UNCERTAINTY IN THE POPULATION DYNAMICS OF ALEWIFE (*ALOSA PSUEDOHARENGUS*) AND BLOATER (*COREGONUS HOYI*) AND ITS EFFECTS ON SALMONINE STOCKING STRATEGIES IN LAKE MICHIGAN.

By

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ABSTRACT

UNCERTAINTY IN THE POPULATION DYNAMICS OF ALEWIFE (*ALOSA PSUEDOHARENGUS*) AND BLOATER (*COREGONUS HOYI*) AND ITS EFFECTS ON SALMONINE STOCKING STRATEGIES IN LAKE MICHIGAN.

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The dynamics of alewife (*Alosa psuedoharengus*) and bloater (*Coregonus hoyi*) in Lake Michigan were investigated and the implications of uncertainty in these dynamics on the outcomes of stocking strategies for salmonines were simulated using a stochastic model. I also analyzed the long-term trends in bloater size at age with a dynamic growth model for evidence of density-dependent growth regulation.

I fit a dynamic von Bertalanffy model and length-weight relationship with time-varying parameters to mean length and weight at ages of bloater from annual surveys. My results support a positive relationship between asymptotic length, L_∞, and the Brody growth coefficient, k, indicating that under conditions supporting larger L_∞, individuals approach L_∞ more rapidly. I explored the relationship between year-specific growth parameters and bloater abundance indices and found evidence of density-dependent growth. However, in the most recent years, L_∞ and yearling length have remained low despite low bloater abundances, suggesting a potential shift in the food web.

I reconstructed the population dynamics of alewife and bloater by fitting dynamic models to historic prey fish survey data (bottom trawl and hydroacoustic indices). These models allowed recruitment variation and accounted for mortality due to salmonine predators. Chinook salmon predation followed a Type II functional response while other

predators were assumed to be consuming at a constant rate. Estimates of consumption based on existing assessments of predators were also used in model fitting. The joint posterior distribution of the stock-recruitment parameters for alewife and bloater and a key parameter of chinook salmon's functional response was approximated using Markov Chain-Monte Carlo methods. While the amount of uncertainty in the parameters of the stock-recruitment relationship for alewife and bloater was large, the uncertainty in the parameter of the functional response was moderate.

To assess the impacts of these uncertainties on the outcomes of salmonine stocking strategies in Lake Michigan, I constructed a stochastic simulation model to forecast the outcomes of stocking strategies on both alewife and chinook salmon population dynamics. Uncertainty in the stock-recruitment relationship for alewife, the functional response of chinook salmon and the response of chinook salmon mortality rates to decreases in growth rate were included in the model. I investigated both fixed and dynamic stocking strategies; for the latter, stocking rates responded to changes in the state of the system. The outcomes of all stocking strategies I considered were highly variable, with a large proportion of undesirable outcomes. The abundance of other salmonine predators had large effects on the dynamics of the system. This suggests that the salmonines require integrated management and our ability to maintain a desirable state long-term through stocking strategies alone may be limited. Removing uncertainty in stock-recruitment parameters for alewife caused the probability of undesirable outcomes to decrease suggesting that ignoring uncertainty in these parameters will cause overly optimistic predictions of future outcomes.

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Szalai, E. B., Fleischer, G. W., and Bence, J.R, 2003. Modeling time-varying growth using a generalized von Bertalanffy model with application to bloater (*Coregonus hoyi*) growth dynamics in Lake Michigan. Can. J. Fish. Aquat. Sci. **60**: 55-66.

Modeling time-varying growth using a generalized von Bertalanffy model with application to bloater (*Coregonus hoyi*) growth dynamics in Lake Michigan

Emily B. Szalai, Guy W. Fleischer, and James R. Bence

Abstract: A concurrent increase in lakewide abundance and decrease in size-at-age of bloater (*Coregonus hoyi*) in Lake Michigan have suggested density-dependent growth regulation. We investigated these temporal patterns by fitting a dynamic von Bertalanffy model and length–weight relationship with time-varying parameters to mean length- and weight-at-ages (ages 1–7) from annual surveys (1965–1999). We modeled yearling length, asymptotic size (L_∞), and the parameters of a power relationship between mean weight and mean length (α and β) as changing slowly over time using a random walk model. The Brody growth coefficient (k) was modeled as a linear function of L_∞ with year-specific random deviations. Our results support a positive relationship between L_∞ and k, indicating that under conditions supporting larger asymptotic lengths, individuals approach the asymptote more rapidly. We explored the relationship between year-specific growth parameters and indices of lakewide bloater abundance and found evidence of density-dependent growth. However, in the most recent years, L_∞ and yearling length have remained low in Lake Michigan despite low bloater abundances, suggesting the occurrence of a fundamental shift in the food web.

Résumé : Chez le cisco de fumage (*Coregonus hoyi*) du lac Michigan, la coïncidence d'une augmentation de l'abondance dans tout le lac et d'une diminution de la taille à un âge donné laisse croire à l'existence d'une régulation de la croissance dépendante de la densité. Nous avons examiné ces structures temporelles en ajustant un modèle dynamique de von Bertalanffy et des relations longueur–masse avec des paramètres qui varient dans le temps aux données de longueur moyenne et de masse à un âge donné (âges 1–7) provenant d'inventaires annuels (1965–1999). Nous avons modélisé la longueur des jeunes de 1 an, la longueur à l'asymptote (L_∞) et les paramètres d'une relation de puissance entre la masse moyenne et la longueur moyenne (α et β) en les faisant varier lentement dans le temps à l'aide d'un modèle de marche aléatoire. Le coefficient de croissance de Brody (k) a été modélisé comme une fonction linéaire de L_∞ avec des déviations aléatoires spécifiques à l'année. Nos résultats indiquent une relation positive entre L_∞ et k, ce qui veut dire que, dans des conditions qui permettent des longueurs à l'asymptote plus élevées, les individus s'approchent plus rapidement de l'asymptote. Nous avons étudié la relation entre les paramètres de croissance spécifiques à l'année et les indices d'abondance des ciscos dans l'ensemble du lac et nous avons trouvé des indications d'une croissance dépendante de la densité. Cependant, durant les dernières années, L_∞ et la longueur des jeunes de 1 an ont été faibles au lac Michigan malgré l'abondance réduite de ciscos, ce qui laisse croire à un changement radical dans le réseau alimentaire.

[Traduit par la Rédaction]

Introduction

Dynamic growth of fishes has many implications and applications in the management of fisheries, and many ecological and practical insights can be gained by examining patterns in fish growth (e.g., Ferreri and Taylor 1996; Fargo and Kronlund 2000; Walters and Wilderbuer 2000). The effects of environmental factors on growth have been examined through both ex-perimental manipulation and observational studies. Although the experimental approach allows the strongest inferences, it is often not feasible for populations or species of interest. In many cases when an observational approach is necessary, a time series of observations of size-at-age and environmental factors are examined (e.g., Mallet et al. 1999; Millar et al. 1999; Fargo and Kronlund 2000). Because of the high variability in mean size-at-age estimates about the population's true

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mean size-at-age, it is often advantageous to identify and fit a growth model to the data to provide smoothed estimates of growth over time.

Such a model-based analysis of data from an observational study generally extends a traditional growth model, usually the von Bertalanffy model, to include time-varying parameters fit to the time series of observations (e.g., Mallet et al. 1999; Millar et al. 1999; Fargo and Kronlund 2000). The time series of observations used to fit the model is generally one of two types, size-at-age data or growth increment data calculated from size-at-age data.

Time-varying parameters have been incorporated into growth models in two general ways, through explicit functions of an environmental variable or by estimating, independently of environmental data, year-specific parameters for the growth model. Applications of the first approach (Millar and Myers 1990; Mallet et al. 1999; Millar et al. 1999) usually model either the L_∞ or k parameter of a von Bertalanffy growth curve as function of an environmental factor, usually temperature. This approach requires identifying both the environmental factor and the functional relationship between this factor and the growth parameters. If the connection between growth and the environment is misspecified, it is possible that spurious patterns in year-specific growth could be identified.

The second approach is to fit a growth model to data on size-at-age independently for each year for which data are available (e.g., Zhao et al. 1997; Fargo and Kronlund 2000). The temporal patterns in the resulting parameter estimates can then be examined in relation to temporal patterns in factors that might cause them to vary. By independently fitting a growth model to each year of size-at-age data, however, this approach ignores the interdependence of growth between years. Here, the model is describing the pattern in size-at-age within a year, not mean growth of a given age between year y and year $y + 1$. The two are only equivalent when growth rates are not changing over time. Hence, this approach causes difficulties in interpretation.

Here we present an alternative method for applying the second approach. We use a von Bertalanffy growth curve with time-varying parameters to predict growth increments from one year to the next. We keep track of the dynamically changing predictions of size-at-age and compare these predictions with a time series of size-at-age observations to estimate the parameters of our model. Thus, the time-varying parameters are estimated independently of any proposed environmental mechanism, in contrast with the first method, and the parameters describe growth rather than year-specific patterns in size-at-age, as in many applications of the second method. Our technique uses a time series approach to model the changes in growth parameters over time and estimates these parameters using a maximum likelihood framework. We apply this approach to the growth dynamics of the bloater (*Coregonus hoyi*) population in Lake Michigan. We then explore the potential mechanisms for changes in bloater growth using the resulting growth parameter estimates.

Bloater is an important member of the Lake Michigan ecosystem. In Lake Michigan, this coregonine is the sole remaining member of an original endemic complex of deepwater forms (Todd et al. 1981). Historically, bloater populations

supported valuable commercial fisheries (Brown et al. 1987; Fleischer 1992) and were forage for the native lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*) populations. Currently, they are forage for the array of stocked salmonids, especially when bloater are younger and smaller (Holey et al. 1998; Madenjian et al. 2002). Changes in bloater populations within Lake Michigan have been dramatic. Bloater abundance increased from near zero in 1970 to dominate the planktivore biomass of the lake by the late 1980s (Madenjian et al. 2002) (Fig. 1a). Bloater abundance remained high during most of the 1990s and subsequently declined to low levels again (TeWinkel et al. 2002). Concurrent with these large changes in abundance, bloater length- and weight-at-age also went through large changes (Figs. 1b–1d). These changes in size-at-age appeared to be correlated with bloater abundance, suggesting that bloaters in Lake Michigan might be exhibiting density-dependent growth (TeWinkel et al. 2002). Because bloater length- and weight-at-age have been monitored continuously since 1965 to present (except 1966 and 1998), these data provided us the opportunity to explore the changes that have occurred in the growth of bloater over time and the potential for density-dependent growth regulation in the Lake Michigan bloater population.

Materials and methods

The Lake Michigan bloater population has been assessed annually since 1962 by the U.S. Geological Survey (USGS) – Great Lake Science Center in a fall bottom trawl survey. This survey is conducted at fixed locations throughout Lake Michigan and provides information on the size (length and weight), age composition, and abundance (through catch-per-unit-effort (CPUE)) of the bloater population along with the exotic alewife (*Alosa pseudoharengus*) population. We used these survey data to construct a time-varying growth model for the bloater population and explored the relationship between the estimated growth parameters and abundance of both bloater and alewife.

Fall trawl survey design

To calculate mean length- and weight-at-age and abundance indices, we analyzed catch data from annual bottom trawl surveys conducted by the USGS – Great Lakes Science Center each fall (e.g., Hatch et al. 1981). The survey was initiated in 1962, but bloater were first aged in 1965 and hence we restricted our analysis to the 1965–1999 period. Trawls were generally 10 min in length and used a ¾ Yankee Standard No. 35 bottom trawl (12 m headrope, 15.5 m footrope, and 13-mm mesh in the cod end) dragged on contour during the day as described by Hatch et al. (1981). Sampling was done offshore of fixed shore locations (Fig. 2). Generally tows were made at each location at 9-m depth intervals and the sampled depths ranged from 6 to 128 m. Not all locations were sampled in each year, usually related to weather conditions, nor were all depths sampled at each location because of irregular bottom features. Although the locations were fixed, the number and identity of sampled locations did change over time. Initially, from 1962 to 1966, trawls were made only off Saugatuck, Mich. (Fig. 2), and in

Fig. 1. (*a*) Relative abundance of yearling bloater (*Coregonus hoyi*) (solid circles), adult (age 2+) bloater (solid triangles), and adult alewife (*Alosa pseudoharengus*) (open squares) in Lake Michigan from 1965 to 1999. Observed (symbols) and predicted (lines) mean length-at-age for (*b*) age 1 (solid circles, lower line) and age 2 (solid triangles, upper line), (*c*) age 3 (solid circles, lower line) and age 4 (solid triangles, upper line), and (*d*) age 5 (solid circles, lower line), age 6 (solid triangles, middle line), and age 7 (solid squares, upper line) over time in Lake Michigan.
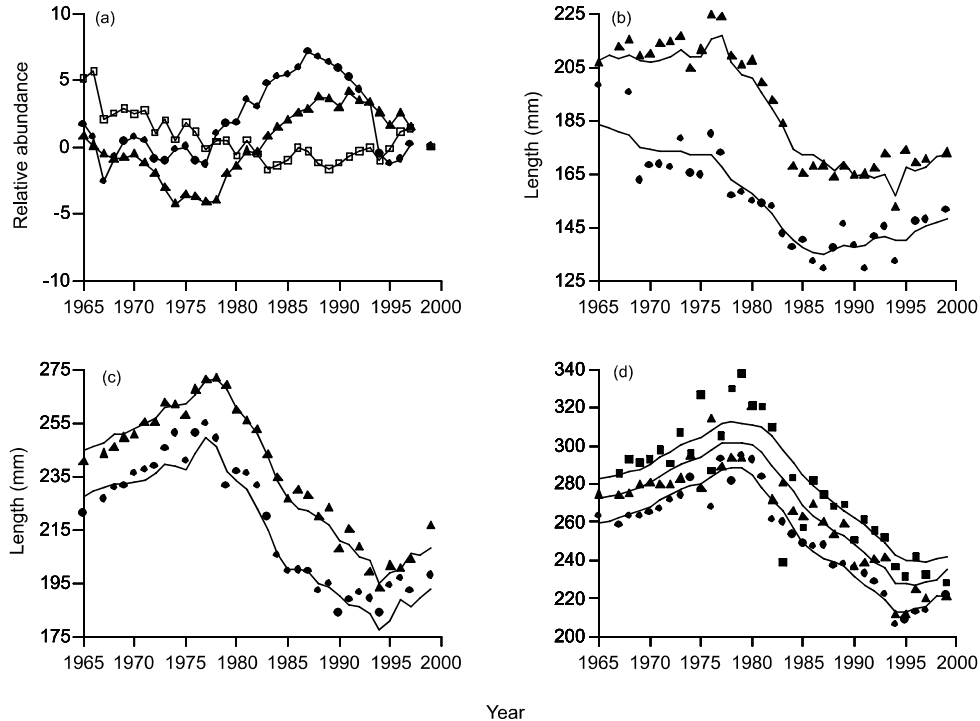
1967, three additional locations were included. Starting in 1973, an additional three locations were added for a total of seven fixed shore locations.

