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Statistical Catch-at-Age Framework for Chinook Salmon in Lake Michigan, 1985-1996

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Abstract.–Successful management of the Lake Michigan salmonine sport fishery requires an understanding of mortality rates, abundance, and age structure. A stock assessment model for chinook salmon is presented in order to estimate the population size and age structure from 1967-1996. The model predicted sport fishery harvest and age structure, fishery effort, and returns to weirs, from 1985-1996. Model parameters were estimated by matching these predictions to observations of these same quantities using a maximum likelihood approach within a statistical catch-at-age analysis framework. Mortality rates were estimated for four sources of mortality: 1) fishing, 2) baseline continuous natural mortality, 3) spawning mortality, and 4) other time-varying natural mortality. Results indicate a large decline in the abundance of chinook salmon ages 2-5 from 1987-1994, in agreement with observed declines in fishery CPUE data. Age structure in the fishery and in the weir harvest shifted towards younger ages and reflected a shift in the population age structure. These declines were caused primarily by an increase in time-varying natural mortality for ages 2-5. Ages 0-1 did not suffer significant time-varying natural mortality. Fishing mortality did not play an important role in the population decline. This model analysis supported existing hypotheses about the role of bacterial kidney disease (BKD) mortality on the Lake Michigan chinook population. Outputs from this modeling exercise could be used to determine stocking levels, and as parameter inputs for multi-species dynamic models and bioenergetics models.

Introduction

The Pacific salmon stocking program in Lake Michigan began in the late 1960s in response to the extirpation of native lake trout (*Salvelinus namaycush*) stocks and high abundance of exotic alewives (*Alosa pseudoharengus*) (Eshenroder et al. 1995). The immediate popularity of these introduced salmonine species to the sport fishery, as well as a growing fishery-related industry, prompted state agencies to maintain an intensive stocking program. Numbers of salmonines planted in Lake Michigan peaked in 1984 at 17 million fish (Holey 1995; Benjamin and Bence 2003). However, beginning in 1987 the thriving salmonine fishery of the mid-1980s underwent a substantial decline in angling success and harvest. This was largely due to a dramatic decline in the chinook salmon (*Onchorhynchus tschawytscha*) population despite the maintenance of consistent stocking levels (Bence and Smith 1999; Benjamin and Bence 2003). While explanations for the decline have included the prevalence of a bacterial kidney disease (BKD), the root of the problem may be that levels of stocking were too high, leading to a scarcity of forage fish, nutritional stress, and BKD-induced mortality (Stewart et al. 1981; Stewart and Ibarra 1991; Koonce and Jones

1994). Few quantitative data exist about the impact of BKD-related mortality on the population (Clark 1996).

The Michigan Department of Natural Resources (MDNR), Fisheries Division expressed the need for using more rigorous modeling analyses to develop lake-wide stocking plans for salmonines (Clark 1996). Similarly, the Lake Michigan Committee of the Great Lakes Fishery Commission called for more mathematical modeling of existing data to help establish detailed management plans, and species-specific harvest levels for salmonines in Lake Michigan (Eshenroder et al. 1995). Ultimately, decisions on what species to stock, how many to stock, and where to stock them could be crucial toward reviving the chinook salmon fishery in Lake Michigan.

The goals of this study were to estimate population size and age structure of chinook salmon in Lake Michigan, and to quantify the contributions of four sources of mortality, (1) fishing mortality, (2) baseline continuous natural mortality, (3) maturation (spawning) mortality, and (4) time-varying natural mortality, to the total annual mortality of chinook salmon from 1985-1996. Furthermore, model parameters and estimates of age-specific abundance could be used as improved inputs in tropho-dynamic models for Lake Michigan (e.g. SIMPLE, Koonce and Jones 1994). This study, which incorporated an integrated modeling and data analysis approach previously used for Lake Huron salmonines (Sitar 1996), was a unique approach to investigating salmonine dynamics in Lake Michigan.

The MDNR has addressed this issue with a multi-species model, CONNECT, which is designed to predict ideal stocking levels required to meet fish community objectives for salmonines in Lake Michigan (Rutherford 1997). The CONNECT model for chinook salmon follows a CAA approach based upon the methods outlined in this paper. Other recent modeling work on chinook salmon in the Great Lakes involves a CAA model built for chinook in Lake Huron (Bence and Meehan, personal communication). The Lake Michigan chinook model presented here built on the information used by CONNECT and the structure of the Lake Huron CAA model.

Methods

The stock assessment model was an age-structured, deterministic model that estimated abundance for multiple cohorts. Initial cohort abundance was assumed to be known, and the model accounted for changes in abundance due to various sources of mortality.

Population Model

Abundance

In the model, population abundance at the start of a given year was equal to the abundance at the start of the previous year, multiplied by the proportion of that population that survives the year. While survival has typically been modeled as a function of a continuous-time instantaneous mortality rate, such that:

$$N_{y+1} = N_y e^{-Z_y}, \qquad (1)$$

much of the mortality of chinook salmon in Lake Michigan occurs over discrete, rather than continuous periods of time within a year. Preliminary analysis of sport harvest data indicates that most of the in-lake fishing mortality occurs in July and August. Similarly, analysis of weir return data suggests that most of the spawning-related mortality occurs in September and October. Chinook salmon population dynamics in Lake Michigan could be more accurately modeled using an approach that combines both continuous-time and discrete-time sources of mortality (Kope 1987; Bence and Meehan, personal communication). Therefore, the model described in Equation 1 was modified for this analysis.

Chinook salmon abundance for a cohort at the start of a calendar year was assumed to be a function of abundance of the cohort at the start of the previous year, minus losses due to natural mortality, fishing mortality, and maturation mortality, such that:

$$N_{a+1,y+1} = N_{a,y} e^{-M_{a,y}} (1 - P_{F_{a,y}})(1 - P_{MAT_a}) \qquad (2)$$

where $M_{a,y}$ was an instantaneous natural mortality rate (for age-a and year-y), $P_{Fa,y}$ was the annual proportion of the population removed by the fishery, and P_{MATa} was the annual proportion of the population that matures and returns to the streams to spawn and die. Standing stock biomass was estimated from the model's estimate of abundance-at-age and the estimated mean weight at annulus formation from the CONNECT model (Rutherford 1997).

Natural Mortality

Natural mortality ($M_{a,y}$) is an instantaneous annual rate and was assumed to operate independently of fishing mortality (Hilborn and Walters 1992). Most CAA models assume a constant natural mortality rate that applies to all ages (Megrey 1989), however, natural mortality rate for chinook salmon in Lake Michigan increased in the late 1980s in response to an outbreak of BKD (Johnson and Hnath 1991). In order to quantify the changes in natural mortality during the study period, mortality was modeled as a sum of a constant component, and a time-varying (TVM) component, such that the total natural mortality rate ($M_{a,y}$) was:

$$M_{a,y} = M_a + M_{TVM_{a,y}} \tag{3}$$

Age-specific natural mortality (M_a) was assumed to be a known constant, estimated prior to the onset of BKD-related mortality (Table 1). An estimate of the age-0 mortality rate was based upon previous modeling work on Lake Michigan salmonines during pre-BKD mortality years (Stewart et al. 1981). Mortality rate estimates for ages 1-3 were based upon estimates from West Coast populations (Rutherford 1997). Mortality rates for ages 4-5 were assumed to be equal to age-3 mortality, because any increase in mortality rates for older fish would be accounted for by TVM and maturation mortality.

Age- and year-specific TVM was estimated by the model, and affected age groups in a logistic fashion, with ages 0-5 being increasingly affected. This assumption reflected observations of BKD mortality (Nelson and Hnath 1990), and approximated assumptions of BKD mortality rates from CONNECT (Rutherford 1997) The logistic mortality function was:

$$M_{TVM\,a,y} = \frac{\gamma_y}{1+e^{-\alpha(a-\beta)}} \tag{4}$$

where a was age, γ_y was a year-specific TVM intensity parameter, and α and β were parameters that determine the shape of the logistic function. The model estimated $\ln(\gamma_y)$, $\ln(\alpha)$, and $\ln(\beta)$ as formal parameters. This logistic model forced a relationship between age-specific rates within years, while the year-specific TVM intensity parameters were unrelated between years. BKD mortality did not appear to be a significant source of mortality in Lake Michigan chinook until about 1987 (Clark 1996). Since that time, BKD-infected chinook have been observed in the population at varying levels of incidence (Clark 1996). Therefore, the model estimated TVM from 1985 to 1996. Initial parameter values were chosen that matched age- and year-specific TVM with age- and year-specific estimates of BKD mortality rates reported in the CONNECT model (Rutherford 1997).

Fishing Mortality

The Lake Michigan salmon fishery more closely resembles a seasonal fishery as opposed to a continuous fishery. Therefore, fishing mortality in the model was assumed to be an instantaneous event, occurring at the end of July. An identical approach was used for Lake Huron chinook (Bence and Meehan, personal communication). The proportion of the population removed by the fishery ($P_{Fa,y}$) was estimated as:

$$P_{F_{a,y}} = 1 - e^{-F_{a,y}} \tag{5}$$

where $F_{a,y}$ was an instantaneous mortality rate per unit time that occurs over an infinitesimally short time unit. Fishing mortality was a function of age-specific fishery selectivity (S_a) and year-specific fishing intensity (f_y) (Megrey 1989), such that:

$$F_{a,y} = S_a f_y \tag{6}$$

Selectivity to the sport fishery was assumed constant over time. Selectivity was also assumed to operate in a logistic fashion where ages 0-5 were increasingly selected for by the fishery, such that:

$$S_a = \frac{1}{1+e^{-\alpha(a-\beta)}} \tag{7}$$

where α and β determined the shape of the logistic curve, and ln(α) and ln(β) were formal parameters estimated by the model. A maximum selectivity value of 1 indicated that an age group was fully selected to the fishery.

Year-specific fishing intensities (f_y) were estimated by the model, with ln(f_y) estimated as formal parameters from 1985 through 1995. For 1967 to 1984, fishing intensity was assumed to increase linearly from zero to the 1985 level estimated by the model (Jones et al. 1993).

