Stocked lake trout		
		Mean CPUE	CV	CV mean	Mean CPUE	CV	CV mean
1971	43	1.072	0.960	0.097	45.461	0.903	0.117
1972	25	3.670	0.809	0.127	69.068	0.910	0.154
1973	15	5.630	0.627	0.164	119.73	0.604	0.199
1974	34	4.786	0.581	0.109	87.399	0.531	0.132
1975	19	4.553	0.580	0.145	84.264	0.776	0.176
1976	36	6.717	0.684	0.106	121.209	0.768	0.128
1977	24	9.974	0.590	0.129	140.195	0.503	0.157
1978	29	14.623	0.866	0.118	117.323	0.634	0.143
1979	14	34.631	0.552	0.169	112.963	0.564	0.205
1980	21	45.075	0.492	0.138	102.533	0.549	0.168
1981	25	41.363	0.510	0.127	63.673	0.784	0.154
1982	33	23.345	0.597	0.110	47.832	0.792	0.134
1983	41	17.990	0.567	0.099	35.905	0.554	0.120
1984	24	19.822	0.393	0.129	31.036	0.617	0.157
1985	21	24.881	0.658	0.138	23.637	0.722	0.168
1986	22	41.231	0.511	0.135	17.288	0.769	0.164
1987	27	33.724	0.483	0.122	5.303	0.680	0.148
1988	60	39.370	0.717	0.082	4.050	0.907	0.099
1989	79	28.517	0.674	0.071	3.784	0.860	0.086
1990	48	41.137	0.741	0.092	3.418	0.841	0.111
1991	46	36.850	0.672	0.093	2.721	1.044	0.113
1992	36	28.522	0.483	0.106	3.173	0.836	0.128
1993	40	22.024	0.624	0.100	2.795	1.000	0.122
1994	32	18.001	0.767	0.112	2.448	0.899	0.136
1995	30	25.388	0.709	0.116	4.342	1.176	0.140
		Mean:	0.634		Mean:	0.769	

Table 13. Number of gill net lifts, mean catch per unit effort (CPUE), coefficient of variation (CV) of CPUE from individual years, and variation of mean CPUE all years combined ($CV\ mean = \overline{CV}\ divided\ by\ \sqrt{lifts}$) for wild and stocked lake trout caught in summer assessments in MI4 of Lake Superior from 1985-1995. Data from Michigan Department of Natural Resources.

Year	# Lifts	Wild lake trout			Stocked lake trout		
		Mean CPUE	CV	CV mean	Mean CPUE	CV	CV mean
1985	5	59.680	0.714	0.330	10.624	0.199	0.385
1986	13	68.998	0.764	0.204	8.194	0.801	0.239
1987	14	50.998	0.676	0.197	5.580	1.063	0.230
1988	14	71.996	0.731	0.197	4.687	0.845	0.230
1989	14	48.171	0.824	0.197	4.687	0.758	0.230
1990	14	50.124	0.633	0.197	3.906	1.017	0.230
1991	14	47.650	0.632	0.197	4.557	1.014	0.230
1992	14	42.833	0.731	0.197	4.947	1.016	0.230
1993	14	53.900	0.925	0.197	3.255	0.962	0.230
1994	14	35.152	0.741	0.197	3.645	0.941	0.230
		Mean:	0.737			0.862	

LIST OF REFERENCES

LIST OF REFERENCES

Baldwin, N.S., R.W. Saalfeld, M.A. Ross, and H.J. Buettner. 1979. Commercial fish production in the Great Lakes 1867-1997. Great Lakes Fishery Commission Technical Report No. 3.

Bence, J.R., A. Gordoa, and J.E. Heightower. 1993. Influence of age-selective surveys on the reliability of stock synthesis assessments. Canadian Journal of Fisheries and Aquatic Sciences 50: 827-840.

Bergstedt, R.A. and C.P. Schneider. 1988. Assessment of sea lamprey (*Petromyzon marinus*) predation by recovery of dead lake trout (*Salvelinus namaycush*) from Lake Ontario, 1982-85. Canadian Journal of Fisheries and Aquatic Sciences 45: 1406-1410.

Bronte, C.R. and M.H. Hoff. 1996. Population status and trends for Lake Superior forage fishes, 1978-1995. Presented at: Lake Superior Committee 1996 annual meeting. Duluth, Minnesota.

Burnham-Curtis, M.K., and G.R. Smith. 1994. Osteological evidence of genetic divergence of lake trout (*Salvelinus namaycush*) in Lake Superior. Copeia 1994: 843-850.

Deriso, R.B., T.J. Quinn II, and P.R. Neal. 1985. Catch-age analysis with auxiliary information. Canadian Journal of Fisheries and Aquatic Sciences 42: 815-824.

Doubleday, W.G. 1976. A least squares approach to analyzing catch at age data. International Commission for the Northwest Atlantic Fisheries Research Bulletin 12: 69-81.