Bloater scales were collected annually for age determinations since 1965 (except for 1966 and 1998). Bloater scale sampling was limited to fish collected at four designated locations (Frankfort, Mich., Saugatuck, Mich., Waukegan, Ill., and Manistique, Mich.) rather than at all locations (except in 1999 when scales were also sampled from Ludington, Mich., and Port Washington, Wis.). From 1965 to 1982, scales were sampled from fish selected at random from the entire bloater size distribution at each of the designated locations. However, since 1983, scale samples have been collected following a stratified sampling design. Scales were collected from a maximum fixed number of fish for each 10-mm length class for each location sampled. The number of scale samples per length class sampled was not constant since 1983, but in most years, about 40 fish were sampled for scales from the most abundant length classes. As would be expected, in some years, very few individuals were sampled from both the smaller and larger length classes. Bloater ages were determined by visual inspection of projected scale images and an age class designation was based on enumeration of observed annuli. Bloater ranged from 0 to 12 years of age. Ageing error was not incorporated in the analysis of size-at-age data. Scored ages were assumed to be true ages

for all fish. The amount of ageing error in scale ageing of bloater populations in the Great Lakes has not been investigated and studies of ageing error in other coregonid species have suggested that the amount of ageing error depends on growth rate, with higher error rates in slower-growing populations (Raitaniemi et al. 1998). Few individuals over age 7 were sampled, and scales were not consistently collected from individuals less than 100 mm in length. Thus, our growth modeling used data for ages 1 to 7 only.

Mean length- and weight-at-age

Because scale samples were not collected at all locations for the entire time period (1965–1999), it was not possible to calculate location-specific mean size-at-age. Previous analysis of the fall bottom trawl data has suggested that the mean size-at-age of bloater differs across the lake (Krause 1999). For this reason, bloater age data were pooled into a northern region (Port Washington, Wis., Sturgeon Bay, Wis., Manistique, Mich., Frankfort, Mich., and Ludington, Mich.) and southern region (Saugatuck, Mich., and Waukegan, Ill.) to calculate regional mean lengths- and weights-at-age (Fig. 2). Bloaters were sampled in both regions for all years except 1965 when only the southern region was surveyed. From 1965 to 1982, when age structures were sampled randomly, the mean length- and weight-at-age in each year and region were calculated by taking the mean of the length and weight, respectively, of all

Fig. 2. Fixed shore locations in Lake Michigan for U.S. Geological Survey – Great Lakes Science Center fall bottom trawl survey. (Inset) Map of the Great Lakes with the international boundary between Canada and the United States of America indicated.
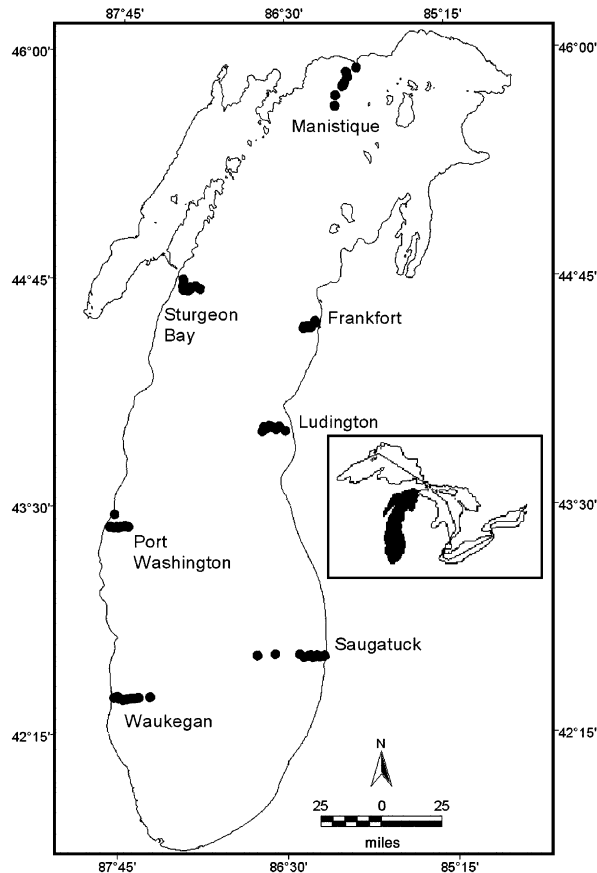
aged fish in each region. From 1983 to 1999 when stratified sampling was used, mean length-at-age $(\bar{L}_{a,y,i})$ in each year and region was estimated by

$$(1) \quad \bar{L}_{a,y,i} = \frac{\sum_{j} p_{a,y,i,j}\, p_{y,i,j}\, \bar{l}_{a,y,i,j}}{\sum_{j} p_{a,y,i,j}\, p_{y,i,j}}$$

where $p_{y,i,j}$ is the proportion of the bloater in length bin j from the length–frequency sample for year y and region i, $p_{a,y,i,j}$ is the proportion of age a in length bin j from the scale sample for year y and region i, and $\bar{l}_{a,y,i,j}$ is the mean length-at-age a in length bin j for year y in region i (Gavaris and Gavaris 1983). For large catches (e.g., greater than 20 kg), the total size of the catch and the number of bloater in each length bin were estimated from subsamples of the total catch (see Krause (1999) for details). Mean weight-at-age $(\bar{W}_{a,y,i})$ in each region and year was estimated similarly with $\bar{l}_{a,y,i,j}$ replaced by $\bar{w}_{a,y,i,j}$ (mean weight-at-age a in length bin j in year y and region i). Because the bloater population is generally treated as one stock rather than as two distinct stocks, the regional estimates of size-at-age were averaged to obtain

a lakewide estimate of mean size-at-age $(\bar{L}_{a,y}$ and $\bar{W}_{a,y}$, respectively) for the bloater population.

Abundance indices of bloater and alewife

CPUE data from the annual USGS fall trawl survey were analyzed to derive year-specific indices of relative abundance for adult (age 2+) bloater and alewife, along with yearling bloater. The natural log of the CPUE data was fit to a general linear model incorporating effects for year, location, and depth and allowing correlations among observations from the same location within a year (see Krause (1999)). The estimates of the fixed effects for year were used as an index of relative abundance. These relative indices are expressed on the natural logarithmic scale and differ from the natural log of CPUE by an additive constant. We used these indices to explore the relationship between the changes in bloater growth over time and abundance of yearling and adult bloater, along with adult alewife.

Growth model

We applied a growth model that allowed mean length-at-age to change between years. We also modeled the length–weight relationship in a way that allowed weight-at-length to vary over time. In combination, this allowed us to consider how both weight- and length-at-age changed over time. Dynamics in mean length-at-age were modeled by generalizing the incremental von Bertalanffy growth model to incorporate time-varying growth parameters. Thus, predicted mean length-at-age in a given year depended on mean length of the same cohort in the previous year and the growth parameters for the previous growing season. These predicted mean lengths-at-age were compared with the observed lengths-at-age over all years and adjustments in the growth parameters were made, using a numerical search, to provide the best agreement between the observed and predicted mean lengths-at-age. We were also interested in how the relationship between mean weight-at-age and mean length-at-age changed over time and thus modeled mean weight as a power function of mean length with parameters that were allowed to vary over time. The parameters determining this time-varying relationship were estimated by using them to predict mean weight-at-age using observed mean length-at-age and comparing these predictions to the observed mean weight-at-age. The parameters of the final model are described in Table 1. The dynamic equations used to predict mean length- and weight-at-age and changes in the growth parameters over time are described in Table 2. The equations presented in these tables are referenced by T$x.y$, where x is the table number and y is the equation number within Table x.

Length-at-age model

In 1965, mean length-at-age for all ages was predicted by the standard form of the von Bertalanffy growth model (eq. T2.1). For all other years, mean length-at-age for ages 2 and older was predicted by the incremental form of the von Bertalanffy model (eq. T2.2). If the incremental form predicted a negative growth increment, then the growth increment was set to zero. This situation never occurred once the parameter values had converged to the best estimates. Because changes in yearling length over time could not be de-

scribed well by the above model, we modeled yearling length separately as a random walk on the log scale (eq. T2.3). The random walk was started in 1965 at the yearling length predicted by eq. T2.1. This approach allows yearling length to change over time but assumes that yearling length in a given year would tend to be similar to the value from the previous year.

Similarly, we modeled L_∞ as a random walk on the log scale, where ε_y is a random change estimated by the model in every year and the random walk was started at L_∞ in 1965 (eq. T2.5). The parameters L_∞ and k were not allowed to vary freely from one another, rather k was assumed to be a linear function of L_∞ with a year-specific random (white noise) deviation (eq. T2.6). This relationship would allow L_∞ and k to have either a positive or negative relationship. The parameters of this relationship and each year-specific random deviation were estimated during the fitting process.

Weight-at-age model

Mean weight-at-age in every year was predicted from observed mean length-at-age ($\bar{L}_{a,y}$) using a length–weight relationship with time-varying parameters (eq. T2.4). Both α_y and β_y were assumed to follow a random walk on the log scale with the starting values in 1965 estimated as parameters during model fitting (eqs. T2.7 and T2.8, respectively).

Model optimization

The model was fitted using AD Model Builder software (Otter Research 2000). AD Model Builder is a superset of C++ that uses automatic differentiation in the application of a quasi-Newton method to fitting nonlinear models, based on a user-specified likelihood equation. In the fitting of this model, the negative log-likelihood function was minimized to obtain parameter estimates. The log-likelihood consisted of seven components:

$$(2) \qquad \ell = \ell_1 + \ell_2 + \ell_3 + \ell_4 + \ell_5 + \ell_6 + \ell_7$$

which correspond to those for the observed mean length- and weight-at-age, the random walks, and the white-noise deviations (Table 3). Mean length- and weight-at-age were both assumed to follow a lognormal distribution (eqs. T3.1 and T3.7). The random deviations from the random walks and from the relationship between L_∞ and k were assumed to follow normal distributions (eqs. T3.2–T3.6). Because the variance terms for ℓ_1–ℓ_7 were either estimated directly during model fitting or provided before fitting, the likelihood components are self-weighting and no additional weighting factors were used.

The variance term, $\sigma_{a,y}^2$, for ℓ_1 (eq. T3.1) was age- and year-specific and composed of two variance components, "measurement error", σ_m^2, and "process error", σ_p^2. The measurement error parameter captures the changes in the reliability of the mean lengths-at-age as sample size changes. The process error parameter captures any errors that are independent of sample size (e.g., the spatial distribution of certain sizes of bloater in the lake differing between years). The measurement error (on the log scale) was not fitted during the minimization process, rather an estimate was obtained based on the variation in observed lengths-at-age ($\sigma_m^2 = 0.0041$) and treated as a constant.

For ℓ_4 (eq. T3.4), the variance term, σ_k^2, could not be estimated during model fitting at the same time as σ_∞^2. Both of these variances refer to process errors for unobserved state variables, and hence there is a singularity in the likelihood surface when their ratio approaches zero or infinity (Schnute and Richards 1995). As an alternative, we modified a strategy used by Schnute and Richards (1995). First we assumed that σ_k^2 was proportional to σ_∞^2 with the proportionality constant, ρ, that was fixed before model fitting. During model fitting, σ_∞^2 was estimated as a parameter and the appropriate value of σ_k^2 was calculated using the estimate of σ_∞^2 and the fixed value of ρ. To choose a value for ρ, we used an iterative approach. First, we fit the model using a wide range of values for ρ to obtain estimates of σ_∞^2 and σ_k^2. We also calculated the "observed" variances based on the variation in our estimates of ε_y and e_y for each value of ρ. By comparing the observed variances in the random deviations to the estimates of the variance components, we found there was only one value of ρ for which these quantities were approximately equal and used this value of ρ in our final model. At this value of ρ, the likelihood profile with respect to ρ is nearly flat. The resulting variances appeared reasonable to us and the resulting model predictions of mean length-at-age were not very sensitive to specific choices for ρ. Although our approach is a repeatable method for obtaining the ratio of these variances, it is an ad hoc approach. Methods for weighting likelihood components when process errors are involved is clearly an area for further research.

The variance components, σ_α^2 and σ_β^2 for ℓ_5 and ℓ_6 (eqs. T3.5 and T3.6, respectively), also could not both be estimated during the fitting process. Instead, as described for variance components of ℓ_4, we allowed σ_α^2 to be estimated during the model fitting process and then assumed that σ_β^2 was proportional to σ_α^2 with a proportionality constant of φ that was fixed during model fitting. The value of φ was chosen using the same procedure described for ℓ_4.

The parameters L_∞, α, and β in the first year, the intercept of the linear relationship between L_∞ and k, and the variance components must be positive and were restricted to the positive real numbers during model fitting by estimating them on the log scale. All other parameters were estimated on the arithmetic scale.

Other model variants explored

The process of choosing the model structure presented above was based on exploring many variants of a standard von Bertalanffy growth model to find a model structure that adequately described the patterns found in the observed length- and weight-at-age data. We attempted to find the most parsimonious model that provided good predictions of mean size-at-age over time. We assessed model fit by visually inspecting residual plots and by using Akaike's information criterion (AIC) to compare different models. In this section we will describe several of the different model structures that we investigated to help guide model choice.

In an initial attempt to model the changes in length-at-age, we allowed only L_∞ to be different in each year, keeping k constant over the entire time period, which produced strong patterns in the residuals that we deemed unacceptable. Subsequently, we allowed both k and L_∞ to vary with time independently of one another, but this model failed to converge

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Table 1. Parameters and fixed constants for the time-varying von Bertalanffy growth model and weight–length relationship.

Parameter	Description
$L_{\infty_{1965}}$	L_∞ for mean length-at-age in 1965
ε_y	Random walk deviations for L_∞
t_0	Age at length 0 in 1965
b	Intercept of linear function between k and L_∞
m	Slope of linear function between k and L_∞
e_y	Year-specific deviations for linear function between k and L_∞
ξ_y	Random walk deviations for $L_{1,y}$
σ_m^2	"Measurement" error in length-at-age data *
σ_p^2	"Process" error in length-at-age data
σ_∞^2	Variance component for L_∞ random walk
σ_1^2	Variance component for $L_{1,y}$ random walk
ρ	Proportionality constant for variance component for $e_v{}^a$
α_{1965}	α from the weight–length relationship in 1965
β_{1965}	β from the weight–length relationship in 1965
υ_y	Random walk deviations for α
δ_y	Random walk deviations for β
σ_w^2	Variance component for weight-at-age data
σ_α^2	Variance component for the α random walk
φ	Proportionality constant for the variance component of the β random walk[a]
n	Number of years
$n_{a,y}$	Sample size of fish aged in each age and year

[a]Parameter fixed during model-fitting process. See text for further explanation.

Table 2. Dynamic equations used to predict mean length- and weight-at-age and changes in growth parameters over time.