Maturation (Spawning) Mortality

Similar to fishing mortality, maturation mortality (MAT) was assumed to be an instantaneous event, occurring immediately after fishing mortality and before additional natural mortality. Age-specific maturation was assumed to increase in a logistic fashion from age 0 to age 4, while MAT for age-5 was assumed to equal 1. The maturation function for ages 0 through 4 was:

$$P_{MAT_a} = \frac{1}{1+e^{-\alpha(a-\beta)}} \tag{8}$$

where ln(α) and ln(β) were estimated as formal parameters. All chinook salmon were assumed to have reached maturity by age-5 because few age-6 fish are observed in the fishery and fishery-independent surveys.

Catch

Sport fishery catch, or harvest, was assumed to occur as an instantaneous event, during which time the population was subject to no other sources of mortality, and after 7 months of natural mortality had taken place (Bence and Meehan, personal communication). A common approach in catch-at-age analysis is to assume that fishing mortality operates in an approximately continuous fashion, thereby warranting the use of the standard Baranov equation to estimate catch (Hilborn and Walters 1992). For intensely seasonal fisheries, the approach taken here can provide a better approximation of catch than the Baranov equation (Mertz and Myers 1996). Catch is the proportion of the population abundance, remaining after seven months, that dies from fishing, and was estimated by:

$$C_{a,y} = N_{a,y} e^{-M_{a,y} 7/12} P_{F_{a,y}} \tag{9}$$

The age composition of mature chinook salmon harvested by the fishery was estimated in order to better estimate age-specific maturation. Mature chinook harvested by the fishery was the proportion of the harvest that had reached maturity, and was estimated by:

$$C_{MAT_{a,y}} = C_{a,y} P_{MAT_a} \tag{10}$$

Effort

Sport fishery effort was related to year-specific fishing intensity divided by an assumed constant catchability coefficient (*q*), such that:

$$E_y = \frac{f_y}{q} \tag{11}$$

where ln(f_y) and ln(q) were formal parameters estimated by the model.

Observed Data and Other Model Inputs

Recruitment

Recruitment to age-0 of chinook salmon in Lake Michigan is from two sources: annual stocking of spring fingerlings and limited natural reproduction. Annual stocking of chinook salmon in Lake Michigan is well documented, and lakewide stocking records dating back to the initial stocking in 1967, were compiled for this report. Natural reproduction of chinook salmon in Lake Michigan was nonexistent at least until 1968.

Chinook salmon are stocked in Lake Michigan each spring as age-0 fingerlings.

Lake-wide stocking data from 1967 to 1996 were collected from the Departments of Natural Resources from Wisconsin, Illinois, Indiana, and Michigan (Benjamin and Bence 2003). Chinook salmon were not stocked in Lake Michigan prior to 1967. Recruitment of age-0 naturally-reproduced chinook salmon increased steadily over time (Clark 1996). Input data for natural recruitment were taken from Rutherford (1997), and were based on estimates of natural reproduction from Carl (1980; 1982; and 1984), Seelbach (1985 and 1986), Zafft (1992), and Hesse (1994). Age-0 recruitment was therefore the sum of stocked fingerlings and estimated wild smolts. Recruitment was an input into the model and is not used as observed data to fit the model. The model assumed that recruitment to age-0 occurred at the beginning of the year.

Sport Fishery Information

Harvest and effort information was compiled from data collected by creel survey programs run by each of the four states surrounding the lake (Benjamin and Bence 2003). An attempt was made to use effort that directly targeted chinook salmon, but was limited by differences in creel survey programs. For Wisconsin data, effort was estimated from interviews in which anglers specifically indicated they were targeting chinook salmon. Illinois and Indiana data included effort targeted at all salmonine species. Michigan effort was estimated from creel data using interviews in which anglers indicated they were targeting chinook salmon, coho salmon, salmon in general, or salmon and trout in general. Fishing effort targeted at either chinook salmon or other salmonines was used in the model to avoid any bias due to possible changes in effort directed at other species, such as yellow perch. Post-hoc comparison, however, of chinook harvest rates calculated from chinook salmon effort versus salmonine effort showed the same trends. Chinook salmon total harvest estimated from total angling effort (including non-targeted effort) was used for each state.

Michigan is the only one of the four states bordering Lake Michigan that collects substantial harvest-age composition data. Wisconsin collects length composition data. Preliminary analysis of length compositions between Michigan and Wisconsin indicated similar harvest length compositions. Therefore, age composition of the lake-wide harvest could reasonably be estimated by the age composition of the Michigan harvest. Chinook salmon migrate widely within Lake Michigan and even between Lake Michigan and Lake Huron (Clark 1996), suggesting that stocks are reasonably mixed, and therefore that the age composition of the population may be fairly homogenous.

Patterns in standardized residuals were used to evaluate model fit to observed age composition data. Standardized residuals were estimated as:

$$SR = \frac{p_{a,y}^{obs} - p_{a,y}^{pred}}{\sqrt{p_{a,y}^{pred}(1 - p_{a,y}^{pred})/n_{eff}}} \qquad (12)$$

where $p_{a,y}$ was the proportion at age a in year y from the observed and predicted age composition data, and n_{eff} was the effective sample size.

Michigan also collects data on maturity of chinook salmon sampled from the fishery. From these data, the age composition of mature fish harvested by the fishery was estimated. These age compositions of mature chinook were based on sampling data from July 15 to August 31. This time period was chosen so that maturation was advanced enough that identification of maturity would not be difficult, though not so advanced that aging error due to scale erosion would be a problem. Model estimates of mature age composition were fit to empirical estimates in order to provide additional information on maturation schedules of chinook.

Weir Harvest Information

Harvest data from Michigan and Wisconsin weirs were available from 1985 to the present. Prior to 1985, only Michigan collected weir information. For the model, an estimate was made of the lake-wide weir harvest age composition for 1985 to 1996, weighted by the number of chinook sampled from each of the weirs around the lake. Questions about the validity of sampled age compositions, coupled with the inconsistencies of reported age compositions between years, prevented the use of weir harvest information in the model prior to 1985.

Fitting the Model to Observed Data

Model estimates of effort, total harvest and mature harvest, harvest and mature harvest age compositions, and weir harvest age compositions were fit to observed data from 1985 to 1996. Model parameters were iteratively and independently adjusted in order to provide the best fit. Fit was measured with a log-likelihood function, and best fit was reached when the log-likelihood function was maximized (Methot 1990). A quasi-Newton search algorithm was used to find the maximum likelihood, with forward differencing used to estimate the partial derivatives of the objective function. Parameters were estimated using quadratic extrapolation. The log-likelihood equation was:

$$L = L_1 + L_2 + L_3 + L_4 + L_5 \qquad (13)$$

where L_1 was the log-likelihood of the model fit to observed fishery effort data, L_2 was the log-likelihood of the model fit to observed fishery harvest, L_3 was the log-likelihood of the model fit to observed fishery harvest age composition, L_4 was the log-likelihood of the model fit to observed fishery mature harvest age composition, and L_5 was the log-likelihood of the model fit to observed weir harvest age composition. No external weighting was applied to any of the likelihood functions (see Methot 1990). Errors were assumed to be log-normally distributed for L_1 and L_2 such that the log-likelihood functions were defined as:

$$L_i = -0.5 \sum_y \frac{[\ln(\lambda_y^{obs}) - \ln(\lambda_y^{pred})]^2}{\sigma_y^2} \qquad (14)$$

where λ_y^{obs} and λ_y^{pred} are the observed and predicted effort (i = 1) and harvest (i = 2). The standard deviation (σ) was set at 0.06 for effort and 0.08 for harvest, and was estimated as:

$$\sigma = \sqrt{\ln[(CV)^2 + 1]} \qquad (15)$$

Law and Kelton (1982). An average coefficient of variation (*CV*) was based on observed annual effort and harvest estimates from Michigan's waters of Lake Michigan (Benjamin and Bence 2003).

Errors were assumed to be multinomially distributed for the age composition log-likelihood functions, such that they were defined (ignoring constants) as:

$$L_{3,4,5} = \sum_y n_y \sum p_{a,y}^{obs} \ln(p_{a,y}^{pred}) \qquad (16)$$

where n_y is the effective sample size in year y, and $p_{a,y}^{obs}$ and $p_{a,y}^{pred}$ were the observed and predicted proportions at age *a* in year *y*. The effective sample size in the likelihood functions for the harvest, mature harvest, and weir harvest age compositions was set to 100, 50, and 50 respectively. These values represented subjective judgements about the accuracy of the observed data. (For a discussion of this issue see Fournier and Archibald (1982)). Observed harvest age compositions were considered to be more accurate than the mature harvest and the weir harvest age compositions because of aging error caused by (1) scale erosion or (2) problems associated with the use of an age-length key to estimate weir harvest age compositions.

Results

Our basic results consisted of parameter estimates that provided a description of the dynamics of the chinook salmon population and fishery in Lake Michigan during 1985 through 1996. These parameter estimates imply a sequence of abundances-at-age and mortality rates as well as modeled values that correspond to observed values of harvest, fishery effort, fishery age-compositions, and weir age-compositions. The validity of the model was partially evaluated by comparing modeled and observed values. Thus, we first present these comparisons before describing our estimated chinook salmon mortality rates and population dynamics in Lake Michigan.

Fishery Effort and Harvest

The model fit the 1989 to 1996 observed fishery effort and harvest data reasonably well, but had more difficulty fitting 1985-1988 data (Figure 1). Chinook salmon effort and harvest increased from 1985 to 1986 before declining through 1994. Effort was relatively constant from 1994 to 1996, while harvest increased. The model was generally able to follow these declines. There was an obvious tradeoff as the model attempted to fit fishery effort and avoid overestimating harvest for 1985-88. The result was an underestimation of the decline in effort and an overestimation of the decline in harvest. A pattern in effort and harvest residuals shows that effort and harvest errors were correlated, which is to be expected because both are related to the fishing intensity parameter, f_y (Figure 2).

Age Compositions

The onset of additional natural mortality in the late 1980s resulted in a decline of older age classes from the population, and this decline was reflected in the fishery and weir age composition data. Fishery harvest consisted primarily of 2 and 3-year old fish from 1985 to 1989, with more 3 and 4-year old fish harvested than 1 and 2-year old fish in most years (Table 2). From 1990 to 1995, the harvest age composition shifted to consist primarily of 1 and 2-year old fish, with 1-year old fish dominating the harvest in some years, and with more 1-year old fish harvested than 3-year old fish in all years.