Dryer, W.R., L.F. Erkkila, and C.L. Tetloff. 1965. Food of the lake trout in Lake Superior. Transactions of the American Fisheries Society 94:169-176.

Ebener, M. P. 1990. Assessment and mark-recapture of lake trout spawning stocks around the Keweenaw Peninsula area of Lake Superior. Great Lakes Indian Fish and Wildlife Commission Biological Services Division Administrative Report 90-8, Odanah, Wisconsin.

Ebener, M.P. 1986. Keweenaw Bay tribal commercial fishery statistics for license years 1984 and 1985. A report prepared for the Keweenaw Bay Tribal Council. Great Lakes Indian Fish and Wildlife Commission. Odanah, Wisconsin.

Ebener, M.P., J.H. Selgeby, M.P. Gallinat, and M. Donofrio. 1989. Methods for determining total allowable catch of lake trout in the 1842 treaty-ceded area within Michigan waters of Lake Superior, 1990-1994. Great Lakes Indian Fish and Wildlife Commission Administrative Report 89-11. 38p.

Eschmeyer, P. H. 1955. The reproduction of lake trout in southern Lake Superior. Transactions of the American Fisheries Society 84: 47-74.

Eshenroder, R.L. and J.F. Koonce. 1984. Recommendations for standardizing the reporting of sea lamprey marking data. Great Lakes Fishery Commission Special Publication 84-1.

Ferreri, C.P. 1995. Role of compensatory mechanisms in the population dynamics of lake trout (*Salvelinus namaycush*) in the U.S. waters of Lake Superior. Doctoral Dissertation. Michigan State University, East Lansing, Michigan.

Fournier, D. and C.P. Archibald. 1982. A general theory for analyzing catch at age data. Canadian Journal of Fisheries and Aquatic Sciences 39: 1195-1207.

Greig, L., D. Meisner, and G. Christie. 1992. Manual for the management protocol for the implementation of integrated management of sea lamprey in the Great Lakes Basin. Version 1.1. Great Lakes Fishery Commission Report.

Goodier, J.L. 1981. Native lake trout (*Salvelinus namaycush*) stocks in the Canadian waters of Lake Superior prior to 1955. Canadian Journal of Fisheries and Aquatic Sciences 38: 1724-1737.

GLFC (Great Lakes Fishery Commission). 1980. A joint strategic plan for management of Great Lakes fisheries. Great Lakes Fishery Commission, Ann Arbor, Michigan.

GLFC (Great Lakes Fishery Commission). 1986. A lake trout restoration plan for Lake Superior. Great Lakes Fishery Commission, Ann Arbor, Michigan.

Hansen, M.J., J.R. Bence, J.W. Peck, and W.W. Taylor. in press. Importance of stocked lake trout to population recoveries in Michigan's waters of Lake Superior.

Hansen, M.J., J.W. Peck, R.G. Schorfhaar, J.H. Selgeby, D.R. Schreiner, S.T. Schram, B.L. Swanson, W.R. MacCallum, M.K. Burnham-Curtis, G.L. Curtis, J.W. Heinrich, and R.J. Young. 1995. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration in 1959-1993. Journal of Great Lakes Research 21(Supplement 1):152-175.

Hansen, M.J., M.P. Ebener, R.G. Schorfhaar, S.T. Schram, D.R. Schreiner, and J.H. Selgeby. 1994. Declining survival of lake trout stocked in U.S. waters of Lake Superior during 1963-1986. North American Journal of Fisheries Management 14:395-402.

Healey, M. C. 1978. The dynamics of exploited lake trout populations and implications for management. Journal of Wildlife Management 42: 307-328.

Hilborn, R. and C.J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York, N.Y.

Hile, R., P.H. Eschmeyer, and G.F. Lunger. 1951. Status of the lake trout fishery in Lake Superior. Transactions of the American Fisheries Society 80: 278-312.

Hile R. 1962. Collection and analysis of commercial fishery statistics in the Great Lakes. Great Lakes Fishery Commission Technical Report 5.

Johnson G. And W. MacCallum. 1987. Otolith acetate replicate pilot project. Ontario Ministry of Natural Resources, Lake Superior Fisheries Unit, Thunder Bay, Ontario. Quick Report 87-3.

Khan, N.Y., and S.U. Qadri. 1970. Morphological differences in Lake Superior lake char. Journal of the Fisheries Research board of Canada 27: 161-167.

Koonce, J.F., R. L. Eshenroder, and G. C. Christie. 1993. An economic injury level approach to establishing the intensity of sea lamprey control in the Great Lakes. North American Journal of Fisheries Management 13: 1-14.

Law, A.M. and W.D. Kelton. 1982. Simulation modeling and analysis. McGraw-Hill, New York, NY.

Lawrie, A.H. and J. F. Rahrer. 1973. Lake Superior: a case history of the lake and its fisheries. Great Lakes Fishery Commission Technical Report 19.

Loftus, K.H. 1958. Studies on river-spawning populations of lake trout in eastern Lake Superior. Transactions of the American Fisheries Society 87: 259-277.