Mean length- and weight-at-age

T2.1 $L_{a,1965} = L_{\infty_{1965}}(1 - e^{-k_{1965}(a-t_0)})$

T2.2 $L_{a+1,y+1} = L_{a,y} + (L_{\infty_y} - L_{a,y})(1 - e^{-k_y})$

T2.3 $\log(L_{1,y+1}) = \log(L_{1,y}) + \xi_y$

T2.4 $\hat{W}_{a,y} = \alpha_y \bar{L}_{a,y}{}^{\beta_y}$

Growth parameters

T2.5 $\log(L_{\infty_{y+1}}) = \log(L_{\infty_y}) + \varepsilon_y$

T2.6 $k_y = b + mL_{\infty_y} + e_y$

T2.7 $\log(\alpha_{y+1}) = \log(\alpha_y) + \upsilon_y$

T2.8 $\log(\beta_{y+1}) = \log(\beta_y) + \delta_y$

Note: $L_{a,y}$ is the predicted mean length-at-age a in year y; $\bar{L}_{a,y}$ is the observed mean length-at-age a in year y; $\hat{W}_{a,y}$ is the predicted mean weight at observed mean length-at-age a in year y; L_{∞_y} is the asymptotic length in year y; k_y is the Brody growth coefficient in year y; and α_y and β_y are the parameters of the weight–length relationship in year y.

on a solution. In an attempt to allow both L_∞ and k to vary over time but in a correlated manner, we attempted to incorporate the functional relationships between L_∞ and k (of the general form $k = qL_\infty^g$) proposed by Jensen (1996), but none of these models would converge on a solution, apparently because the assumed negative relationship does not agree with the observed data. We then fitted a model where k was

a linear function L_∞, which was able to converge on a solution but still had strong patterns in the residuals, particularly for yearlings (age 1). To remove these patterns in the residuals, we arrived at the model presented above. We also attempted to capture the change in mean weight-at-age by allowing only α or β to vary with time, but we found that the AIC for the model in which both α and β were allowed to vary with time was lower than either of these simpler models.

Finally, we also fit a cohort-based model (i.e., growth parameters differed between cohorts but remained constant across a given cohort's life) because the growth patterns appeared to be correlated across years. However, we found that this model structure produced very strong patterns in the residuals and was unable to capture the changes in growth that occurred in the late 1990s. For this reason, we deemed this type of model unacceptable.

Results

Model fit

Although the measurement error variance (σ_m^2) was 6.81 times larger than the process error (σ_p^2; Table 4), the contribution of measurement error to total variance in predicted mean length-at-age declines rapidly with increasing sample size. For example, for a sample size of 10, the measurement error contributes ~40% to the total variance in predicted mean length-at-age, but its contribution declines to ~21% for a sample size of 25. Across all years and ages, 28% of the observed sample sizes (65 of 234 age–year samples) were

Table 3. Log-likelihood components (ignoring constants) for bloater growth model.

T3.1	ℓ_1: mean length-at-age	$$\sum_y \sum_a -0.5\left((\log(\sigma_{a,y}^2)) + \frac{(\log(L_{a,y}) - \log(\bar{L}_{a,y}))^2}{\sigma_{a,y}^2} \right)$$ $$\sigma_{a,y}^2 = \sigma_p^2 + \sigma_m^2/n_{a,y}$$
T3.2	ℓ_2: random walk in L_∞	$$-\frac{n-1}{2}\log(\sigma_\infty^2) - \frac{0.5}{\sigma_\infty^2}\sum_y \varepsilon_y^2$$
T3.3	ℓ_3: random walk in $L_{1,y}$	$$-\frac{n-1}{2}\log(\sigma_1^2) - \frac{0.5}{\sigma_1^2}\sum_y \xi_y^2$$
T3.4	ℓ_4: year-specific deviations in k	$$-\frac{n}{2}\log(\sigma_k^2) - \frac{0.5}{\sigma_k^2}\sum_y e_y^2$$
T3.5	ℓ_5: random walk in α	$$-\frac{n-1}{2}\log(\sigma_\alpha^2) - \frac{0.5}{\sigma_\alpha^2}\sum_y \upsilon_y^2$$
T.3.6	ℓ_6: random walk in β	$$-\frac{n-1}{2}\log(\sigma_\beta^2) - \frac{0.5}{\sigma_\beta^2}\sum_y \delta_y^2$$
T3.7	ℓ_7: mean weight at mean length	$$\sum_y \sum_a -0.5\left(\log\left(\frac{\sigma_w^2}{n_{a,y}}\right) + \frac{(\log(\hat{W}_{a,y}) - \log(\bar{W}_{a,y}))^2}{\frac{\sigma_w^2}{n_{a,y}}} \right)$$

Note: Parameters are defined in the text and Table 1.

less than 25. There was a higher percentage of sample sizes less than 25 in the yearling (33.3%) and older ages (age 5, 24%; age 6, 45%; age 7, 72%) than in the intermediate ages (age 2, 15%; age 3, 6%; and age 4, 3%). The model fit indicates a positive correlation between L_∞ and k (Table 3), implying that in years when L_∞ was high, k is also high (Fig. 3c). This result is contrary to many theoretical and empirical studies, which describe an inverse relation between L_∞ and k (Pauly 1980; Jensen 1996).

The residuals for both mean length-at-age and mean weight-at-age from this model were generally moderate in size, with most within ±2 standard deviations (SD), and only in three cases was the value outside the range ±3 SD. Moreover, the residuals generally exhibited no pattern with year at each age. We examined those specific cases in which there appeared to be a potential temporal pattern in the residuals. The first case was mean length-at-age 4, where there appeared to be a slight trend of negative residuals in the earlier years changing towards positive residuals in the later years. Because these residuals were relatively small in magnitude, they may simply represent a minor departure from the assumed von Bertalanffy growth model. We did not deem this minor departure of sufficient magnitude to explore a more flexible growth model such as the model proposed by Schnute (1981). The second and third cases, mean weight-at-ages 1 and 7, showed opposite trends. In predicting mean weight-at-age 1, the model slightly overestimated mean weight in the earlier years and underestimated it for later years in the series. For mean weight-at-age 7, the model tended to underestimate mean weight in the earlier years and overestimate it in later years. We interpret these results to indicate that our model may not have captured all of the com-

Table 4. Parameter estimates and asymptotic standard errors (in parentheses) ($\rho = 18.16$ and $\varphi = 2.75 \times 10^{-3}$).

Parameter	$\sigma_m^2 = 0.0041$
t_0	–3.641 (0.477)
b	2.164×10^{-22} (7.65×10^{-17})
m	5.98×10^{-4} (7.68×10^{-5})
σ_p^2	7.40×10^{-4} (1.20×10^{-4})
σ_∞^2	4.51×10^{-5} (1.21×10^{-5})
σ_1^2	2.56×10^{-4} (1.03×10^{-4})
σ_w^2	0.199 (2.66×10^{-2})
σ_α^2	8.76×10^{-5} (3.18×10^{-5})

Note: This table contains all of the parameters that do not vary with time.

plexities in changes in the bloater length–weight relationship over time and that the factors that influenced the weight at mean length of younger and older bloaters may be different.

Bloater growth dynamics

The trends in estimates of both L_∞ and yearling length show a substantial decline over the latter portion of the study period (Figs. 1b, 3a). Estimates of L_∞ peaked in 1976–1977 at a value of 354 mm, then declined steadily through the 1980s and 1990s to 302 mm by 1999 (Fig. 3a). Yearling length declined from a maximum of 183 mm in 1965 to 135 mm in 1987 but subsequently has increased slightly (Fig. 1b). The estimates of k show a similar decline in the 1980s (Fig. 3b). Predicted and observed mean length-at-ages 2–7 showed an increasing mean length through the 1970s

Fig. 3. Estimates of (*a*) L_∞, (*b*) *k*, (*d*) α, (*e*) β, and (*f*) predicted mean weight of a 200-mm bloater (*Coregonus hoyi*) over time. (*c*) The estimated relationship between *k* and L_∞ in the Lake Michigan bloater population.
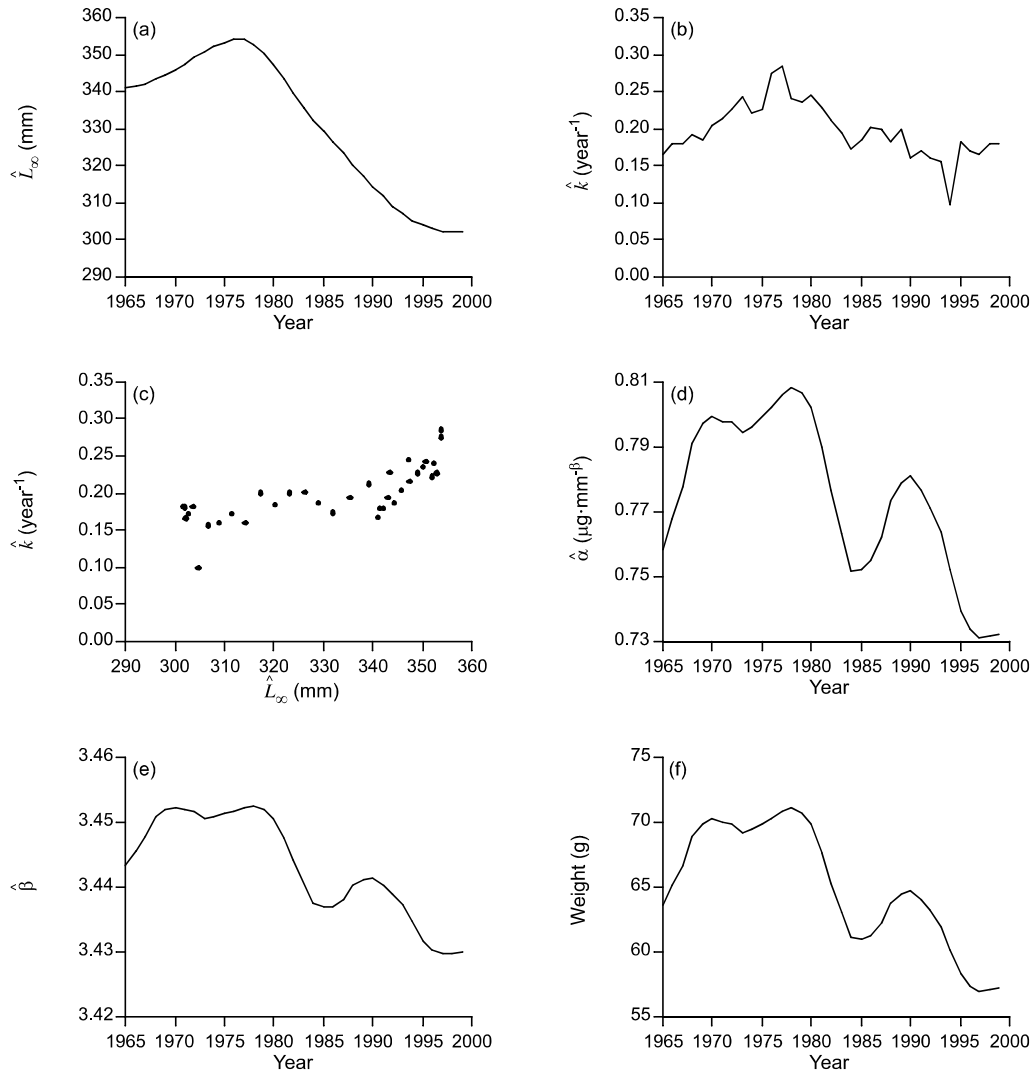
and then declined sharply through the 1980s (Figs. 1*b*–1*d*). In recent years, mean length for all ages appears to be increasing slightly.

Estimates of α and β from the length–weight relationship show similar patterns of change over time (Figs. 3*d*, 3*e*). Both increased during the late 1960s and remained relatively high throughout the 1970s. During the 1980s they declined initially and then increased during the late 1980s before declining again in the 1990s. The predicted weight of an intermediate-sized bloater (200 mm) over time increased through the early 1980s and subsequently declined after a slight recovery in the early 1990s (Fig. 3*f*).

To assess the role that density-dependent mechanisms may play in regulating bloater growth, we graphically explored the relationships between the estimates of growth parameters and bloater population abundance. Estimates of L_∞ and the relative abundance of adult (age 2+) bloater appears to be in-

versely related during most of the study period (Fig. 4*a*). However, as adult bloater abundance peaked and then declined during the 1990s, estimates of L_∞ did not respond in an anticipated density-dependent fashion. In contrast, *k* shows a more regular linear decline with increased adult abundance (Fig. 4*b*) There appears to be a slight change in this trend at high relative adult abundance. If we factor out the effects of changes in L_∞ by only looking at the estimated random deviations (e_y), this feature is more apparent (Fig. 4*c*).

The temporal pattern in the bloater length–weight relationship through the mid-1980s also suggests density-dependent effects. Our estimates of the mean weight at 200 mm from 1965–1984 appear to follow a similar pattern with higher weight during periods of lower bloater abundance (Fig. 4*d*). However, during the late 1980s and early 1990s, mean weight increased despite the higher adult bloater abundances. This transient temporal response of mean weight at 200 mm was

Fig. 4. Relationship between estimates of (a) L_∞, (b) k, and (c) deviations (e_y) from the linear relationship between L_∞ and k and (d) predicted mean weight of a 200-mm bloater (*Coregonus hoyi*) and the relative abundance of adult (age 2+) bloater in Lake Michigan, 1965–1999.

Adult abundance
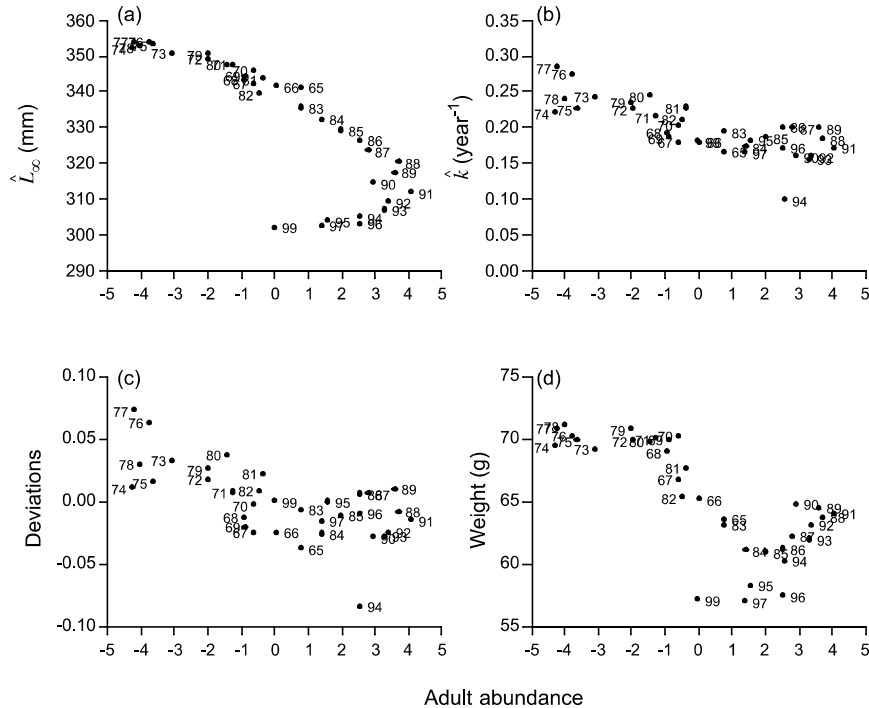
not seen in the von Bertalanffy parameters. Subsequently, mean weight at 200 mm returned to low levels and, like L_∞, did not increase in the late 1990s despite lower bloater abundance.

Density-dependent growth also appears to occur for yearling bloaters. The relationship between estimated yearling length and yearling relative abundance shows decreased yearling size with increased abundance of yearlings (Fig. 5 a). However, in the most recent years (1994–1999), as was seen for the adult growth parameters, this relationship appears to have broken down. Juvenile bloater growth and adult alewife abundance are positively correlated from 1965 to 1999, with larger yearling length achieved in times of high alewife abundance (Fig. 5 b).

Discussion

We were able to capture the dramatic changes in bloater size-at-age by modeling changes in L_∞, k, α, β, and yearling length. The model, in general, predicted mean length- and weight-at-age that agreed very well with observed data. Some patterns were detected in the residuals, but these patterns appear to be only minor deviations from our growth model. Although limits with regard to estimability were encountered (e.g., we could not estimate k independently for each year), we were still able to capture the dynamics and infer the mechanisms of the changes in bloater growth over time.