Similar trends were seen in the age composition of mature fish harvested by the fishery and in the weirs. Age 3-4 fish dominated the mature harvest from 1985 to 1989 (Table 3). In 1990, the age composition shifted to mostly age 2-3 fish along with an equal proportion of age-1 and age-4 fish. Weir harvest age compositions were comprised of age 2-4 fish from 1985 to 1990, but shifted to age 1-3 fish from 1991 to 1996 (Table 4).

The model had difficulty fitting the fishery age composition data, as evidenced by clear patterns in the standardized residuals (Figure 3). The proportion of age-0 fish in the harvest was consistently overestimated, while the proportion of age-1 fish was consistently underestimated. The model also consistently overestimated the proportion of age-2 fish. Residuals were more randomly distributed and the magnitude of the residuals decreases for ages 3-5. These patterns were probably a result of the difficulty the model had when estimating the true selectivity with a logistic function. The logistic function cannot follow the slope of the true selectivity function, so it compromises by overestimating age-0, underestimating age-1, and overestimating age-2.

Similar patterns in the standardized residuals are also evident in the weir harvest age composition data. Most notable was the model's tendency to overestimate age-0 and underestimate age-1 fish, and was likely due to the inability of the logistic function to follow the true maturation rates. Residual patterns for age 2-4 fish showed a definite transition between 1990 and 1991, and reflected the model's inability to follow the abrupt change in the observed age composition data (Figure 4).

Abrupt changes in age composition data were also reflected in the standardized residuals for the fishery mature harvest age compositions. Most notable was the increase in the residuals for age-1 fish from 1989 to 1990, as the model could not follow the rapid increase in age-1 harvest from 1990 to 1993 (Figure 5). Residuals appeared to be randomly distributed for ages 2-4. The model consistently overestimated the proportion of age-0 and age-5 fish, although differences from observed data were small.

Fishing Mortality

Fishing mortality was estimated by the model for ages 0-5 from 1967 to 1996. Fishing mortality had relatively little impact on age 0 and age 1 chinook salmon, with mortality never exceeding 3% in any year for either age class (Table 5). Thus although the model did not accurately estimate harvest of the younger ages (0, 1), these errors had only a minor influence on the predicted dynamics. Age-2 fishing mortality reached a peak of 13% in 1986, and declined to 5% by 1992. Ages 3-5 chinook salmon suffered peak fishing mortality levels in 1986, from 30% and 41%, and declined to 13-18% by 1992.

Maturation

Model-estimated proportions of chinook salmon that matured for ages 0-4 were 0.00, 0.02, 0.13, 0.51, and 0.87. Age-5 maturity was set to 1 (Table 6). Note that these proportions do not indicate the proportion that return to the streams, since some mature fish are harvested by the fishery. Total harvest of mature fish from weirs and from the fishery were not fit to observed data because observed weir harvest data does not account for all chinook that run up all streams tributary to Lake Michigan. Therefore, only the age compositions of the fishery mature harvest and weir harvest were used to compare with observed data (Table 3; Table 4).

Natural Mortality

BKD-related deaths of chinook salmon were not observed in Lake Michigan until 1986, although the model was allowed to estimate TVM beginning in 1985. The model estimated a TVM rate of 0.00 for ages 0 and 1, and estimated that the same TVM rate applied for ages 2 to 5. TVM increased for ages 2 to 5 from 0.00 in 1985 to a peak of 1.70 in 1993 before declining to 0.29 in 1996 (Table 7).

Total Mortality

The model did not allow survival past age 5, therefore total annual mortality of age 5 was 100%. Age 0 and age 1 chinook salmon were exposed to no TVM mortality and to very little fishing mortality, thus total annual mortality of these ages remained relatively steady from 1967 to 1995, at 53% and 28% for age 0 and age-1, respectively (Table 8). Estimated TVM had the greatest effect on ages 2 and 3. Pre-TVM mortality averaged 25% and 61% for ages 2 and 3, respectively. Total annual mortality increased substantially for these age groups during TVM years, averaging 66% and 83% for ages 2 and 3, respectively. Annual mortality before 1985 for age 4 chinook salmon averaged 91%, and increased to 96% after 1985. Highest total annual mortality for all ages was observed from 1991 to 1994, which corresponds with the lowest harvest years, though not the highest fishing mortality years.

A comparison of total number of deaths in each year from 1985 to 1996 indicated that relative contributions of different sources of mortality shifted over time after 1985. For age-3 fish, for example, natural mortality accounted for 12% of the total deaths, but increased to 54% after 1985. Fishing mortality accounted for 20% prior to 1985 and declined to 15% after 1985. Spawning mortality comprised 68% of the total annual mortality for age-3 fish prior to 1985, but declined to 31% after 1985 as natural mortality increased. It is clear that the increase in natural mortality caused a decline in maturation deaths and harvest, as most BKD infected fish did not survive to reach the weirs or to be caught by anglers.

Population Abundance

Assuming that fishing intensity (f_y) increased linearly from 1967 to 1985, the model estimated abundance from 1967 to 1996 (Table 9). Chinook salmon were first stocked into Lake Michigan in 1967; therefore, age-5 fish did not appear in the population until 1972. Total recruitment reached a peak in 1989 at 10 million chinook salmon. Recruitment fluctuated between 7.5 million and 10 million from 1986 to 1996, and was driven by stocking and steady increases in estimated natural reproduction. The model estimated that the population size was less than 1 million in 1967, and surpassed 10 million by 1978. Population size fluctuated between 13.5 million and 17.9 million from 1980 to 1996, with a peak abundance in 1990.

Stock biomass increased from 1967 to a peak level of 50 million pounds in 1986 before high mortality rates on older chinook salmon caused the biomass to decline beginning in 1987 (Figure 6; Table 10). Stock biomass declined by nearly 50% from 1986 to 26 million pounds by 1993. Natural mortality rates declined in 1995 and 1996, and stock biomass has increased to 39 million pounds in 1996.

Uncertainty of Parameter Estimates

The 95% confidence intervals for each parameter were estimated by inverting the likelihood ratio test (Seber and Wild 1989) (Table 7). Uncertainty for the time-varying mortality parameter (TVM_y) was variable across years, with the largest uncertainty associated with the 1985 and 1996 parameters. High variability for the 1996 parameter was probably due to the lack of information on mortality in 1997. Estimating uncertainty about the parameters determining the shape of the mortality function proved difficult. Nevertheless, the model showed a strong tendency to set age 0-1 mortality to zero and make age 2-5 mortality equivalent, although this could be accomplished with various combinations of α and β. The lower 95% confidence limit on the logistic function parameter α resulted in zero TVM for age 0 and a small level of time-varying natural mortality for age 1 chinook salmon, with essentially equal (and higher) TVM for ages 2-5. The upper 95% confidence limit went to infinity as mortality of ages 0-1 went to zero and mortality of ages 2-5 was constant (i.e. a step function). Confidence limits on the logistic function parameter β could not be estimated because the model would increase α until the denominator in the TVM function (Equation 4) approached zero, causing the model to crash.

Discussion

Severe declines in the Lake Michigan chinook salmon fishery in the late 1980s prompted fishery managers to evaluate chinook salmon management efforts in an attempt to revive the fishery (Clark 1996). Declines in the chinook salmon fishery were likely due to density-dependent mortality, as evidenced by an outbreak of BKD and declines in fishery catch rates at high population levels, and were probably caused by nutritional stress due to declines in the alewife population.

This model is a first attempt to quantify relationships between different sources of mortality on chinook salmon during a period of critical and substantial changes in chinook salmon population dynamics. In order to use this model to make predictions or projections for the future, the model requires additional assumptions about how these population dynamics will operate in the future. One assumption would be that these rates would remain constant at their 1996 values. Accurate forecasts would need to account for how vital rates change in response to chinook salmon abundance and other factors, and this would require an improved mechanistic understanding. However, mortality and abundance estimates made by the model could be used to improve existing Lake Michigan multi-species models (e.g., Stewart et al. 1981; Jones et al. 1993; Rutherford 1997).

There is some concern that the logistic model applied to TVM may have been too restrictive. In particular, the fact that the model estimates equal values for ages 2 to 5 may suggest that TVM for older ages, if given the freedom, might actually decline. To test this, the baseline CAA model was compared to a similar model that estimated TVM separately for each age and year. Outputs from both models were compared with a likelihood ratio test (Seber and Wild 1989). Allowing the model to independently estimate TVM for each age and year significantly improved model fit ($P<0.005$). TVM estimates for ages 0 and 1 continued to be relatively small, but estimates for ages 2 to 5 were markedly different across ages, with no consistent trends across ages or years. If there is time-varying mortality among ages, it should have some systematic pattern so that in a given year close ages would respond the same way. Instead, estimated mortality rates varied without pattern. This may not reflect time-varying mortality but rather an over-parameterization of this alternative model, which used these new parameters to explain other process errors such as differential catchability or aging errors.

A sensitivity analysis was performed on the age-0 baseline natural mortality rate (0.75). Age-0 natural mortality was increased and decreased by 25% and the model was re-fit to the data for both trials. Model output from both trials was compared to the original results to see if adjusting the natural mortality rate would result in the same qualitative conclusions of chinook salmon population dynamics. Both trials in fact yielded the same qualitative results as the original model (Table 11). However, a

25% reduction in age-0 natural mortality appeared to significantly improve model fit, and raised concerns about the appropriate estimate of natural mortality. This topic warrants further investigation. We did not simply decrease age-0 natural mortality in order to improve model fit because empirical evidence (declines in observed weir returns per fish stocked; Benjamin and Bence 2003) pointed to an increase in age-0 mortality in the 1980s.

The results of this model suggest that chinook salmon suffered very high mortality in the late 1980s and early 1990s, with most of the mortality due to increasing natural mortality. Ages 2 through 5 were subject to equivalent TVM rates within years, and all four age groups suffered severe declines in abundance over a year. Consequently, the mode in the age composition of the harvest shifted from age 3 to age 2.