LSLTTC (Lake Superior Lake Trout Technical Committee). 1986. A lake trout rehabilitation plan for Lake Superior. Pages 47-62 *in* S.D. Morse, editor. Lake Superior Committee 1986 annual meeting minutes. Great Lakes Fishery Commission, Ann Arbor, Michigan.

Marshall T.R., R.A. Ryder, C.J. Edwards, G.R. Spangler. !987. Using the lake trout as an indicator of ecosystem health- application of the dichotomous key. Great Lakes Fishery Commission Technical Report 49.

Mattes, W.P., M.P. Gallinat, and M. Donofrio. 1996. Biological and commercial catch statistics from the Chippewa inter-tribal gill net fishery within Michigan Waters of Lake Superior During 1995.

Methot, R.D. 1990. Synthesis model: an adaptable framework for analysis of diverse stock assessment data, p.259-277. *In* L. Low, editor. Proceedings of the symposium on applications of stock assessment techniques to Gadids. International North Pacific Fisheries Commission Bulletin 50.

Nute, G.L. 1944. Lake Superior. The American Lakes Series. Bobbs-Merrill, Indianapolis. 376 p.

Peck, J.W. 1979. Utilization of traditional spawning reefs by hatchery lake trout in the upper Great Lakes. Michigan Department of Natural Resources Fisheries Research Report 1871.

Peck, J.W., and R.G. Schorfhaar. 1994. Lake trout assessment and management in Michigan waters of Lake Superior, 1988-92. Michigan Department of Natural Resources Fisheries Research Report 2010.

Peck, J.W., and R.G. Schorfhaar. 1991. Assessment and management of lake trout stocks in Michigan waters of Lake Superior. Michigan Department of Natural Resources Fisheries Research Report 1956.

Pycha, R.L. 1980. Changes in mortality of lake trout (*Salvelinus namaycush*) in Michigan waters of Lake Superior in relation to sea lamprey (*Petromyzon marinus*) predation, 1968-78. Canadian Journal of Fisheries and Aquatic Sciences 37:2063-2073.

Pycha, R.L., and King, G.R. 1975. Changes in the lake trout population of southern Lake Superior in relation to the fishery, the sea lamprey, and stocking, 1950-70. Ann Arbor, MI. Great Lakes Fishery Commission Technical Report 28.

Pycha, R.L., W.R. Dryer, and G.R. King. 1965. Movements of hatchery-reared lake trout in Lake Superior. Journal of the Fisheries Research board of Canada 22: 999-1024.

Rahrer, J.F. 1965. Age, growth, maturity, and fecundity of "humper" lake trout, Isle Royale, Lake Superior. Transactions of the American Fisheries Society 94:75-83.

Rahrer, J.F. 1968. Movements of adult lake trout in Lake Superior. Transactions of the American Fisheries Society 97: 481-484.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191:382p.

Sakagawa, G.T. and R.L. Pycha. 1971. Population biology of lake trout (*Salvelinus namaycush*) of Lake Superior before 1950. Journal of the Fisheries Board of Canada 28:65-71.

Seber, G.A.F. and C.J. Wild. 1989. Nonlinear Regression. John Wiley and Sons, New York, NY.

Selgeby, J.H. 1992. Status of forage populations in Lake Superior. In *Minutes Lake Superior Committee (1992 Annual Meeting)*, Duluth, Minnesota, Great Lakes Fishery Commission. March 17-18, 1992.

Selgeby, J.H. 1981. Decline of lake herring (*Coregonus artedii*) in Lake Superior: an analysis of the Wisconsin Herring Fishery, 1936-78. Canadian Journal of Fisheries and Aquatic Sciences 39: 554-563.

Sitar, S.P. 1996. Estimation of lake trout (*Salvelinus namaycush*) abundance and mortality due to sea lampreys (*Petromyzon marinus*) and fishing in the main basin of Lake Huron, 1984-1993. Masters Thesis. Michigan State University, East Lansing, Michigan.

Smith, B.R., and Tibbles. 1980. Sea lampreys (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936-78. Canadian Journal of Fisheries and Aquatic Sciences 37: 1780-1801.

Swanson, B.L. 1973. Lake trout homing, migration, and mortality studies, Lake Superior. Wisconsin Department of Natural Resources Fish Management Report 65.

Technical Fisheries Review Committee. 1992.Status of the fishery resource-1991. A report by the Technical Fisheries Review Committee on the assessment of lake trout and lake whitefish in treaty-ceded waters of the upper Great Lakes: State of Michigan. Mimeo. Rep. 97p.

Walters, C.J., G. Steer, and G. Spangler. 1980. Responses of lake trout (*Salvelinus namaycush*) to harvesting, stocking, and lamprey predation. Canadian Journal of Fisheries and Aquatic Sciences 37: 2133-2145.

Warren, W.W. 1957. History of the Ojibway nation. Ross and Haines Inc., Minneapolis, Minn. 527p.