Our model shares features with some previous attempts to fit dynamic growth models to mean length-at-age data (Millar and Myers 1990; Millar et al. 1999). Unique features of our

approach included using a time series approach to describe changes in growth parameters over time (i.e., random walks) rather than assuming relationships with environmental factors and combining length- and weight-at-age information in the description of changes in growth over time. By using a dynamic growth model, such as the model presented here, the noise inherent in mean size-at-age data can be smoothed, eliminating the negative growth increments that are often observed when calculated directly from observed size-at-age. Furthermore, the parameters of the growth model provide a useful and parsimonious way of summarizing how growth is changing over time and allow researchers to investigate mechanisms for changes in growth over time using information from all ages rather than a selected few.

The incremental growth model presented here allowed all fish of the same size, regardless of their previous growth history, to achieve the same growth. This feature allowed for fish to recoup size-at-age even after previous poor growth if conditions improved. As such, this model would not be able to emulate stunting (the phenomenon of previous growth history influencing current growth potential; Ylikarjula et al. 1999). Although we did not see evidence for stunting in the Lake Michigan bloater population, our ability to detect this condition may be obscured because of the relatively slow change in conditions over time and the observation that most individuals experiencing poor growth conditions in early life also experience poor growth conditions as an adult. If further evidence suggests that stunting may be important in bloater growth dynamics, then the dynamic growth model would need to be adjusted to incorporate this process. Millar and

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Fig. 5. Relationship between estimated yearling length and (a) relative abundance of yearling bloater (*Coregonus hoyi*) in Lake Michigan, 1965–1999, and (b) relative abundance of adult (age 2+) alewife (*Alosa pseudoharengus*) in Lake Michigan, 1965–1999.

mated seemed to decline in concert with increasing bloater abundance. However, since the beginning of the 1990s, a change in this relationship appears to have occurred. During this time, bloater growth in length and mean weight at 200 mm remained low despite relatively low abundances of both adult and juvenile bloater. We note that these recent changes in bloater growth were coincident with the invasion and expansion of zebra mussels (*Dreissena polymorpha*) and the disappearance of *Diporeia* spp. in Lake Michigan (Nalepa et al. 2000; Fleischer et al. 2001). *Diporeia* represents a major link between pelagic production and upper trophic levels in Lake Michigan and is also an important component of adult bloater diet in Lake Michigan, exhibiting higher lipid content than other benthic macroinvertebrates (Gardner et al. 1985; Rand et al. 1995; Davis et al. 1997). Zebra mussels may also be having profound effects on the primary productivity of Lake Michigan because of energetic demands (Madenjian 1995; Stoekmann and Garton 1997) that may manifest in lower productivity in lower trophic level fishes.

Interestingly, the changes in bloater growth in the 1990s are evident in the estimates of L_∞ and yearling length but not in the estimates of k. This suggests that although all three growth parameters may be affected by intraspecific density, changes in the food web can influence them differently. Such a difference could arise if the change in the food web caused approximately the same effect on incremental growth (in length), irrespective of fish size (see Walters and Post 1993). Only future monitoring of bloater length-at-age will tell if these trends continue in the future and if these changes in bloater growth are a harbinger of future changes to the Lake Michigan ecosystem.

Our inability to model changes in growth of both adult and juvenile bloater with a common set of parameters suggests that these life stages of bloater may be responding to different environmental conditions. This result is not unexpected because of the different bathymetric habitats occupied by the two life stages. Juvenile bloater occupy more nearshore, shallower depths and feed primarily on zooplankton, whereas adult bloater are limited to a hypolimnetic distribution and feed primarily on hypolimnetic prey (Davis et al. 1997). Consequently, intraspecific density-dependent growth in bloaters appears to be life stage specific (i.e., juvenile growth appears to respond strongly to juvenile abundance but not to adult abundance, and adult growth seems to respond primarily to adult abundance).

Previous studies have concluded that the invasion of the exotic alewife (*Alosa pseudoharengus*) has had profound effects on the bloater population in Lake Michigan (e.g., Crowder and Crawford 1984; Eck and Wells 1987). For example, Crowder and Crawford (1984) suggested that competition between the pelagic juvenile bloater and adult alewife for pelagic resources has caused bloater to switch to benthic resources at an earlier age (from age 3 to age 2). If competition between juvenile bloater and adult alewife was strong, we would expect that in times of high alewife abundance, juvenile bloater growth would be reduced. In fact, young bloater growth rate, as indicated by predicted yearling length, increased in concert with adult alewife abundance. This suggests that any negative interaction between juvenile bloater and adult alewife does not appear to affect juvenile

Myers (1990) have explored one model that incorporates stunting and could be used in an analysis similar to ours.

Our analysis indicates a positive relationship between L_∞ and k in the Lake Michigan bloater population. Previous studies of fish growth have shown that the relationship between L_∞ and k is generally negative (Pauly 1980; Jensen 1996). However, Pauly (1980) looked at this relationship across populations, whereas we looked within one individual fish population. We have tried several functional forms to force a negative relationship between L_∞ and k; however, none of these models was able to converge on a solution. The positive relationship that we observed, although initially counterintuitive, simply implies that when growth conditions are favorable for bloaters, they respond with both fast growth rates and larger maximum sizes.

Our analysis corroborates a previously reported density-dependent growth response of bloater in Lake Michigan (TeWinkel et al. 2002). All of the growth parameters esti-

bloater length, at least within the densities of alewife and bloater observed during the study period (1965–1999).

The implications of density-dependent growth in bloater for the Lake Michigan ecosystem may be profound. Since the mid-1980s, concern about the balance between the predatory demands of stocked salmonids and the productivity of the forage base has risen. Several observations indicate that the forage available to the salmonids, particularly the chinook salmon (*Oncorhynchus tshawytscha*), may not be sufficient to maintain the large populations of the 1980s (Stewart and Ibarra 1991; Holey et al. 1995). Bloater, especially smaller individuals, represent a potentially important alternative forage item for the salmonids (Madenjian et al. 1998). Therefore, in the future, an understanding of the forces governing bloater dynamics will be important in balancing predatory demand and forage availability. Changes in size-at-age may have many effects on their population dynamics, including mortality rates and fecundity. Our ability to accurately assess the availability of forage for salmonids depends in part on our understanding of bloater population dynamics.

Acknowledgments

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Chapter 2

QUANTIFYING UNCERTAINTY IN LAKE MICHIGAN ALEWIFE AND

BLOATER POPULATION DYNAMICS, 1962-1999

Introduction

With the increasing acknowledgment of the importance of ecological interactions

in the management of fisheries resources, focus has shifted from single-species stock

assessments to integrated assessments of the effects of management actions on fish

communities and ecosystems. Such assessments require not only the ability to assess the

current status of a key species of interest but also the ability to assess other species

involved in interactions with this species and the form of these interactions.   Recognition

that predation mortality can play an important role in the dynamics of a fish population

by altering natural mortality rates over time has led to the development of several

approaches to incorporating this source of mortality in fisheries stock assessments.

These approaches have ranged from extending traditional stock assessment

methodologies, such as virtual population analysis (Tsou and Collie 2001) or statistical

catch-at-age analysis (Livingston and Methot 1998), to incorporate the effects of

predation to the development of new trophic mass-balance models, such as Ecopath (Cox

et al. 2002) for fish communities.

One of the first approaches expanded virtual population analysis (VPA) into

multi-species models that can incorporate species interactions including predation

commonly known as multispecies virtual population analysis (MSVPA ; Pope 1991;

Tsou and Collie 2001). This method uses catch at age and stomach content data to

reconstruct the population abundances of each species over time. Predation mortality for a given prey type is calculated from the abundance of each predator type, the consumption rate of each predator type, a prey-specific suitability index, and the abundance of all prey types. Consumption rates (per predator) of each predator species are assumed known and estimated externally to the MSVPA. In practice, these consumption rates are generally assumed constant over time. While MSVPA provides a reconstruction of the population abundance of the species of interest that accounts for predation, it suffers from inability to capture how predator consumption rates change with changes in prey abundance (e.g. a functional response), assumes that consumption rates are known without error, and lacks a strong statistical framework to derive uncertainty estimates about the population reconstruction.

A second approach to incorporating predation mortality into stock assessments is to generalize the statistical catch-at-age framework and treat predators as another type of fishery operating on the species of interest (Livingston and Methot 1998; Hollowed et al. 2000). Predator abundances indices play an equivalent role to fishery effort data while data on the age composition of the stomach contents of the predator plays an equivalent role to catch age composition data. Predator consumption rates were initially assumed by Livingston and Methot (1998) to increase linearly with increases in prey abundance as in a Type I functional response (Holling 1959) but Hollowed et al. (2000) has extended the approach to incorporate asymptotic consumption rates. Additionally, because of the likelihood-based approach used in model fitting, it is possible, although not necessarily simple, to obtain uncertainty estimates for model predictions. While the applications of Livingston and Methot (1998) and Hollowed at al. (2000) incorporated multispecies interactions through the effect of several predators on a single prey population, they did

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not incorporate how changes in the alternative prey availability affect these interactions.

Here we present an extension of the Livingston and Methot (1998) approach to incorporate the dynamic links between two species sharing a common suite of predators. We utilize a multispecies Type II functional response to model changes in predator consumption rates with changes in the abundance of both species and incorporate estimates of the biomass consumed by predators from bioenergetic models as an additional source of data. Incorporation of this novel source of data allows us to estimate key parameters of the functional response. Additionally, our formulation lacks a fishery operating on either species of interest and predation mortality serves as the sole time-varying mortality source. Consumption estimates along with fishery independent survey data provide enough information to reconstruct the historical abundances of the two species of interest. This suggests that the basic approach underlying the statistical catch-at-age methodology may have applications to non-fishery based populations where a measure of the absolute abundance of a source of time-varying mortality exists (e.g. predator abundance).

In particular, we applied our methodology to reconstruct the historical abundances of the bloater (*Coregonus hoyi)* and alewife (*Alosa pseudoharengus*) in Lake Michigan. Alewife and bloater serve as important prey items for the five stocked salmonine species in Lake Michigan (Madenjian et al. 2002). Because the abundance of all five salmonine species is maintained primarily through stocking, the natural feedback between the abundance of prey and the abundance of predators does not exist. Therefore, concern that excessive stocking could lead to a collapse of the prey base arose (Stewart et al. 1981; Stewart and Ibarra 1991). Additionally, a potential imbalance between predatory demand and prey production was suggested by the collapse of the

Lake Michigan chinook salmon (*Oncorynchus tshawytscha)* fishery in the late 1980s. This collapse coincided with an outbreak of bacterial kidney disease, believed to be aggravated by nutritional stress (Holey et al. 1998; Benjamin and Bence in press a and b). The ability to manage the Lake Michigan ecosystem to support a successful salmonine fishery without compromising the prey fish community depends critically on understanding the dynamics of the prey fish community and the dynamic link between the prey fish and their salmonine predators.

Alewife are an exotic invader of Lake Michigan and are believed to have had profound effects on the Lake Michigan ecosystem. Alewife originally invaded Lake Michigan from their native marine environment in the late 1940's through the Welland Canal from Lake Ontario (Smith 1970). By the late 1960s, the alewife population had exploded and become the dominant species in the prey fish community. Concurrent with the high abundance of alewife, declines in several native prey species (e.g. bloater, emerald shiner (*Notropis atherinoides)* and yellow perch (*Perca flavescens*)) were observed, presumably due to egg and larval predation by the exotic alewife (Brown et al. 1987). Alewife dieoffs occurred during the late 1960s, with dead alewife littering beaches and interfering with water intake systems (Brown 1972). Fishery managers responded to the problem of abundant alewife with a plan to stock Pacific salmonines into Lake Michigan with the goal, in part, of controlling alewife abundance (Tody and Tanner 1966). Since the late 1960s, alewife abundance has declined dramatically and has remained at relatively low levels since the late 1980s (Madenjian et al. 2002). Nevertheless, alewife remain the most important prey item in the diet of the five stocked salmonines (Madenjian et al. 2002).

Although bloater does not comprise a large fraction of salmonine diets, juvenile

bloater are thought to be an important alternative prey source for the stocked salmonines, particularly during times of high bloater recruitment (Elliot 1993). Bloater populations in Lake Michigan have gone through several cycles of increases and declines since the late 1960s (Brown et al. 1987; Madenjian et al. 2002). Concurrent with these large shifts in abundance have been large changes in the growth rates of bloater suggesting density-dependent regulation (Szalai et al. 2003).

Early attempts to assess the effects of the salmonine community on the prey fish in Lake Michigan relied on the comparison of estimates of predatory consumption from bioenergetics modeling to estimates of the lakewide biomass of prey fish from fall trawl surveys (Stewart et al. 1981; Stewart and Ibarra 1991). However, this approach was limited because it could not dynamically predict how prey populations would respond to changes in salmonine abundance in that there was no underlying model of prey fish dynamics or a link between predator consumption and prey abundance. Additionally, since consumption by the salmonine predators was expressed on an annual basis and the abundance of prey was expressed as biomass rather than production, it was difficult to determine if there was sufficient prey production to sustain the estimated level of consumption.

Jones et al. (1993) recognized the need for a dynamic model of salmonine and prey fish populations to assess the effects that changes in stocking levels would have on the dynamics of the prey fish community. Koonce and Jones (1994) constructed multispecies dynamic models, called the SIMPLE models, of Lakes Michigan and Ontario that incorporated dynamic links between predator and prey population through a functional response model. Through the construction of these models, they recognized the importance of understanding the dynamics of the prey fish population and

emphasized the need to investigate this area further. Additionally, they emphasized the effect that incorporating uncertainty in these dynamic models may have on the outcomes of different stocking scenarios.

To address these two needs, we have attempted to quantitatively reconstruct alewife and bloater populations in Lake Michigan from 1962 to 1999 while estimating key parameters governing their dynamics using available survey data. We have incorporated a functional response model into our estimation model to capture the dynamic link between alewife and bloater and their salmonine predators. Additionally, by using information from predator assessment models, we were able to estimate key parameters of this dynamic predator-prey relationship. We have also used Bayesian statistical techniques to quantify the uncertainty in all of our estimated parameters for use in future investigations of stocking policies in Lake Michigan.

Methods

We reconstructed alewife and bloater population dynamics in Lake Michigan, accounting for the effects of predation by the stocked salmonine populations. We did this by modifying the statistical catch-at-age (SCAA) approach used in fisheries stock assessment to incorporate predation mortality as the primary time-varying mortality source. Our estimation model contains two sub-models, a dynamic population model for alewife and bloater and an observation sub-model. The dynamic population sub-models track abundance at age of both alewife and bloater using predictions of recruitment, natural mortality rates and predation mortality rates over time. Predation mortality was modeled using a Type II functional response, which allowed mortality rates to respond to changes in both prey and predator population abundances. The observation sub-model predicts values for the survey and assessment data used in model fitting based on the current abundances at age for alewife and bloater. We then compare our predictions to observed survey indices for both prey populations and assessment estimates of salmonine consumption to estimate key parameters governing alewife and bloater dynamics, including those describing the stock-recruitment relationships and the functional response. Uncertainty in these parameters was assessed using Bayesian statistical techniques to describe the joint posterior probability distributions of all estimated parameters.