Initial values for time-varying mortality were obtained from existing estimates of BKD mortality rates (Rutherford 1997). However, because the model does not fit any observed data on BKD mortality, inferences about BKD mortality based on model-estimated time-varying mortality should be carefully made. In particular, the model estimated an annual increase in TVM from 1985 to 1993, followed by a decline from 1993 to 1996 (Figure 7). In contrast, observed data show greater levels of BKD incidence in the late 1980s, followed by declines in the early 1990s (Clark 1996; Marcquenski 1997). This discrepancy between the model estimates of mortality and observed incidence rates of BKD could mean one of two things. First, observed incidence rates of BKD are not an index of BKD mortality rates (Clark 1996). Second, causes of mortality rates may be more complex than originally thought, and cannot be estimated by simply observing one of the symptoms (i.e., BKD incidence).

High in-lake natural mortality rates on age 2-5 chinook salmon are a real problem in Lake Michigan, and the reduction of natural mortality, should be an immediate management goal. If natural mortality of chinook salmon is density dependent (Clark 1996), then reducing the population density of chinook salmon is a viable method for reducing mortality and improving the fishery. Because chinook salmon recruitment is governed by stocking in Lake Michigan, management decisions regarding stocking will influence population abundance.

Conclusions

The chinook salmon population in Lake Michigan underwent dramatic changes between 1986 and 1996. These changes were most directly felt by the sport fishery, as harvest and harvest rates for chinook salmon began declining in 1987, triggering a decline in sport fishery effort, which led to a cycle of further declines in harvest.

The sport fishery was not the only place where changes in the chinook salmon population were seen. Dead chinook salmon washed up on the southern Lake Michigan shoreline in the late 1980s, suggesting an increase in lake-wide natural mortality. While most of these fish ultimately died from BKD, it is likely that another environmental or nutritional stress affected their resistance to disease. Regardless of the cause, modeling results show that this increase in lake-wide natural mortality was a significant source of mortality in older (age 2-5) chinook salmon, accounting for upwards of 70% of the deaths in some years. The increased mortality of older chinook salmon could not be explained by overfishing, which is often to blame for fishery collapses. Because of increased natural mortality of older fish, fishery harvest declined, and fishery and weir harvest age compositions shifted towards younger ages, as fewer older fish survived to be harvested. Finally, estimated standing stock biomass declined by about 50% from peak levels in the mid-1980s, to the early-1990s. The population appeared to recover somewhat by 1996, as harvest and harvest rates increased, and age compositions slowly shifted towards older fish.

What is the future of chinook salmon in Lake Michigan? As the fishery grew in the 1970s and 1980s, chinook salmon became an indispensable species in the fish community. Fish community objectives, as outlined by the Great Lakes Fishery Commission (Eshenroder et al. 1995), called for a diverse salmonine fish community capable of sustaining an annual yield of 6 to 15 million pounds. Included was a short-term goal of annual yields of chinook salmon of about 6.8 million pounds. Also included was the goal of an increased reliance upon naturally reproduced salmonines. With what appears to be a recovery in the chinook salmon population in recent years, their popularity in the fishery, and their ability to naturally reproduce, chinook salmon will continue to be an integral part of the Lake Michigan fish community.

Management of chinook salmon in the next 10 years will continue to be challenged by a number of issues and unanswered questions remain. For example, chinook salmon health continues to be monitored by measuring BKD incidence rates in surveys and at the weirs, although it is not clear what the relationship is between incidence rates and mortality rates. Reducing stocking rates could alleviate mortality rates (Keller et al. 1990; Clark 1996), but exactly how many fish should be stocked and in what species combinations continues to be an area for further research.

Acknowledgments

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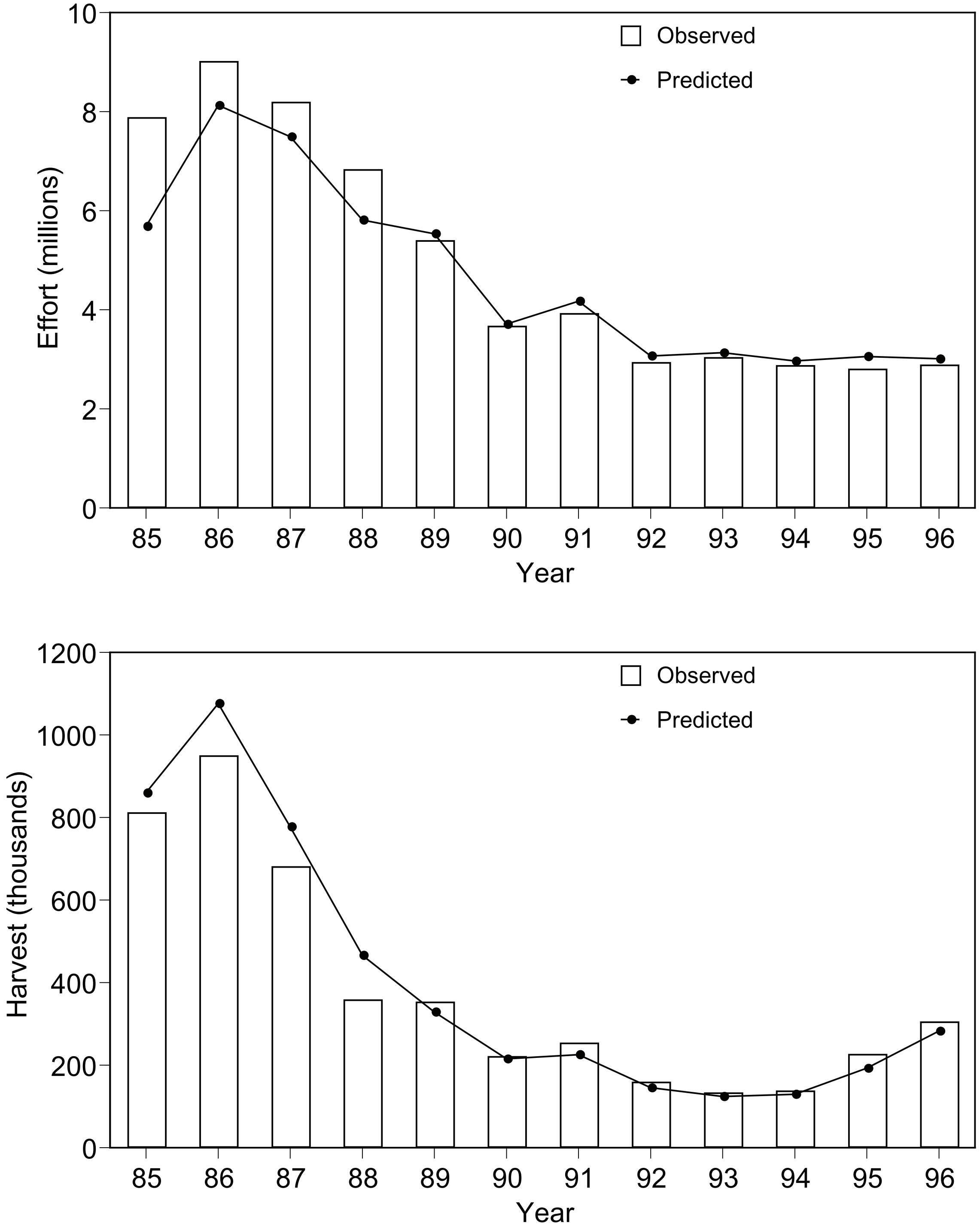

Figure 1.–Observed and predicted values of sport fishery effort in millions of angler-hours (top) and chinook salmon harvest in thousands of fish (bottom).

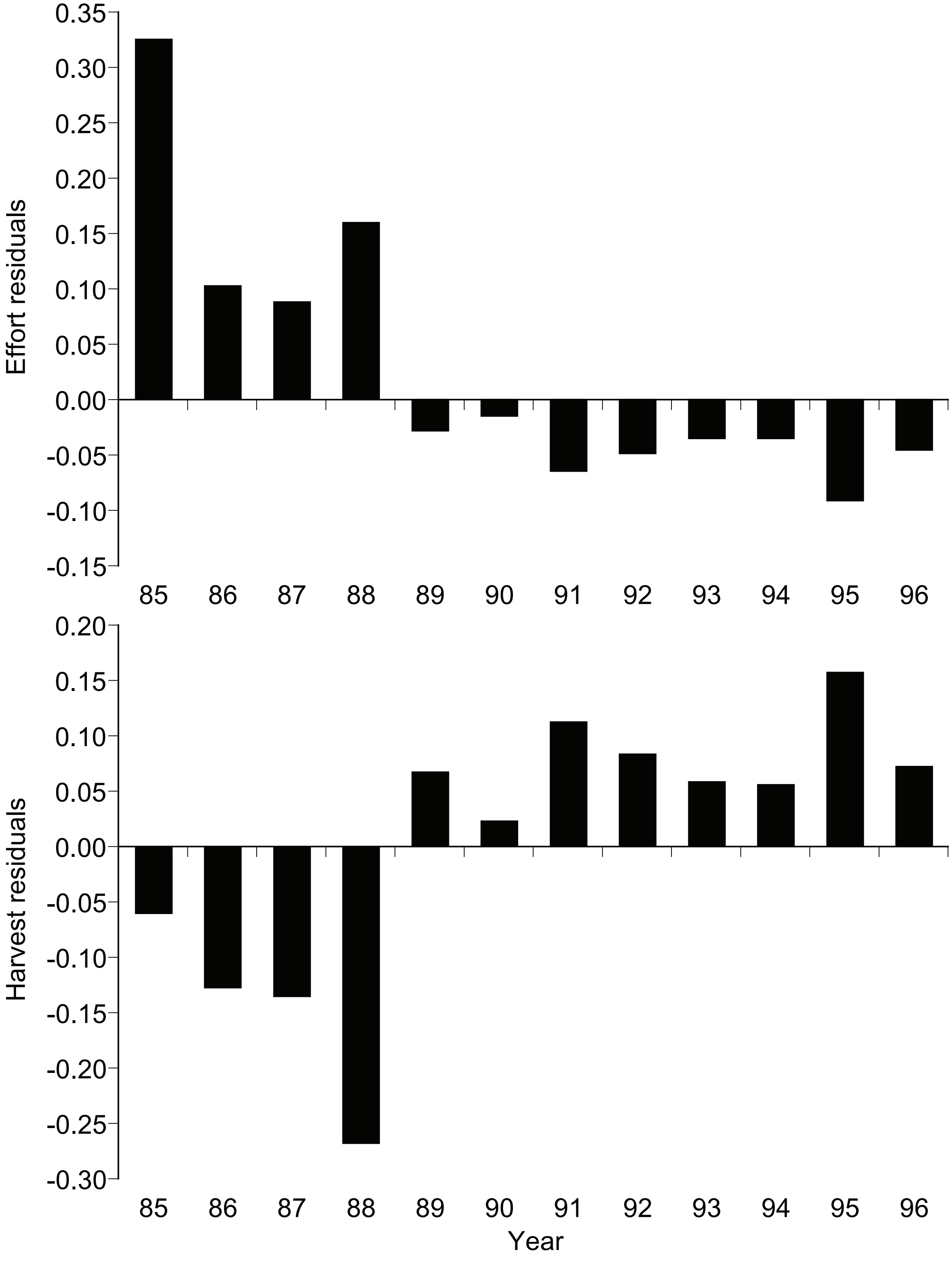

Figure 2.–Log$_e$-based residuals from model predictions of fishery effort (top) and chinook salmon harvest (bottom) for the Lake Michigan sport fishery.

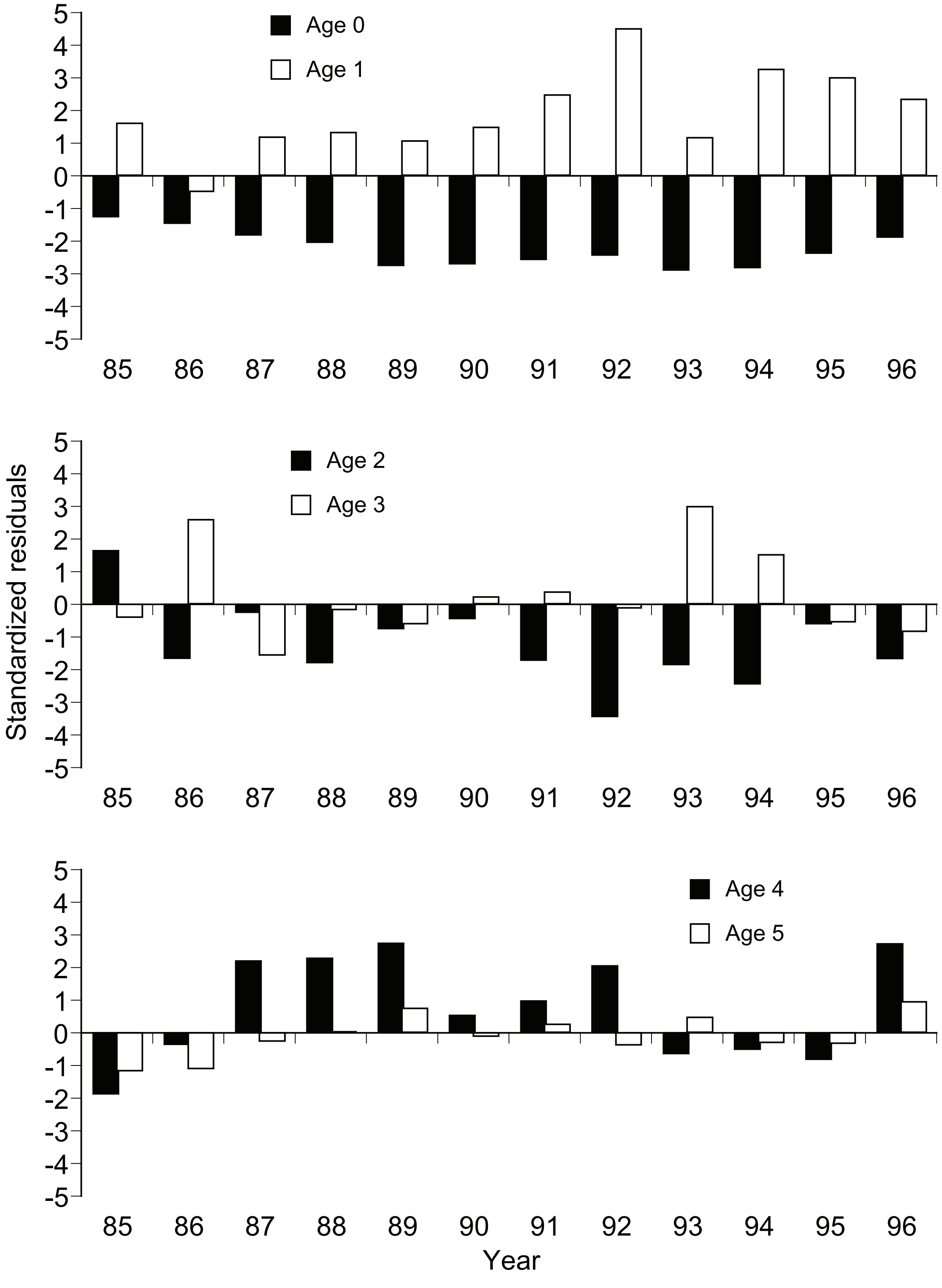

Figure 3.–Standardized residuals for fishery harvest age compositions of chinook salmon in Lake Michigan. See text for calculation of standardized residuals.

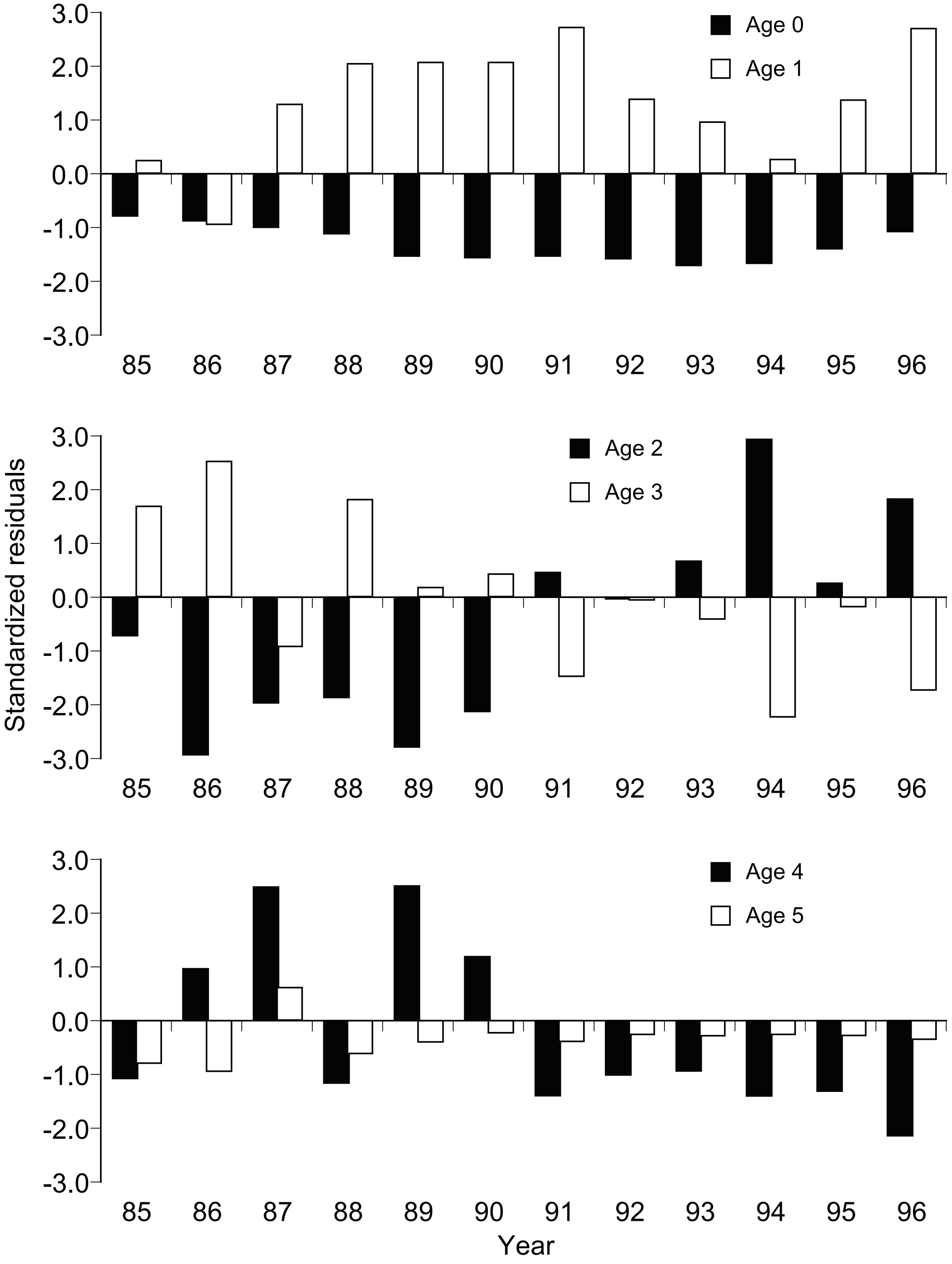

Figure 4.–Standardized residuals for weir harvest age compositions of chinook salmon from Lake Michigan. See text for calculation of standardized residuals.