Prey fish surveys

The United States Geological Survey-Great Lake Science Center (USGS-GLSC) has been monitoring the prey fish community in Lake Michigan since 1962. A lakewide fall bottom trawl survey has collected information on age, length, weight and abundance of alewife and bloater as part of the ongoing prey fish assessment. In addition, from

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1992 to 1996, the prey fish community was also sampled using a fall hydroacoustic survey. Both of these surveys provide information on the changes in abundance, age composition and length distribution over time.

Fall bottom trawl survey

Fall bottom trawl surveys have been conducted annually since 1962 at fixed locations throughout Lake Michigan by the USGS-GLSC. The surveys provide information on size (length and weight), age composition, and abundance (through catch per unit effort-CPUE) of the alewife and bloater populations along with several other prey fish species (deepwater sculpin (*Myoxocephalus thompsoni*), rainbow smelt (*Osmerus mordax*), and slimy sculpin (*Cottus cognatus*)). Trawls were generally 10 minutes in length and used a $\frac{3}{4}$ Yankee Standard No. 35 bottom trawl (12-m headrope, 15.5-m footrope, and 13-mm mesh in the cod end) dragged on contour during the day as described by Hatch et. al (1981). Sampling was done offshore at up to seven fixed shore locations distributed geographically around the lake. Generally tows were made at each location at 9 m depth intervals and the sampled depths ranged from 6 m to 128 m. Not all locations were sampled in each year, usually related to weather conditions, nor were all depths sampled at each location due to irregular bottom features. All trawl catches were processed to estimate the total weight of the catch by species (Krause 1999).

Both alewife and bloater populations were sampled for age determination using the fall bottom trawl survey. Scales were used to determine age from 1965 to 1982. Since 1982, otoliths rather than scales have been used for alewife age determination while scales continued to be used for bloater. All fish below a length cutoff which varied over time (100-120 mm for alewife, 100-140 mm for bloater) were assumed to be young

of the year (Krause 1999). Ages ranged from zero to nine for alewife and zero to twelve for bloater. However, very few fish over age 6 were captured for alewife and few fish over age 7 were captured for bloater.

The age samples were used to construct age-length keys for alewife and bloater for each year (and where appropriate lake region) and these keys were used to convert catch per length bin to catch per age class (Krause 1999). Catch per unit effort (CPUE) by age class for alewife and bloater were analyzed to derive year-specific relative indices of abundance. The natural log of the CPUE by age class data was fit to a general linear model incorporating effects for year, location and depth allowing for correlated errors among samples from the same location within a year (Krause 1999). The estimates of the fixed effects for year were used as an index of relative abundance at age for both alewife and bloater from 1962 to 1999. These relative indices are expressed on the natural logarithmic scale and differ from the natural log of CPUE by an additive constant.

Because very few bloater over age 7 were captured in the trawl survey, all bloater over age 7 were combined to produce a relative index of abundance for age 7+ bloater. Concerns over the large aging errors in adult alewife when scale structures were aged, as observed by O'Gorman et al. (1987), caused us to analyze the adult alewife CPUE data as a composite age 3+ age class rather than individual age classes. Additionally, age 1 and age 2 alewife are incompletely sampled by the bottom trawl survey, so the CPUE data for these age class may not reflect trends in true abundance (C. Madenjian, USGS-GLSC, Ann Arbor, Michigan, personal communication). Therefore, we only utilized age 0 and age 3+ relative indices of abundance for alewife in our model.

Both alewife and bloater length and weight at age were calculated from the fall bottom trawl data. Since bloater weight and length at age has varied substantially over

time, we used the predicted mean weight and length at age from Szalai et al. (2003)'s time-varying growth model. Alewife mean length and weight at age was calculated from the fall bottom trawl surveys by averaging across all years.

Hydroacoustic survey

From 1992 to 1996, the Lake Michigan prey fish community was assessed by the USGS-GLSC using a fall hydroacoustic survey. Acoustic measurement were made at night along a selected transect with a second vessel following to perform a midwater trawl to determine species composition (Argyle et al. 1998). Survey transects were located throughout Lake Michigan (excluding Green Bay and Grand Traverse Bay) and were selected to provide good geographic coverage of the lake basin. Alewife abundance estimates were divided into two life stages (young of the year and age 1+) while bloater abundance estimates were combined across all age classes (Argyle et al. 1998). Variance estimates were then calculated for the lakewide estimates of abundance (Argyle et al. 1998). Due to inclement weather, the number of transects completed in 1992 was insufficient to provide lakewide spatial coverage and subsequently we chose not to utilize these estimates during model fitting (Argyle et al. 1998).

Predator abundance and consumption

Estimates of age-specific abundance of lake trout (*Salvelinus namaycush*, ages 1-10+), coho salmon (*O. kisutch*, ages 1-2), chinook salmon (ages 0-5), brown trout (*Salmo trutta*, ages 1-5+) and steelhead (*O. mykiss*, ages 1-5+) at the beginning of the year (prior to any mortality occurring) were obtained from the most recent predator assessments for Lake Michigan (Appendix A). In our calculations of the mortality rates on alewife and bloater due to predators, we used geometric mean predator abundances (over the year) derived from these assessments (Appendix A). Chinook salmon weight and length at age

was varied over time, whereas the other predators were assumed to have constant size at age in all years, because available size at age data did not indicate trends over time (Appendix A). Predator length and weight at age were obtained from the same stock assessments (Appendix A).

Estimates of total fish consumption and total consumption by prey type, small (<120 mm) alewife, large alewife, and other fish, in metric tonnes by all five salmonid predators were obtained from Madenjian et al. (2002), derived using a production-efficiency method as described by Ney (1990).

Alternative prey

Four other types of alternative prey besides alewife and bloater were included in the predation model. These prey types included small (<100 mm) and large rainbow smelt, slimy sculpin and deepwater sculpin. These species were not modeled dynamically, instead their abundance, as estimated by swept-area methods using the fall bottom trawl survey data from 1972-1999, were treated as known inputs (Madenjian et al. 2002). The average of their abundance from 1972-1977 was used as an estimate of their abundance from 1965-1971. The average length and weight of small and large rainbow smelt, slimy sculpin and deepwater sculpin was estimated as the average across all years (1972-1999) of length and weight data from the fall bottom trawl survey. Abundance in numbers for each prey type was calculated by dividing the biomass estimates by the average weight of each prey type.

Estimation model

Symbols used in model development are defined in Table 1. Equations governing alewife and bloater population dynamics and for the prediction of survey indices and assessment estimates of consumption are in Tables 2 and 3. These equations are

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referenced in the text by *Tx.y*, where *x* is the table number and *y* is the equation number

within Table *x*. Appendix B contains the data used in model fitting and the values of

assumed known constants.

Numbers at age for alewife and bloater were modeled from 1962-1999. For

alewife, the ages modeled ranged from age 0 to age 6+, where the final age group

accumulated all older surviving alewife. For bloater, the ages modeled ranged from age

0 to age 7+, where the final age group also accumulated all older surviving bloater.

Recruitment to age 0 for both species was estimated as a free parameter for each year.

Numbers at age in the first year for both species were treated differently. For bloater, the

number at age in the first year for ages 1 to 7+ were estimated independently as model

parameters. For alewife, the abundance of age 1 was estimated as a model parameter,

and the abundances at ages 2 to 6+ was assumed to follow a stable age distribution

predicted by background natural mortality rates and recruitment at age 1 equal to the

estimated age 1 abundance for the first year.

Numbers at age of alewife and bloater for later years and ages greater then zero

were calculated by eq. T2.1. Older alewife and bloater were accumulated in the last age

group (*l*) by eq. T2.2.

Mortality rates

Instantaneous total mortality rates for alewife and bloater consisted of two

additive sources, background natural mortality rates and predation mortality rates (eq.

T2.3). Background natural mortality rates were not estimated during model fitting but

supplied as known quantities. We assumed natural mortality took one value for age 0 fish

and another for all older fish. Initial estimates for age 1+ background natural mortality

rates were derived from Pauly's equation and for age 0 the background natural mortality

rates were double that of age 1+ (Pauly 1980). Several scenarios were investigated

where both the natural mortality rates of age 0 and age 1+ for alewife and bloater were

increased and decreased by 25% and 50%. Final estimates of alewife and bloater natural

mortality rates were chosen by the scenario where the objective function was lowest and

are reported in Table 4. We also explored several models where natural mortality rates

declined gradually with age but these models performed poorly. Natural mortality rates

were assumed constant over time for both alewife and bloater with one exception. The

large dieoff in 1967 for alewife was simulated by estimating an additional instantaneous

mortality rate to decrease the survival of age 1+ alewife in 1967 by eq. T2.4

Predation mortality rates for each alewife and bloater age class were calculated

separately for each age class of the five salmonid species. Consumption rates per

predator (kg) of lake trout, brown trout, coho salmon and steelhead were assumed to be

constant from 1965 through 1999 because no consistent trend has been detected in their

weight at age from 1965 to present (Appendix A). Therefore consumption rates per

predator by predator type j were set at the average consumption per predator for 1965-

1999 from Madenjian et al. (2002). We refer to the rate for predator type j as $C_{\max, j}$

because we assume that these predators are consuming at or near the asymptotes of their

functional responses. These consumption rates were then distributed among the various

prey types and converted to numbers based on the predator's attack rate for each prey

type and the abundance of each prey type by eq. T2.6a.

Consumption rates per predator for chinook salmon were assumed to follow a

Type II functional response as these predators showed a declining size at age with

declining alewife abundance. The instantaneous consumption rate ($A_{i,j,y}$) for an age j

chinook on prey type i in year y is predicted by eq. T2.6b. The maximum consumption

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rates per predator of chinook salmon were estimated from the maximum observed

consumption per predator by Madenjian et al. (2002).

Attack rates for each predator-prey combination were the product of three

components as in Jones et al. (1993): the effective searching efficiency of each predator

type on an optimal sized prey, the size preference of a predator for a prey type, and the

habitat overlap between the prey and predator type (eq. T2.7). The effective searching

efficiency of each predator was calculated as a length-based scalar , γ , which was

estimated as a model parameter, times the length of the predator. As in Jones et al.

(1993), the size preference function is based on the length ratio of the prey type to the

predator type, $\ell_{i,j}$ by eq. T2.8. It is a bell-shaped function that peaks at a preference of 1

at the optimal ratio, ℓ_{opt} , of 0.25 and the width of the bell is controlled by the parameter

ϖ , which was fixed at 0.01. To account for predator growth throughout the year, we

used the geometric average length at age (of beginning of the year length and end of the

year length) of a predator to approximate its mid-year length.

Habitat overlaps were assumed to be constant across predator ages and only

varied with predator species and prey type and age categories. Habitat overlaps for all

predator species with all ages of alewife were assumed to be one based on the

observation that alewife remained an important component of the predator's diet even

when abundance was low. Similarly, habitat overlaps of all predators with both small

and large rainbow smelt were assumed to be one. Habitat overlaps between all predators

with the exception of lake trout and brown trout, and adult bloater (age 2+), slimy, and

deepwater sculpin were assumed to be zero based on the different bathymetric

distributions of these species. Both brown trout and lake trout had nonzero habitat

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overlaps (0.1 and 1, respectively) with adult bloater due to the observation that these two species have the potential to occupy similar bathymetric distributions as adult bloater. Only lake trout had a nonzero habitat overlap with slimy and deepwater sculpin (0.1 for both prey types) as they are the only predators that feed at the depths occupied by these species. Since juvenile bloater (ages 0,1) are pelagic, they are potentially available as prey for all predators. The habitat overlap between lake trout and juvenile bloater was assumed to be one while the habitat overlap between the other predators and juvenile bloater was assumed to be 0.1.

Instantaneous predation rates on alewife and bloater by age were calculated by eq. T2.5 using the "average" abundance of each prey type. The consumption of age 0 to 6+ alewife and age 0 to 7+ bloater was calculated using Baranov's catch equation (eq. T3.1) by applying these rates to beginning of the year abundance. We devised an iterative method to find an "average" abundance of alewife and bloater that produced the appropriate amount of consumption. The following steps were repeated until total consumption in biomass of alewife and bloater changed by less than 1% of the total consumption calculated in the previous iteration :

1. Instantaneous predation rates were predicted using "average" abundance for alewife and bloater (beginning of the year abundance in the first iteration)

2. The instantaneous predation rates were used to calculate end-of-year abundances of alewife and bloater along with total consumption of alewife and bloater.

3. The geometric mean abundance of alewife was calculated and used as the new "average" abundance in step 1.

The total consumption of alewife and bloater ($C_{awbl,j}$) by predator type j is predicted by summing across the consumption of each species and age predicted by eq

T3.1. However, since rainbow smelt, slimy sculpin, and deepwater sculpin are not modeled dynamically, the consumption of each predator type on these species cannot be predicted using eq. T3.1. From eqs. T2.6 a and b, we can calculate the relative proportion of each prey type in the diet. These relative proportions can then be used to approximate total consumption of all prey species by eq. T3.2. Total consumption by all predator types ($\hat{C}_y$) is then predicted by eq. T3.3 for comparison with observed quantities. Additionally, we also predicted the consumption (in weight) per predator ($\hat{C}_{a,y}^{chs}$) for ages 1-3 chinook salmon for comparison with observed quantities (eq. T3.4). We also predicted the proportion of total consumption (by weight) on small (ages 0 and 1) and large (ages 2+) alewife, and other fish ($\hat{\theta}_y$) for comparison with observed quantities.

Predicting survey abundance indices

The observed indices of abundance for the fall bottom trawl survey were on the log-scale and were calculated relative to the abundance in 1999, and the trawl survey usually occurred in October of each year (but see below). Therefore, we predicted indices as the log of the ratio of abundances at age in each year to the abundance at age in 1999, after accounting for mortality that occurred over 10/12ths of the year. Indices for ages 0 to 7 bloater and for ages 3+ alewife for 1962-1997 were predicted by eq. T3.5a.

The timing of the fall bottom trawl survey shifted from an October mid-date in the 1960s through 1980s to a mid-date of mid-September in the 1990s. This shift appears to have influenced the catches of alewife (particularly age 0 alewife) caught in the trawl survey which seems plausible if the vertical distribution of young alewife changes during this period (Figure 1). For this reason, we attempted to account for the apparent change in the catchability of age 0 alewife by estimating a relative catchability coefficient for age

0 alewife after 1990 and modifying the predicted trawl indices from 1962-1990 as in eq.
T3.5b.

Fall hydroacoustic survey indices were predicted by the biomass of bloater (all ages), age 0 alewife, and age 1+ alewife present at the time of the survey (again after 10/12ths of the years mortality). The hydroacoustic indices were assumed to be only relative indices of abundance so a catchability coefficient (q_i) was estimated for young of the year alewife, age 1+ alewife and bloater.