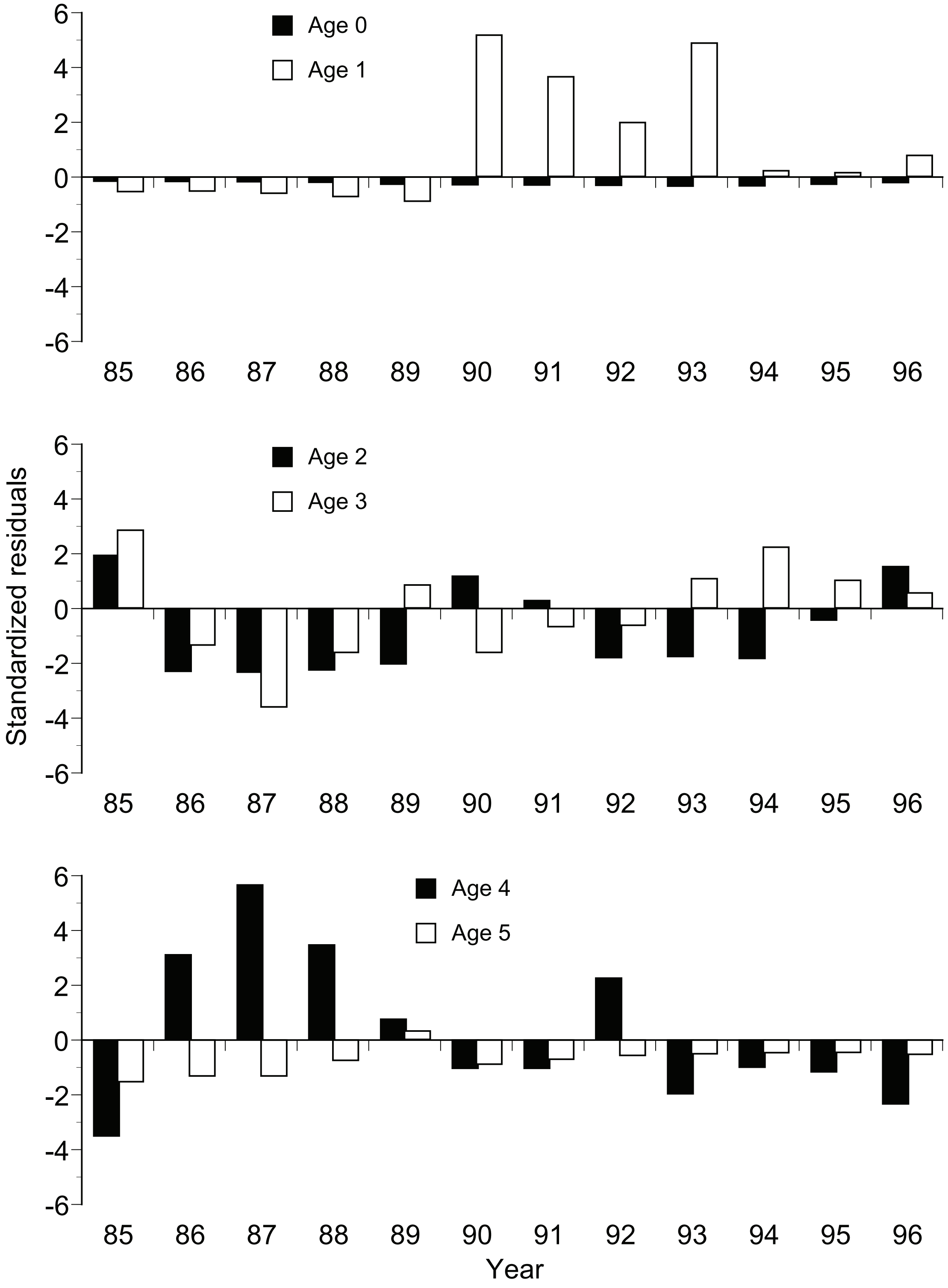

Figure 5.–Standardized residuals for fishery mature harvest age compositions of chinook salmon in Lake Michigan. See text for calculation of standardized residuals.

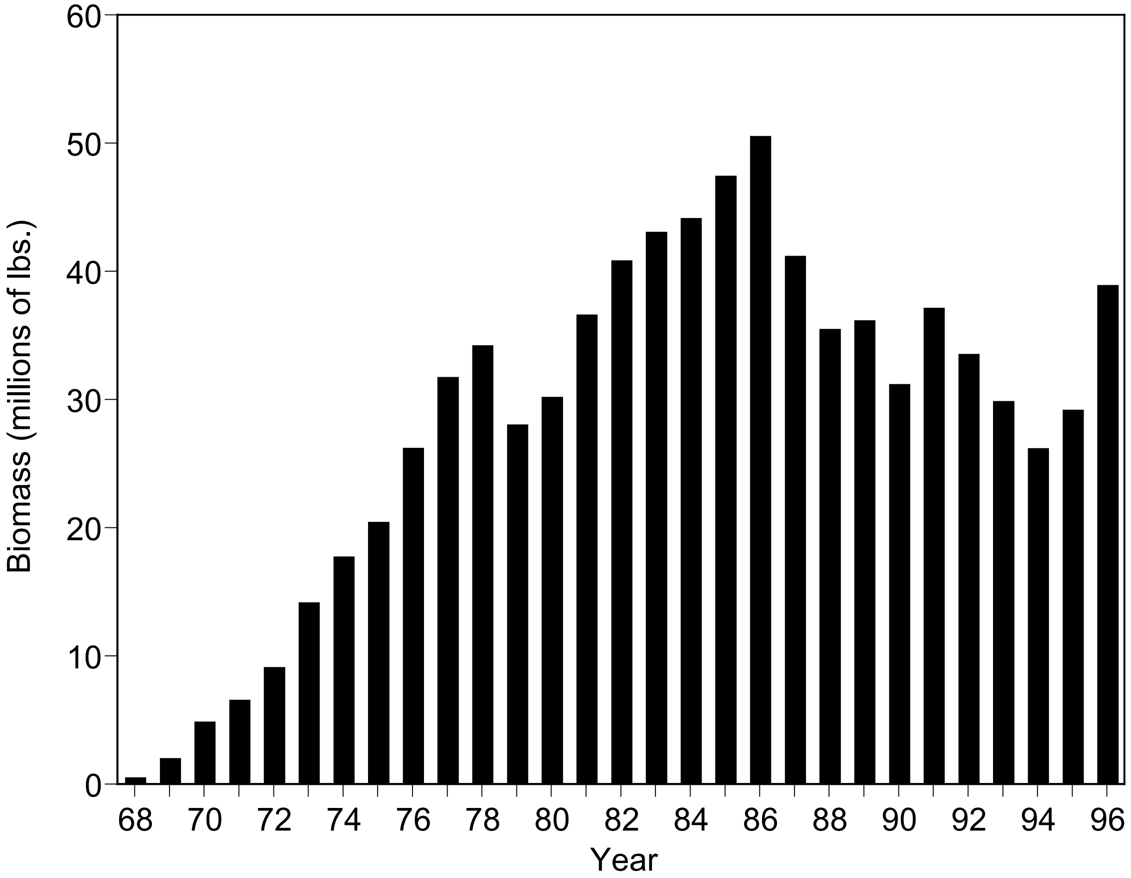

Figure 6.–Standing stock biomass (pounds) as estimated from abundance-at-age from the CAA model and using mean weight at annulus formation from CONNECT (Rutherford 1997).

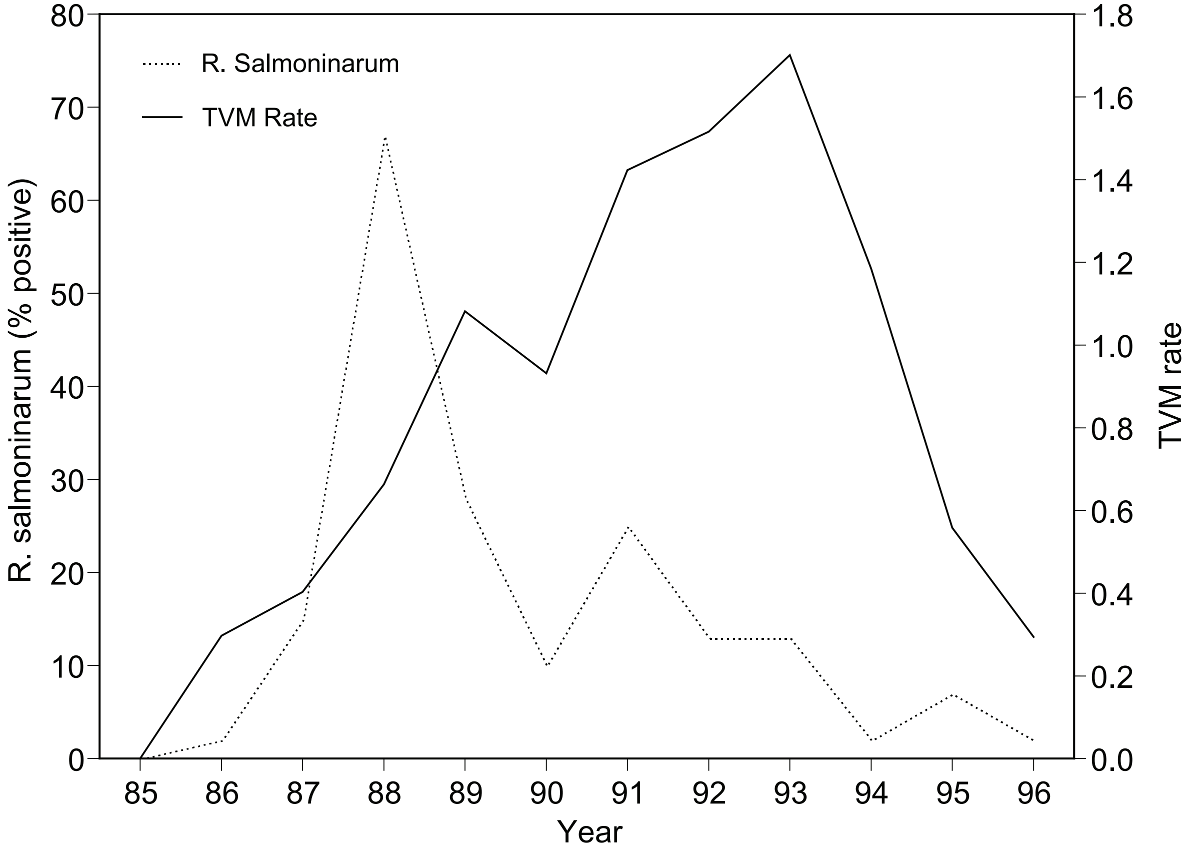

Figure 7.–Observed estimates of prevalence of *Renibacterium salmoninarum*, the causative of agent of BKD, versus model-estimated time-varying instantaneous natural mortality rate (TVM). Observed data were obtained from mature chinook salmon sampled at Strawberry Creek, Sturgeon Bay, Wisconsin (Marcquenski 1997).