Estimating model parameters

The parameters of the model were estimated using AD Model Builder software (Otter Research 2000). Using automatic differentiation, AD Model Builder fits statistical nonlinear models with user specified likelihood equations and performs Markov Chain Monte Carlo (MCMC) sampling using a Metropolis-Hastings algorithm to sample from the joint posterior distribution of the specified parameters. All parameters were estimated on the log scale and diffuse, flat, bounded priors (on the log scale) were utilized so the resulting posterior distributions would be driven by the data used in model fitting. The log likelihood for our model consisted of eight likelihood components: one for each of the seven data sources and one penalty function to prevent the model from converging on impossible solutions (Table 5).

$$\ell = \frac{N_{tot}}{2} Log(\sum_{i=1}^{6} \ell_i) + \ell_7 + \ell_8 \qquad (1)$$

The first six components ($\ell_1 - \ell_6$) were all assumed to follow normal or log-normal distributions and were incorporated into the log likelihood by a concentrated

likelihood. This allowed us to easily specify weighting factors (λ^i) for each component,
while the overall scale of the variances was set to be consistent with model fit. The
bottom trawl survey indices and the hydroacoustic indices were weighted by the inverse
of the observed variances of each index ($\tau_{j,y}^{aw}$, $\tau_{a,y}^{bl}$, υ_y^{bl} , $\upsilon_{j,y}^{aw}$; Table 5). Since no
uncertainty estimates were available for the consumption data provided by predator
assessments, the weighting factor for these components (λ^C and λ^{CP}) were fixed at one,
which gives these data sources approximately equal weight as both the survey data
sources. The final data source, the proportion of total consumption from small and large
alewife and other fish was assumed to follow a Dirchlet distribution (Table 5; Williams
and Quinn 1998). The effective sample size of a Dirchlet distribution is equal to $\gamma - 1$
and we modified McAllister and Ianelli's (1997) iterative method to find the appropriate
effective sample size (38.54). The final likelihood component was a penalty function to
prevent the estimated recruitments of alewife and bloater in 1998 and 1999 to be
extremely different from the average recruitment between 1994-1997. This penalty
function was necessary early in model fitting to prevent the model from becoming
trapped in implausible areas of the parameter space and was not included during the final
phase of model fitting, so it had no impact on final parameter estimates.

A stock-recruitment function for both alewife and bloater was fit externally to the
estimation model using the estimated series of abundances at age. The stock-recruitment
function for both species was fit to the linearized version of a Ricker function and the
parameters of α_S , β_S , and $\sigma_{S,r}^2$ were estimated for both species (Quinn and Deriso
1999). For alewife, stock size was indexed by the abundance of age 2+ alewife and for
bloater, because size-at-age changed over time, stock size was calculated using the

equation reported by TeWinkel et al. (2002) which relates the weight of mature females to the number of eggs produced.

Posterior distributions of the estimated parameters, those from the population model and the stock-recruitment functions, were generated using a two-step MCMC procedure as in Haeseker et al. (in press). First, the Metropolis-Hastings algorithm within AD Model Builder was used to sample the parameters estimated directly in the population model along with the stock size of alewife and bloater in each year. The MCMC chain was run for 3 million samples saving every 300th sample with the step sized scaled to produce moderate acceptance rates (0.25-0.5) for a total saved sample size of 10,000.

The second step was used to add the stock-recruitment parameters to this MCMC sample. We appended a single sample from an approximate posterior distribution for the stock-recruitment parameters to each of the 10,000 saved MCMC samples, given the time series of stock sizes and recruitments associated with each sample. First, maximum likelihood estimates of α_S, β_S and $\sigma^2_{s,r}$ were obtained from each MCMC sample by linear regression as described above. Then, we drew samples of α_S and β_S for each species by drawing one sample (for each species) from a multivariate normal distribution with a mean and covariance matrix set at the maximum likelihood estimates for a given stock-recruitment time series (i.e., one of the 10,000 samples). We also generated a single sample for each of the 10,000 saved MCMC samples from the posterior of $\sigma^2_{s,r}$ for each species by drawing a sample from an inverted scaled χ^2 distribution with degrees of freedom of 34 (number of observations minus 2) and the scale parameter equal to the maximum likelihood estimate of $\sigma^2_{s,r}$ (see Gelman et al. 1995, pg. 480 for details).

Samples taken during the burn-in period (1000 of the saved steps in the MCMC

chain) were discarded. MCMC chain convergence was checked with three methods.

First, trace plots of each estimated parameter were constructed to ensure the chain was

well-mixed and not exhibiting any substantial "stickiness"over long portions of the chain.

Second, the chain was divided into thirds and the mean of each third was calculated and

the distributions plotted. Substantial differences in the means or distributions would

indicate that the chain has not converged upon the posterior distribution. Finally, the

effective number of samples for each parameter was calculated following the procedure

described by Theibaux and Zwiers (1984).

Results

To assess overall model fit to the observed data, we compared the predicted values based on parameters that maximize the posterior likelihood. Predictions of fall bottom trawl survey abundance indices generally matched the observed values well (Figures 1, 2). For adult alewife (age 3+), the predicted trawl indices did not decline as rapidly as the observed trawl indices during the 1970s and then increased more rapidly during the 1990s (Figure 1). The predicted relative size of the 1967 year class was much larger than observed values and the predicted relative year class sizes were generally lower than those observed for late 1970s (Figure 1). For age 0 bloater, the predicted trawl indices were higher than the observed trawl indices during the early 1960s and the predicted indices for age 1 bloater did not reach as high a peak as the observed indices in the late 1980s (Figure 2a). The predicted trawl indices for age 2+ bloater generally matched the trends in the observed indices well (Figures 2b, c). However, the predicted indices for age 7+ bloater did not decline as rapidly as the observed indices in the 1970s (Figure 2c).

Fit to the trends in the hydroacoustic survey indices was in general not as good as to the trawl indices (Figures 3, 4). While the trends in the age 0 alewife hydroacoustic index were reflected in the predicted values, the predicted values of the age 1+ hydroacoustic index did not reflect the increased abundance observed in the hydroacoustic survey in 1995 and 1996 (Figure 3). For bloater, the predicted hydroacoustic survey indices suggested a more gradual decline in the abundance of bloater than that observed (Figure 4).

Predictions of total consumption by all salmonine predators matched well with the time series of observed values (Figure 5). However, the model slightly overestimates

consumption during the final three years (1997-1999, Figure 5). The model had more

difficulty matching the proportion of total consumption by prey type (Figure 6). The

predicted proportion of large alewife was larger than the observed proportion in both the

early 1980s and the 1990s but the proportion decreased more dramatically and to a lower

level than observed during the mid 1980s (Figure 6). The predicted proportion of small

alewife generally remained more constant than the observed proportion of small alewife

(Figure 6). The model was able to capture the dynamic changes in chinook salmon

consumption per predator at age over time for ages 1 through 3 (Figure 7a). There were

some difficulties in predicting consumption per predator for age 2 chinook, with the

model consistently overestimating consumption for the entire time series (Figure 7a).

Additionally, the predicted consumption per predator for age 1 chinook salmon was

consistently higher than the observed values from mid 1980s on. The predicted

consumption per predator for age 3 chinook salmon was consistently lower than the

observed values from the 1960s through 1980 and the predicted consumption per

predator for age 3 did not reach the high level observed in some years in the mid 1990s

(Figure 7a).

Estimates of the instantaneous predation rates by age on alewife and bloater, at

the parameter values that maximize the posterior likelihood, allow us to summarize the

effects predation has had on the dynamics of these two populations. In general, alewife

have sustained much larger predations rates than bloater throughout the time series

(Figures 8, 9). Predation rates on adults (age 1+) of both species peaked in the mid 1980s

concurrent with the peak in predator abundance in Lake Michigan (Figures 8, 9).

Additionally, predation rates on adults (age 1+) in the late 1990s are similar to or larger

than those observed during the peak predator abundance in the mid 1980s (Figures 8, 9).

Peak predation rates on age 0 alewife and bloater occurred during the late 1970s. For alewife, instantaneous predation rates have been greater then two times background natural mortality rates since the 1980s (Figure 8). Instantaneous predation rates on bloater, even in the mid 1980s, have never been larger then one half the background natural mortality rates (Figure 9).

Uncertainty in the key model parameters was quantified using Bayesian techniques to estimate the posterior distributions for each parameter and we summarized these distributions using 95% credibility intervals (Table 6). In general, the effective sample sizes from the MCMC chain were several thousands with smaller effective sample sizes from the posterior distributions of the stock-recruitment parameters for alewife (Table 6). The trace plots for each parameter generally showed no long range (> 120,000 chain steps) autocorrelation, suggesting that the chain was sampling the entire range of the posterior, and the beginning, middle and end thirds of the chains had similar means and distributions of the sampled parameters, suggesting that the chain had converged upon the posterior distribution. There was covariance among parameters in the posterior distribution, and this is summarized by the correlation matrix among the different parameters in the MCMC sample (Table 7). In general, the correlations were very low, with the exception of high correlation observed between the parameters of the stock-recruitment function for each species and a high correlation between the survival of age 1+ alewife during the 1967 dieoff and the stock-recruitment parameters for alewife.

The estimated posterior distributions for the catchability of bloater and alewife in the hydroacoustic survey suggest that the survey measures a much higher proportion of the true abundance of age 0 alewife and bloater than it does for age 1+ alewife (Figures 10, 11). The uncertainty in the catchability of age 1+ alewife, with a coefficient of

variation (CV) of 39.1%, is higher than that for the catchability of age 0 alewife, with a CV of 18.3%, and bloater, with a CV of 26.0%. The effect of the shift to an early start for the fall bottom trawl survey appears to be large, with the posterior of the catchability for trawl survey being skewed strongly towards zero and very little density above a value of 0.1 (Figure 10c). However, the uncertainty in this parameter is large with a CV of 106.5%.

The estimated posterior distribution of the length-based scalar (γ) for the effective searching efficiency on an optimal sized prey of chinook salmon suggests the parameter is fairly well-determined with a CV of 17.2%. The posterior distribution for this parameter is relatively symmetric suggesting there is an approximately equal chance of the value of the parameter being either above or below the maximum posterior estimate (Figure 12). To assess the degree of food limitation in the chinook salmon population over time, we calculated the proportion of $C_{max,chs}$ consumed each year by an age 3 chinook salmon based on the parameters that maximized the posterior likelihood along with 95% credibility intervals (Figure 7b). During the early 1970s age 3 chinook were consuming at annual rates close to their maximum. However, as the abundance of alewife declined in the late 1970s and early 1980s, the proportion of $C_{max,chs}$ consumed declined quickly to a low of 0.31 in 1986. After a slight recovery in the late 1980s, the proportion of $C_{max,chs}$ consumed has remained relatively constant at approximately 0.5 of $C_{max,chs}$.

The estimated posterior distributions for the stock-recruitment parameters for alewife in Lake Michigan suggests there is considerable uncertainty remaining in these parameters, particularly in the degree of compensation (Figure 13). For alewife, the CV of $\ln(\alpha_{aw})$ is relatively low at 23.9% while the CV's of $\sigma^2_{aw,r}$ (41.9%) and β_{aw}

(65.4%) are larger. There are also differences in the shape of the posterior distributions for these parameters. While the posterior distribution for $\ln(\alpha_{aw})$ is relatively symmetric about the maximum posterior estimate, the posterior distribution of β_{aw} is skewed highly towards low values, indicating a significant probability of relatively weak compensation at high stock sizes (Figures 13a, b). The posterior distribution of the parameters describing variability in recruitment about the stock recruitment relationship($\sigma^2_{aw,r}$) is also skewed, with a long tail extending towards high levels of recruitment variability (Figure 13c). The maximum posterior estimates of the stock-recruitment relationship for alewife reveals a moderate amount of recruitment variability unexplained by stock size (Figure 15a).

The estimated posterior distributions for the parameters of the bloater stock-recruitment parameters are all relatively symmetric with only the posterior of $\sigma^2_{bl,r}$ having an extended tail towards large values (Figure 14). The level of uncertainty in the parameters of the bloater stock-recruitment is generally higher than that for the parameters of the alewife stock-recruitment. In particular, both the parameters describing the productivity at low stock size ($\ln(\alpha_{bl})$) and the degree of compensation (β_{bl}) have CVs larger than 100% (158.7% and 107.5%, respectively). The estimates of the parameter describing amount of variability about the stock-recruitment relationship ($\sigma^2_{bl,r}$) have much lower uncertainty with a CV of 27.8%. The maximum posterior estimates of the stock-recruitment relationship for bloater shows a high level of recruitment variability and a low degree of compensation at high stock sizes (Figure 15b).

The estimated posterior of the survival of age 1+ alewife from the 1967 dieoff confirms that the alewife population most likely suffered a large dieoff (Figure 16).

However, the degree of uncertainty in this parameter is high with a CV of 84.5%.

Therefore, the estimated posterior distribution suggests that there is also a positive

probability that the alewife population might have only suffered a mild dieoff in 1967

(Figure 16).

Discussion

We were able to achieve our goal of reconstructing alewife and bloater dynamics in Lake Michigan from current prey fish survey data and predator assessment models by modeling the predation process using a dynamic multispecies functional response that allowed the instantaneous predation mortality rates to respond to changes in both predator and prey abundance. Through this modeling process we discovered that there are many gaps in our knowledge regarding how the predation process occurs and that the assumptions made in the face of this lack of knowledge can have important consequences on the reconstruction process. Clearly, reconstructing the population dynamics of a fish species that is strongly influenced by interactions with other species requires a suite of information not commonly available for most species (Kitchell et al. 1999; Hollowed et al. 2000; Cox et al. 2002; Link 2002). The availability of a long-term monitoring program for the prey fish in Lake Michigan and up-to-date assessments of the main predator species were invaluable in this process. As fisheries management continues to focus on ecosystem and food web management, the need for these types of assessments will increase (Link 2002).

The ability to predict how changes in abundances of predator and prey populations will effect the consumption rates of the prey population remains an area of active investigation in fisheries research (Eby et al. 1995; Hollowed et al. 2000; Cox et al. 2002; Essington et al. 2002). Maintaining a balance between predatory demand and prey production to support satisfactory growth rates of predators and preserve diverse prey populations relies on our ability to make these predictions (Jones et al. 1993; Spencer and Collie 1997; Heikinheimo 2001; Cox et al. 2002; Essington et al. 2002). However, attempts at estimating parameters governing the functional response of a fish

predator from large-scale observational data rather than small-scale experimentation have been limited and the uncertainty associated with the estimated parameters has not been quantified (Eby et al. 1995; Cox et al. 2002). In our approach, the utilization of both current predator stock assessments and existing prey fish assessments allows us to estimate some of the parameters governing the predation process and quantify our uncertainty in these parameters.

The Lake Michigan ecosystem provides an interesting opportunity to investigate how predation structures a pelagic prey fish species. Prior to 1965, the invasive alewife existed in a system essentially lacking large piscivores. With the introduction of substantial numbers of five salmonine species through stocking, predation pressure rose rapidly, causing declines in the overall abundance of alewife in the system (Figures 1, 8). These declines in alewife abundance led to consequent declines in the consumption rates of chinook salmon (Figure 7b). This apparent food limitation of chinook salmon coincided with collapse of the chinook salmon population in the late 1980s (Holey et al. 1998). Our current estimates of predation pressure show that levels in the late 1990s are rapidly approaching the levels seen during the period preceding the chinook salmon collapse (Figure 8). If, as suggested by Holey et al. (1998), the collapse of the chinook salmon population was, in part, caused by food limitation, then the system may again be approaching conditions where such a collapse is a serious risk.

Both adult alewife and bloater sustained peak levels of predation during the late 1980s, while age 0 alewife and bloater predation rates peaked in the 1970s. The difference in the timing of the peak predation pressure between age 0 alewife and older alewife results primarily from two different sources. First, the predation rates on age 0 alewife rise more rapidly in the late 1960s and early 1970s because the predator

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population is dominated by younger fish, which preferentially prey upon the age 0 alewife because of their smaller size. Secondly, while age 1+ alewife abundance declined steadily from the late 1970s through the mid 1990s, the abundance of age 0 alewife increased from the 1970s through the 1990s causing a decreasing per capita predation rate despite the growing abundance of salmonine predators. Similarly, the abundance of age 0 bloater declined throughout the 1970s causing increasing per capita predation rates during this time. However, in the mid 1980s during the period of increased salmonine abundance, the recruitment of bloater to age 0 increased substantially to cause a decreasing per capita predation rate.