Table 1.–Estimated annual instantaneous natural mortality rates of chinook salmon in Lake Michigan, 1967-1996.

Year	Age					
	0	1	2	3	4	5
1967-85	0.750	0.300	0.100	0.100	0.100	0.100
1986	0.750	0.300	0.397	0.397	0.397	0.397
1987	0.750	0.300	0.503	0.503	0.503	0.503
1988	0.750	0.300	0.763	0.763	0.763	0.763
1989	0.750	0.300	1.182	1.182	1.182	1.182
1990	0.750	0.300	1.031	1.031	1.031	1.031
1991	0.750	0.300	1.523	1.523	1.523	1.523
1992	0.750	0.300	1.616	1.616	1.616	1.616
1993	0.750	0.300	1.801	1.801	1.801	1.801
1994	0.750	0.300	1.285	1.285	1.285	1.285
1995	0.750	0.300	0.658	0.658	0.658	0.658
1996	0.750	0.300	0.394	0.394	0.394	0.394

Table 2.–Observed and predicted fishery harvest age compositions of chinook salmon from Lake Michigan, 1985-1996.

Year	Age-0	Age-1	Age-2	Age-3	Age-4	Age-5
Observed Fishery Harvest Age Composition						
1985	0.00	0.13	0.33	0.43	0.10	0.00
1986	0.00	0.07	0.22	0.54	0.17	0.00
1987	0.00	0.14	0.27	0.35	0.23	0.01
1988	0.00	0.18	0.24	0.35	0.22	0.01
1989	0.00	0.22	0.32	0.29	0.17	0.01
1990	0.00	0.30	0.37	0.25	0.07	0.00
1991	0.00	0.36	0.33	0.24	0.06	0.00
1992	0.01	0.45	0.28	0.20	0.07	0.00
1993	0.00	0.33	0.33	0.32	0.02	0.00
1994	0.00	0.39	0.36	0.24	0.02	0.00
1995	0.00	0.29	0.43	0.26	0.02	0.00
1996	0.00	0.21	0.30	0.35	0.13	0.00
Predicted Fishery Harvest Age Composition						
1985	0.02	0.08	0.26	0.45	0.17	0.02
1986	0.02	0.08	0.29	0.41	0.18	0.01
1987	0.03	0.10	0.28	0.43	0.15	0.01
1988	0.04	0.13	0.32	0.36	0.14	0.01
1989	0.07	0.18	0.35	0.31	0.09	0.01
1990	0.07	0.24	0.39	0.24	0.06	0.00
1991	0.06	0.25	0.42	0.23	0.04	0.00
1992	0.07	0.25	0.44	0.20	0.03	0.00
1993	0.08	0.28	0.42	0.20	0.03	0.00
1994	0.07	0.25	0.48	0.18	0.02	0.00
1995	0.06	0.18	0.46	0.28	0.03	0.00
1996	0.04	0.13	0.38	0.39	0.07	0.00

Table 3.–Observed and predicted harvest age compositions of mature chinook salmon from Lake Michigan, 1985-1996.

Year	Age-0	Age-1	Age-2	Age-3	Age-4	Age-5
Observed Mature Harvest Age Composition						
1985	0.00	0.00	0.15	0.73	0.12	0.00
1986	0.00	0.00	0.00	0.41	0.59	0.00
1987	0.00	0.00	0.00	0.29	0.71	0.00
1988	0.00	0.00	0.02	0.40	0.57	0.01
1989	0.00	0.00	0.06	0.60	0.31	0.03
1990	0.00	0.13	0.29	0.42	0.16	0.00
1991	0.00	0.11	0.28	0.50	0.11	0.00
1992	0.00	0.08	0.19	0.49	0.25	0.00
1993	0.00	0.16	0.19	0.62	0.03	0.00
1994	0.00	0.04	0.23	0.66	0.07	0.00
1995	0.00	0.02	0.24	0.68	0.06	0.00
1996	0.00	0.02	0.24	0.68	0.06	0.00
Predicted Mature Harvest Age Composition						
1985	0.00	0.00	0.08	0.53	0.35	0.04
1986	0.00	0.00	0.09	0.50	0.38	0.03
1987	0.00	0.01	0.09	0.54	0.33	0.03
1988	0.00	0.01	0.12	0.51	0.34	0.02
1989	0.00	0.01	0.16	0.54	0.27	0.02
1990	0.00	0.02	0.22	0.53	0.21	0.01
1991	0.00	0.03	0.26	0.55	0.16	0.01
1992	0.00	0.03	0.30	0.53	0.14	0.00
1993	0.00	0.03	0.30	0.54	0.12	0.00
1994	0.00	0.03	0.35	0.50	0.11	0.00
1995	0.00	0.02	0.26	0.61	0.11	0.00
1996	0.00	0.01	0.16	0.64	0.18	0.00

Table 4.–Observed and predicted weir harvest age compositions of chinook salmon from Lake Michigan, 1985-1996.

Year	Age-0	Age-1	Age-2	Age-3	Age-4	Age-5
Observed Weir Harvest Age Composition						
1985	0.00	0.06	0.17	0.60	0.16	0.01
1986	0.00	0.02	0.07	0.62	0.29	0.00
1987	0.00	0.12	0.12	0.40	0.33	0.03
1988	0.00	0.18	0.16	0.53	0.12	0.00
1989	0.00	0.23	0.13	0.39	0.25	0.00
1990	0.00	0.29	0.22	0.34	0.14	0.00
1991	0.00	0.35	0.43	0.21	0.01	0.00
1992	0.00	0.28	0.43	0.27	0.02	0.00
1993	0.00	0.28	0.46	0.25	0.02	0.00
1994	0.00	0.21	0.68	0.11	0.00	0.00
1995	0.00	0.20	0.45	0.35	0.01	0.00
1996	0.00	0.20	0.45	0.35	0.01	0.00
Predicted Weir Harvest Age Composition						
1985	0.01	0.06	0.21	0.48	0.22	0.02
1986	0.01	0.05	0.24	0.45	0.23	0.02
1987	0.02	0.07	0.24	0.47	0.19	0.02
1988	0.02	0.09	0.28	0.41	0.19	0.01
1989	0.04	0.13	0.32	0.37	0.13	0.01
1990	0.04	0.18	0.37	0.31	0.09	0.01
1991	0.04	0.20	0.40	0.30	0.06	0.00
1992	0.05	0.20	0.43	0.27	0.05	0.00
1993	0.05	0.22	0.41	0.27	0.04	0.00
1994	0.05	0.19	0.47	0.24	0.04	0.00
1995	0.04	0.13	0.43	0.36	0.04	0.00
1996	0.02	0.09	0.32	0.47	0.09	0.00

Table 5.–Estimated age- and year-specific annual fishing mortality ($P_{Fa,y}$).

	Age					
Year	0	1	2	3	4	5
1967	0.000					
1968	0.000	0.002				
1969	0.001	0.003	0.015			
1970	0.001	0.004	0.020	0.052		
1971	0.001	0.005	0.025	0.064	0.088	
1972	0.001	0.006	0.030	0.077	0.104	0.111
1973	0.001	0.007	0.034	0.089	0.121	0.128
1974	0.001	0.008	0.039	0.101	0.137	0.145
1975	0.002	0.009	0.044	0.113	0.153	0.162
1976	0.002	0.011	0.049	0.125	0.168	0.178
1977	0.002	0.012	0.054	0.136	0.183	0.194
1978	0.002	0.013	0.058	0.148	0.198	0.210
1979	0.002	0.014	0.063	0.159	0.213	0.225
1980	0.003	0.015	0.068	0.170	0.227	0.240
1981	0.003	0.016	0.072	0.181	0.241	0.255
1982	0.003	0.017	0.077	0.192	0.255	0.270
1983	0.003	0.018	0.082	0.202	0.268	0.284
1984	0.003	0.019	0.086	0.213	0.282	0.298
1985	0.004	0.020	0.091	0.223	0.295	0.311
1986	0.005	0.028	0.127	0.303	0.393	0.413
1987	0.005	0.026	0.118	0.283	0.369	0.388
1988	0.004	0.020	0.093	0.228	0.300	0.317
1989	0.003	0.019	0.088	0.218	0.288	0.305
1990	0.002	0.013	0.060	0.152	0.204	0.216
1991	0.003	0.015	0.067	0.169	0.226	0.240
1992	0.002	0.011	0.050	0.128	0.172	0.182
1993	0.002	0.011	0.051	0.130	0.175	0.186
1994	0.002	0.010	0.048	0.123	0.167	0.177
1995	0.002	0.011	0.050	0.127	0.171	0.182
1996	0.002	0.011	0.049	0.125	0.169	0.179

Table 6.–Estimated maturation and fishery selectivity. Values were estimated by logistic functions, with parameters estimated by the CAA model.

	Age-0	Age-1	Age-2	Age-3	Age-4	Age-5
Maturation (MAT_a)	0.00	0.02	0.13	0.51	0.87	1.00
Selectivity (S_a)	0.01	0.05	0.25	0.67	0.92	0.99

Table 7.–Parameters and 95% confidence intervals as estimated by the model. See Methods for a discussion of confidence interval estimates.

Parameter	Symbol	Lower 95%	Estimate	Upper 95%
TVM	γ_{1985}	0.000	0.000	0.052
	γ_{1986}	0.086	0.297	0.507
	γ_{1987}	0.192	0.403	0.615
	γ_{1988}	0.426	0.663	0.904
	γ_{1989}	0.833	1.082	1.336
	γ_{1990}	0.675	0.931	1.193
	γ_{1991}	1.163	1.423	1.689
	γ_{1992}	1.255	1.516	1.782
	γ_{1993}	1.440	1.701	1.969
	γ_{1994}	0.941	1.185	1.433
	γ_{1995}	0.277	0.558	0.838
	γ_{1996}	0.000	0.294	0.747
	α	7.859	45.014	∞
	β	*	1.281	*
Fishing Intensity	f_{1985}	0.288	0.378	0.511
	f_{1986}	0.418	0.541	0.710
	f_{1987}	0.381	0.499	0.661
	f_{1988}	0.295	0.387	0.514
	f_{1989}	0.281	0.368	0.490
	f_{1990}	0.188	0.247	0.329
	f_{1991}	0.211	0.278	0.371
	f_{1992}	0.155	0.204	0.273
	f_{1993}	0.158	0.209	0.279
	f_{1994}	0.150	0.197	0.264
	f_{1995}	0.154	0.203	0.273
	f_{1996}	0.151	0.200	0.269
Selectivity	α	1.646	1.789	1.942
	β	2.385	2.609	2.863
Maturation	α	1.805	1.913	2.024
	β	2.898	2.984	3.072
Catchability Coefficient	q	5.142E-08	6.653E-08	8.747E-08

Table 8.–Estimated total annual mortality (A) of chinook salmon in Lake Michigan, 1967-1995.

	Age					
Year	0	1	2	3	4	5
1967	0.529					
1968	0.529	0.277				
1969	0.529	0.278	0.227			
1970	0.530	0.279	0.230	0.578		
1971	0.530	0.279	0.234	0.583	0.897	
1972	0.530	0.280	0.238	0.589	0.899	1.000
1973	0.530	0.281	0.242	0.594	0.900	1.000
1974	0.530	0.282	0.246	0.600	0.902	1.000
1975	0.530	0.282	0.249	0.605	0.904	1.000
1976	0.530	0.283	0.253	0.610	0.906	1.000
1977	0.530	0.284	0.257	0.615	0.907	1.000
1978	0.530	0.285	0.261	0.620	0.909	1.000
1979	0.530	0.285	0.264	0.625	0.911	1.000
1980	0.530	0.286	0.268	0.630	0.912	1.000
1981	0.531	0.287	0.272	0.635	0.914	1.000
1982	0.531	0.288	0.275	0.640	0.916	1.000
1983	0.531	0.288	0.279	0.645	0.917	1.000
1984	0.531	0.289	0.283	0.650	0.919	1.000
1985	0.531	0.290	0.286	0.654	0.920	1.000
1986	0.532	0.296	0.491	0.769	0.949	1.000
1987	0.531	0.294	0.537	0.787	0.952	1.000
1988	0.531	0.290	0.633	0.823	0.959	1.000
1989	0.531	0.290	0.757	0.882	0.973	1.000
1990	0.530	0.285	0.709	0.851	0.964	1.000
1991	0.530	0.286	0.824	0.911	0.979	1.000
1992	0.530	0.283	0.836	0.915	0.979	1.000
1993	0.530	0.283	0.864	0.929	0.983	1.000
1994	0.530	0.283	0.772	0.881	0.971	1.000
1995	0.530	0.283	0.573	0.777	0.946	1.000

Table 9.–Model estimated abundance-at-age. Age-0 abundance is equivalent to recruitment.

	Age						
Year	0	1	2	3	4	5	Total
1967	802,390	0	0	0	0	0	802,390
1968	686,692	377,697	0	0	0	0	1,064,389
1969	717,585	323,177	273,070	0	0	0	1,313,831
1970	1,913,492	337,653	233,405	211,215	0	0	2,695,765
1971	2,265,198	900,210	243,602	179,632	89,179	0	3,677,822
1972	2,102,128	1,065,474	648,774	186,543	74,843	9,213	4,086,974
1973	3,245,767	988,588	767,065	494,330	76,695	7,591	5,580,037
1974	3,978,053	1,526,136	710,959	581,541	200,553	7,637	7,004,879
1975	4,875,782	1,870,105	1,096,384	536,312	232,818	19,606	8,631,006
1976	4,002,057	2,291,707	1,342,070	822,924	211,874	22,346	8,692,978
1977	3,618,561	1,880,692	1,642,890	1,002,297	320,807	19,965	8,485,212
1978	6,165,263	1,700,160	1,346,812	1,220,827	385,571	29,679	10,848,313
1979	5,984,271	2,896,177	1,216,240	995,811	463,432	35,021	11,590,952
1980	7,305,924	2,810,634	2,069,638	894,774	373,021	41,326	13,495,317
1981	6,247,799	3,430,740	2,006,382	1,515,002	330,745	32,658	13,563,325
1982	7,646,427	2,933,319	2,446,454	1,461,358	552,608	28,429	15,068,594
1983	7,791,913	3,589,304	2,089,529	1,772,982	525,998	46,634	15,816,360
1984	9,229,792	3,656,919	2,554,109	1,506,746	629,732	43,580	17,620,879
1985	7,475,523	4,330,946	2,599,468	1,832,548	528,099	51,224	16,817,808
1986	7,692,678	3,507,131	3,075,331	1,855,469	633,700	42,167	16,806,476
1987	7,800,757	3,603,561	2,468,933	1,565,936	427,794	32,366	15,899,346
1988	7,616,870	3,655,622	2,542,507	1,143,267	334,139	20,440	15,312,845
1989	10,059,479	3,573,163	2,594,625	933,360	202,614	13,644	17,376,885
1990	9,876,937	4,719,836	2,538,605	629,375	110,149	5,536	17,880,438
1991	8,643,262	4,639,423	3,374,990	738,005	93,629	3,913	17,493,222
1992	8,030,679	4,058,771	3,312,037	595,667	65,802	1,978	16,064,934
1993	7,729,950	3,773,688	2,908,863	542,438	50,815	1,355	15,007,109
1994	8,092,950	3,632,229	2,703,935	395,358	38,334	866	14,863,671
1995	8,790,976	3,803,194	2,604,125	617,832	47,190	1,106	15,864,424
1996	8,393,377	4,130,990	2,725,821	1,112,095	137,478	2,535	16,502,296

Table 10.–Standing stock biomass (pounds) of chinook salmon in Lake Michigan as estimated from abundance-at-age from the CAA model, and mean weight at annulus formation from CONNECT (Rutherford 1997).

	Age					
Year	1	2	3	4	5	Total
1967	0	0	0	0	0	0
1968	453,237	0	0	0	0	453,237
1969	387,812	1,556,497	0	0	0	1,944,310
1970	405,184	1,330,407	3,062,616	0	0	4,798,206
1971	1,080,252	1,388,530	2,604,671	1,426,872	0	6,500,325
1972	1,278,569	3,698,010	2,704,880	1,197,483	176,351	9,055,293
1973	1,186,306	4,372,272	7,167,789	1,227,124	145,304	14,098,795
1974	1,831,363	4,052,469	8,432,350	3,208,851	146,188	17,671,220
1975	2,244,126	6,249,386	7,776,523	3,725,091	375,309	20,370,434
1976	2,750,049	7,649,801	11,932,392	3,389,984	427,752	26,149,977
1977	2,256,831	9,364,473	14,533,312	5,132,909	382,180	31,669,705
1978	2,040,192	7,676,829	17,701,993	6,169,140	568,132	34,156,287
1979	3,475,413	6,446,070	10,854,342	6,580,737	630,376	27,986,937
1980	3,372,761	10,969,081	9,753,040	5,296,894	743,869	30,135,646
1981	4,116,888	10,633,823	16,513,517	4,696,580	587,839	36,548,647
1982	3,519,982	12,966,204	15,928,801	7,847,028	511,723	40,773,738
1983	4,307,165	11,074,504	19,325,505	7,469,176	839,409	43,015,758
1984	4,388,303	13,536,777	16,423,534	8,942,200	784,434	44,075,248
1985	5,197,135	13,777,181	19,974,778	7,499,012	922,027	47,370,133
1986	4,208,557	16,299,253	20,224,616	8,998,544	759,010	50,489,981
1987	4,324,273	13,085,343	17,068,700	6,074,676	582,585	41,135,577
1988	4,386,746	13,475,286	12,461,609	4,744,777	367,921	35,436,339
1989	4,287,796	14,789,362	13,533,716	3,241,821	261,182	36,113,877
1990	5,663,803	14,470,050	9,125,936	1,762,384	105,964	31,128,137
1991	5,567,307	19,237,444	10,701,077	1,498,058	74,902	37,078,789
1992	4,870,525	18,878,611	8,637,176	1,052,834	37,860	33,477,005
1993	4,528,426	16,580,517	7,865,353	813,045	25,940	29,813,281
1994	4,358,675	15,412,428	5,732,688	613,344	16,577	26,133,711
1995	4,563,833	14,843,515	8,958,561	755,037	21,181	29,142,127
1996	4,957,188	15,537,178	16,125,380	2,199,645	48,533	38,867,924

Table 11.–Parameter estimates from a sensitivity analysis of age-0 baseline natural mortality (M_0) of chinook salmon in Lake Michigan compared with estimates obtained using the default value. M_0 was increased and decreased by 25% from the default value for M_0 of 0.75. Parameter estimates for M_0 unchanged from the default value are the same as estimates reported in Table 7.

Parameter	M_0 unchanged	M_0 increased 25%	M_0 decreased 25%
Fishing Intensity			
f_{1985}	0.378	0.462	0.309
f_{1986}	0.541	0.597	0.456
f_{1987}	0.499	0.548	0.420
f_{1988}	0.387	0.434	0.325
f_{1989}	0.368	0.409	0.310
f_{1990}	0.247	0.274	0.207
f_{1991}	0.278	0.311	0.233
f_{1992}	0.204	0.228	0.172
f_{1993}	0.209	0.233	0.175
f_{1994}	0.197	0.220	0.166
f_{1995}	0.203	0.226	0.171
f_{1996}	0.200	0.223	0.168
Selectivity			
α	1.789	1.784	1.755
β	2.609	2.576	2.642
Maturation			
α	1.913	1.909	1.910
β	2.984	2.978	2.947
TVM			
γ_{1985}	0.000	0.002	0.000
γ_{1986}	0.297	0.003	0.338
γ_{1987}	0.403	0.457	0.418
γ_{1988}	0.663	0.590	0.678
γ_{1989}	1.082	1.021	1.087
γ_{1990}	0.931	0.871	0.932
γ_{1991}	1.423	1.384	1.420
γ_{1992}	1.516	1.472	1.510
γ_{1993}	1.701	1.651	1.695
γ_{1994}	1.185	1.145	1.177
γ_{1995}	0.558	0.495	0.555
γ_{1996}	0.294	0.239	0.291
α	45.014	31.325	41.752
β	1.281	1.183	1.468
Catchability Coefficient			
q	6.653E-08	7.406E-08	5.592E-08

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