The full implications of our uncertainty about prey fish dynamics in Lake Michigan on the consequences of different stocking policies for salmonid predators remains to be seen. Although the expected recruitment of alewife at low stock sizes is well estimated, large variations in alewife recruitment that are not explained by the stock-recruitment relationship suggest that this process variation may play an important but unpredictable role in the future dynamics of alewife population (Figure 13). Thus, it may not be possible to maintain the alewife population at a relatively constant level by selecting an "optimal" stocking level for predators. Effective stocking policies may need to be responsive to changes in alewife abundance. A formal evaluation of the consequences of our uncertainty regarding prey fish dynamics in Lake Michigan on stocking policy decisions, using techniques such as decision analysis (Raiffa 1968), will be necessary to answer these questions.

The use of functional response in ecological modeling has recently drawn criticism from Walters (2000) because of the lack of fish captured with full stomachs and low proportions of maximum consumption estimated by bioenergetics modeling . This

suggests that the phenomenon of satiation and the tradeoff between time spent handling prey and time spent searching for prey may not be applicable to some aquatic ecosystems. Rather, Walters (2000) argues that fish consumption is driven by a predator balancing the need to search for food versus the risk of being consumed during foraging activities, producing rates of consumption that are driven not only by the abundance of food but also by the energy state of the predator and the level of risk. While Walters' (2000) arguments may apply to many aquatic ecosystems, this lack of evidence for satiation does not appear to apply in the Lake Michigan ecosystem. The lack of a predator on large salmonines in Lake Michigan suggests that the influence of predation risk on foraging of Lake Michigan salmonines should be minimal and would only remain through previous evolutionary pressure on salmonine species to avoid high predation risk. Diet studies of Lake Michigan salmonine predators have found predators with full stomachs, indicating that satiation can occur (Elliot 1993). Further, most salmonine diet assessments in Lake Michigan target actively searching salmonines, which are less likely to be satiated, so indices of stomach fullness in Lake Michigan are most likely biased towards unsatiated fish (R. Elliott, USFWS, Green Bay, Wisconsin, personal communication). Bioenergetics models also suggest that some Lake Michigan salmonines (e.g. coho salmon) also consume at rates of 70-80% of the possible maximum consumption (personal observation). Additionally, the consumption rates of chinook salmon are highly correlated with the abundance of their primary prey, alewife. These observations suggests that the use of a saturating functional response model is appropriate for modeling Lake Michigan salmonine predation.

There is, however, significant uncertainty in the form of the functional response that describes process of predation by salmonines in Lake Michigan. Our modeling has

assumed that chinook salmon consumption rates follow a Type II functional response while all other salmonine predators consume at a constant rate. Both of these assumption may be inappropriate. Clearly, for lake trout, brown trout, steelhead, and coho salmon, the use of a completely flat functional response is invalid across all potential prey abundances. However, across the wide range of prey abundances observed in Lake Michigan since the 1960s, lower growth rates for these predators have not been linked to lower prey abundances (Appendix A). Thus, the prey abundance at which the consumption rates of these predators declines remains unknown.

Some lack of fit observed when fitting our model could be explained by a departure from a Type II functional response for chinook salmon. Our predation model underestimates the contribution of alewife to total salmonine consumption during the collapse of the alewife population in the mid to late 1980s and overestimates this contribution during the recovery of the population in the 1990s (Figure 6). This suggests the possibility of an increase of preference (relative search rate) for alewife when they become scarce. This could, for example, result from concentrated feeding in areas where alewife density remains high. The assumptions made in this study were chosen to represent our current understanding of the mechanisms governing predator searching behavior in the system. However, these assumptions have an uncertain basis and the data we used in model fitting were uninformative on this topic. More detailed diet information combined with a quantitative analysis of the abundances of prey types in the lake could provide more information on the foraging behavior of salmonine predators.

Additionally, there is an apparent conflict between the observed alewife trawl survey abundance and the abundance of alewife necessary to produce the patterns in salmonine consumption used in our model. Our model estimates indicate that alewife

abundance declined less rapidly and recovered more quickly than the observed trawl survey data suggests (Figure 1). One potential explanation is that predators, particularly chinook salmon, had lower energy density when alewife abundance was declining, rather then the constant energy density assumed in the bioenergetics models used as a basis for estimating consumption in the predator assessments. If energy density was declining, this assumption would cause us to overestimate consumption that was occurring during this period and consequently overestimate the abundance of alewife in the system needed to support our estimates of consumption. Additionally, if the energy density of chinook remained low despite increasing growth rates during the 1990s, this could also account for our overestimate of the abundance of alewife in the late 1990s. Lipid levels and energetic status of fish have been demonstrated to vary spatially and temporally and these variations are linked to overall fish health (Adams 1999; Madenjian et al. 2002). In Lake Michigan, recent evidence suggests that chinook salmon energy density has changed from year to year and is now low enough to be a potential fish health concern (A. Peters, Michigan State University, East Lansing, Michigan,unpublished data). Thus, historical changes in the energy density of chinook salmon are plausible.

The role that predators play in structuring fish communities has been shown to be important to understanding the ecosystem consequences of fisheries management (Cox et al. 2002, Essington et al. 2002, Link 2002 , Link and Garrison 2002). The modeling approach presented here provides an extension of statistical catch-at-age methodology for exploring predator and prey assessment data simultaneously and provides a methodology for quantifying uncertainty in the resulting parameter estimates. It does however, require large amounts of data from both predator and prey fish assessments. The availability of long term monitoring of both predator and prey populations may be a significant

limitation to the application of this approach to other systems (Link 2002). Additionally, even in systems such as Lake Michigan where these types of data are available, several key uncertainties remain, particularly regarding the dynamic link between predator and prey populations. Clearly, the uncertainties surrounding this dynamic link are not unique to the Lake Michigan ecosystem and our analysis has highlighted several areas of future research to further understanding of predator-prey interactions in pelagic fish communities. Additionally, the consequences of these uncertainties on the management practices to balance predatory demands and prey production remain unknown. However, the Bayesian statistical framework utilized in this modeling effort allows the qualification of some of these uncertainties for future formal analysis of their effects on management decisions.

Table 1. List of variables and parameters used in the estimation model (*a:* age, *y:* year).

$N_{s,a,y}$	Beginning of the year numbers at age of prey species s
$Z_{s,a,y}$	Total instantaneous mortality rate for prey species s (y^{-1})
$M_{s,a}$	Background instantaneous natural mortality rate for prey species s (y^{-1})
$P_{s,a,y}$	Instantaneous total predation mortality rate for prey species s (y^{-1})
S_{67}	Instantaneous mortality rate associated with the 1967 dieoff (y^{-1})
$C_{\max,j}$	Maximum annual consumption rate (kg y^{-1}) per predator by predator type j
$A_{i,j,y}$	Instantaneous consumption rate (in numbers per year) per predator of predator type j on prey type i
$A_{s,a,j,y}$	Instantaneous consumption rate (in numbers per year) per predator of predator type j on prey species s
$w_{i,y}$	Mid-year weight (kg) of prey type i
$p_{oth,j,y}$	Proportion in weight of alternative prey in diet of predator type j
$\alpha_{i,j}$	Instantaneous attack rate (y^{-1}) of predator type j on prey type i
$\tilde{N}_{i,y}$	Approximate mid-year abundance of prey or predator type i
γ	Length-based scalar for a predator's effective search area (cm^2 y^{-1})
$\ell_{i,j}$	Length ratio between prey type i and predator type j
l_j	Mid-year length of predator type j (cm)
$F_{i,j}$	Size preference of predator type j for prey type i
$HO_{i,j}$	Habitat overlap of predator type j and prey type i
ℓ_{opt}	Optimal predator-prey length ratio
ϖ	Parameter controlling the width of the size preference function
$C_{s,a,j,y}$	Predicted consumption (kg) of species s by predator type j
$\hat{C}_y$	Predicted total consumption (kg) of all prey types by all predator types
$C_{tot,j}$	Total consumption (kg) of all prey types by predator type j
$\hat{\theta}_{i,y}$	Predicted proportion of prey category i in $\hat{C}_y$
$\hat{C}^{chs}_{a,y}$	Predicted consumption (kg) per chinook salmon predator
$\hat{T}^s_{k,y}$	Predicted trawl survey index for species s and age category k
$\hat{H}^s_{k,y}$	Predicted hydroacoustic survey index for species s and age category k
$B^s_{k,y}$	Biomass of species s and age category k at time of hydroacoustic survey

Table 2. Model equations describing the alewife and bloater population dynamics.

Population dynamics model

$$N_{s,a+1,y+1} = N_{s,a,y}e^{-Z_{s,a,y}} \tag{T2.1}$$

$$N_{s,l,y+1} = N_{s,l-1,y}e^{-Z_{s,l-1,y}} + N_{s,l,y}e^{-Z_{s,l,y}} \tag{T2.2}$$

$$Z_{s,a,y} = M_{s,a} + P_{s,a,y} \quad y \neq 1967 \cap s \neq aw \tag{T2.3}$$

$$Z_{aw,a,1967} = M_{aw,a} + P_{aw,a,1967} + S_{67} \tag{T2.4}$$

$$P_{s,a,y} = \sum_j \frac{A_{s,a,j,y} * \tilde{N}_{j,y}}{N_{s,a,y}} \tag{T2.5}$$

Predator other than chinook salmon:

$$A_{i,j,y} = \frac{C_{\max,j}}{w_{i,y}} \frac{\alpha_{i,j}\tilde{N}_{i,y}}{\sum_i \alpha_{i,j}\tilde{N}_{i,y}} \tag{T2.6a}$$

Chinook salmon: $A_{i,j,y} = \dfrac{\alpha_{i,j}\tilde{N}_{i,y}}{1+\sum_i \left(\alpha_{i,j}\tilde{N}_{i,y}w_{i,y} \middle/ C_{\max,i} \right)}$ \qquad (T2.6b)

$$\alpha_{i,j} = \gamma * l_j * F_{i,j} * HO_{i,j} \tag{T2.7}$$

$$F_{i,j} = \exp\left((\ell_{i,j} - \ell_{opt})^2 \middle/ spw \right) \tag{T2.8}$$

Table 3. Model equations used in the observation sub-model.

$$C_{s,a,j,y} = \frac{A_{s,a,j,y}}{Z_{s,a,y}} N_{s,a,y} (1 - e^{-Z_{s,a,y}}) * w_{i,y} \qquad \text{(T3.1)}$$

$$C_{tot,j} = \frac{\sum_s \sum_a C_{s,a,j,y}}{p_{oth,j,y}} \qquad \text{(T3.2)}$$

$$\hat{C}_y = \sum_j C_{tot,j} \qquad \text{(T3.3)}$$

$$\hat{C}_{a,y}^{chs} = C_{tot,chs} / \tilde{N}_{chs,a,y} \qquad \text{(T3.4)}$$

$$\hat{T}_{k,y}^s = Log\left(\frac{\sum_a N_{s,a,y} e^{-10/12 Z_{s,a,y}}}{\sum_a N_{s,a,1999} e^{-10/12 Z_{s,a,1999}}} \right) \qquad \text{(T3.5a)}$$

For age 0 alewife, 1962-1990:

$$\hat{T}_{k,y}^s = Log\left(\frac{\sum_a N_{s,a,y} e^{-10/12 Z_{s,a,y}}}{\sum_a q_{tr} N_{s,a,1999} e^{-10/12 Z_{s,a,1999}}} \right) \qquad \text{(T3.5b)}$$

$$H_{k,y}^s = q_k B_{k,y}^s \qquad \text{(T3.6)}$$

Table 4. Values for parameters assumed known during model fitting (LT: lake trout, CHS: chinook salmon, CO: coho salmon, ST: steelhead, and BT: brown trout).

Species	Natural mortality rates per year									
	age 0					age 1+				
Alewife	0.44626					0.22313				
Bloater	0.47237					0.47237				
	Maximum annual consumption rates (kg) by age									
	0	1	2	3	4	5	6	7	8	9
LT	n/a	0.495	1.98	3.59	4.93	5.37	6.17	6.69	6.99	12.78
CHS	2.15	9.30	26.7	55.1	108.7	n/a	n/a	n/a	n/a	n/a
CO	n/a	2.46	5.14	n/a	n/a	n/a	n/a	n/a	n/a	n/a
ST	n/a	1.54	6.39	4.58	7.8	n/a	n/a	n/a	n/a	n/a
BT	n/a	1.44	5.09	4.98	0.02	n/a	n/a	n/a	n/a	n/a

Table 5. Negative log likelihood components utilized during model fitting. CL indicates the likelihood component was incorporated using the concentrated likelihood form.

Component	Equation	Distribution
Alewife trawl survey	$\ell_1 = \sum\limits_{y} \sum\limits_{k=1}^{2} \lambda_{k,y}^{aw}(\hat{T}_{k,y}^{aw} - T_{k,y}^{aw})^2$ $\lambda_{k,y}^{aw} = \dfrac{1}{\tau_{k,y}^{aw}}$	Normal (CL)
Bloater trawl survey	$\ell_2 = \sum\limits_{a,y} \lambda_{a,y}^{bl}(\hat{T}_{a,y}^{bl} - T_{a,y}^{bl})^2$ $\lambda_{a,y}^{bl} = \dfrac{1}{\tau_{a,y}^{bl}}$	Normal (CL)
Alewife hydroacoustic survey	$\ell_3 = \sum\limits_{y} \sum\limits_{k=1}^{2} \lambda_{k,y}^{aw}(\ln(\hat{H}_{k,y}^{aw}) - \ln(H_{k,y}^{aw}))^2$ $\lambda_{k,y}^{aw} = \dfrac{1}{\upsilon_{k,y}^{aw}}$	Lognormal (CL)
Bloater hydroacoustic survey	$\ell_4 = \sum\limits_{y} \lambda_{y}^{bl}(\ln(\hat{H}_{y}^{bl}) - \ln(H_{y}^{bl}))^2$ $\lambda_{y}^{bl} = \dfrac{1}{\upsilon_{y}^{bl}}$	Lognormal (CL)
Total Consumption	$\ell_5 = \sum\limits_{y} \lambda^{C}(\ln(\hat{C}_{y}) - \ln(C_{y}))^2$	Lognormal (CL)
Chinook consumption per predator	$\ell_6 = \sum\limits_{a,y} \lambda^{cp}(\hat{C}_{a,y}^{chs} - C_{a,y}^{chs})^2$	Normal (CL)
Consumption prey type composition	$\ell_7 = -\sum\limits_{y} \left[\ln\Gamma(\gamma) - \sum\limits_{j=1}^{3}\left[\ln\Gamma(\gamma_{j,y}) + (\gamma_{j,y} - 1)\ln\theta_{j,yy}\right] \right]$ $\gamma_{j,y} = \gamma\hat{\theta}_{j,y}$	Dirichlet
Recruitment penalty function	$\ell_8 = \sum\limits_{y} \dfrac{1}{\varsigma}((\hat{R}_{y}^{aw} - \overline{R}^{aw})^2 + (\hat{R}_{y}^{bl} - \overline{R}^{bl})^2)$	Normal

Table 6. Mean, variance, 95% credibility intervals (CI) and effective sample size (N_{eff}) for the posterior distributions of all estimated parameters.

Parameter	Mean	Variance	95% CI	N_{eff}
$\ln(\alpha_{aw})$	2.456	0.34	(1.44, 3.38)	878
β_{aw}	0.306	0.04	(0.66, 0.03)	620
$\sigma^2_{aw,r}$	4.07	2.91	(1.99, 7.33)	1201
$\ln(\alpha_{bl})$	0.315	0.25	(-0.51, 1.12)	8602
β_{bl}	0.186	0.04	(-0.14, 0.54)	5087
$\sigma^2_{bl,r}$	5.39	2.24	(3.42, 8.08)	6560
γ	1.54E-06	7.0E-14	(1.29E-06, 1.8E-06)	2178
q_{ad}	0.140	0.003	(0.07, 0.24)	3005
q_{yoy}	0.771	0.02	(0.51, 0.97)	6111
q_{bl}	0.665	0.03	(0.39, 0.95)	1980
q_{tr}	0.023	0.0006	(0.007, 0.062)	1668
S_{67}	-1.65	1.35	(-3.91, -0.15)	1723

Table 7. Correlations between pairs of parameters in MCMC samples drawn from the posterior distributions.

	$\ln(\alpha_{aw})$	β_{aw}	$\sigma^2_{r,aw}$	$\ln(\alpha_{bl})$	β_{bl}	$\sigma^2_{r,bl}$	γ	S_{67}	q_{ad}	q_{yoy}	q_{bl}	q_{tr}
$\ln(\alpha_{aw})$	1.00											
β_{aw}	0.754	1.00										
$\sigma^2_{r,aw}$	-0.415	-0.381	1.00									
$\ln(\alpha_{bl})$	0.004	0.007	-0.008	1.00								
β_{bl}	0.021	0.015	0.005	0.605	1.00							
$\sigma^2_{r,bl}$	0.005	0.010	0.019	-0.085	0.024	1.00						
γ	0.130	0.087	0.040	-0.009	0.096	0.025	1.00					
S_{67}	0.388	0.515	-0.381	0.006	-0.006	0.011	-0.074	1.00				
q_{ad}	0.058	0.026	0.003	-0.014	0.026	0.006	0.243	-0.039	1.00			
q_{yoy}	0.010	0.012	0.008	0.013	0.009	0.006	0.013	0.003	0.012	1.00		
q_{bl}	0.074	0.048	-0.034	0.002	0.070	0.011	0.117	-0.019	0.086	0.004	1.00	
q_{tr}	0.004	0.007	-0.048	-0.012	0.000	0.001	0.038	-0.006	0.003	-0.010	-0.008	1.00
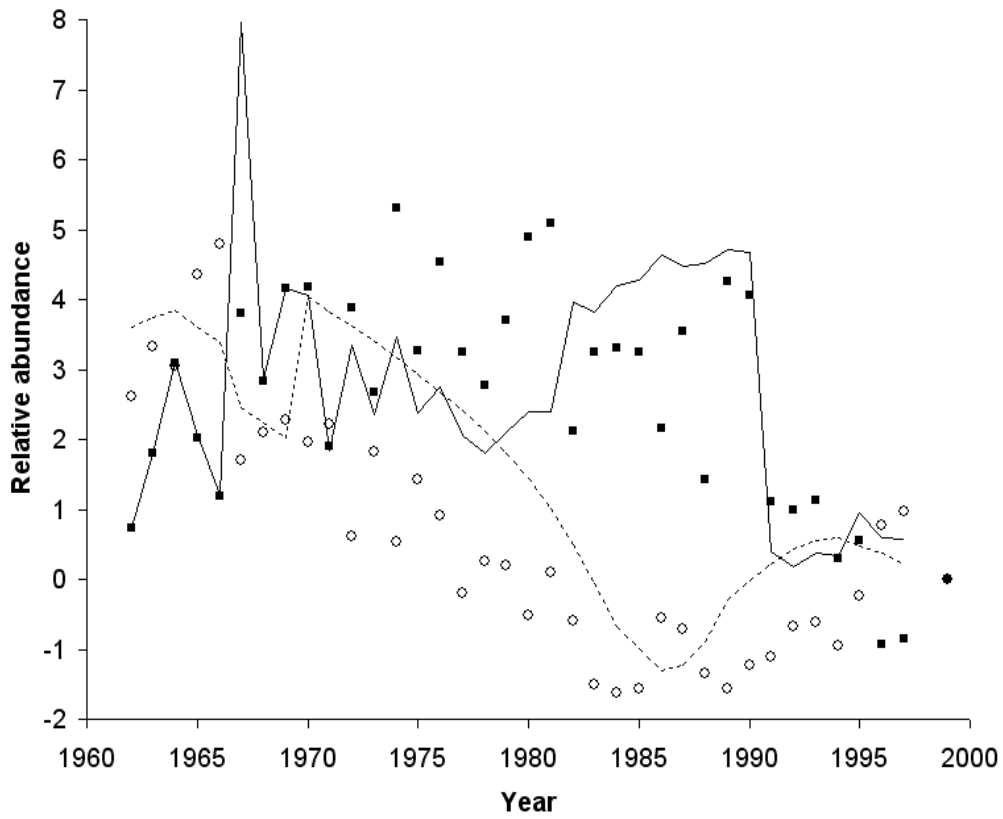
Figure 1. Observed (symbols) and predicted (lines) fall bottom trawl survey indices for age 0 (squares and solid line) and age 3+ (circles and dashed line) alewife in Lake Michigan, 1962-1999.
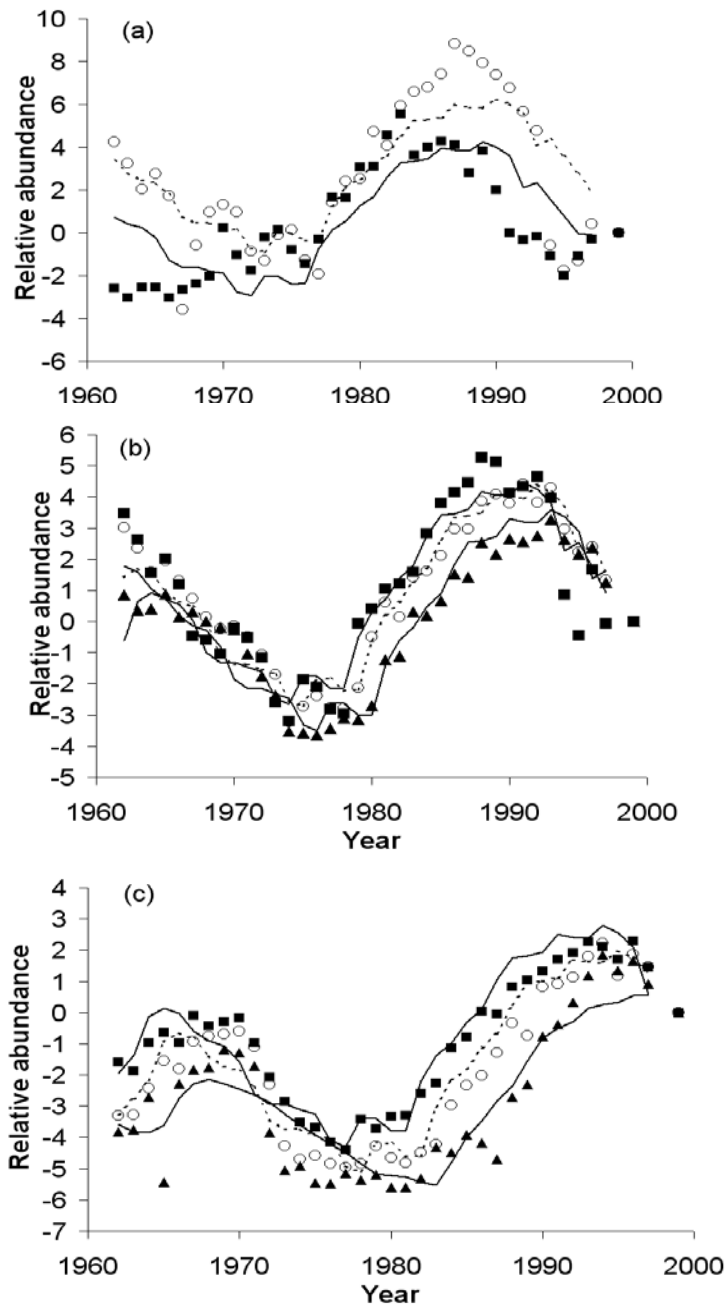
Figure 2. Observed (symbols) and predicted (lines) trawl survey indices for (a) age 0 (squares, solid), age 1 (circles, dashed), (b) age 2 (squares, solid), age 3 (circles, dashed), age 4 (triangles, solid), and (c) age 5 (squares, solid), age 6 (circles, dashed), and age 7 (triangles, solid) bloater in Lake Michigan, 1962-1999.
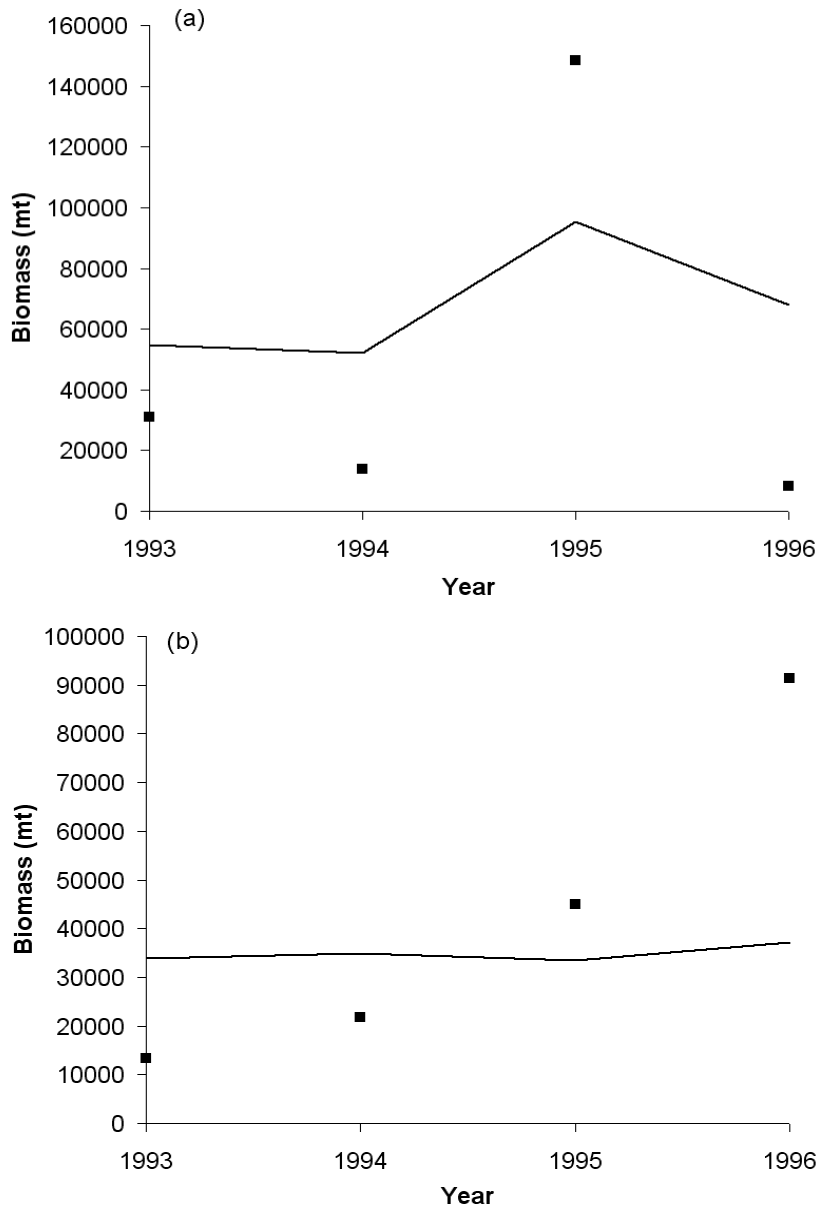
Figure 3. Observed (symbols) and predicted (lines) fall hydroacoustic biomass estimates

of (a) age 0 and (b) age 1+ alewife in Lake Michigan, 1993-1996.
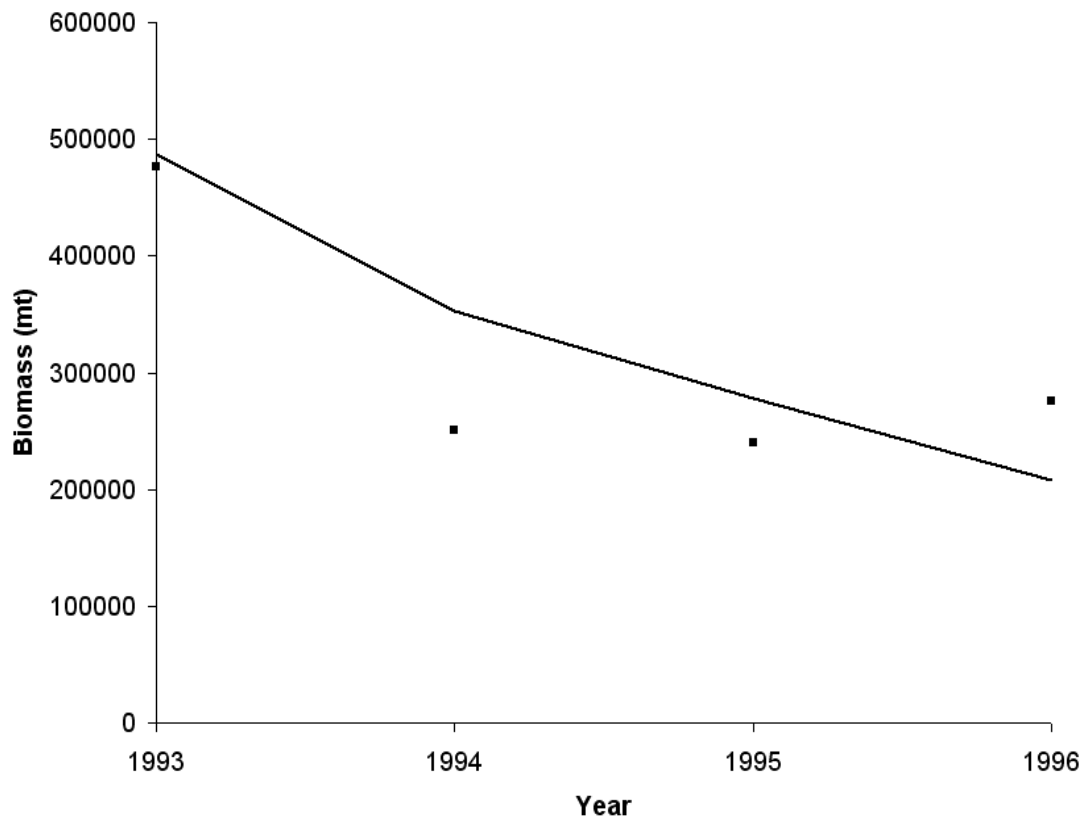
Figure 4. Observed (squares) and predicted (line) hydroacoustic biomass estimates for bloater in Lake Michigan, 1993-1996.
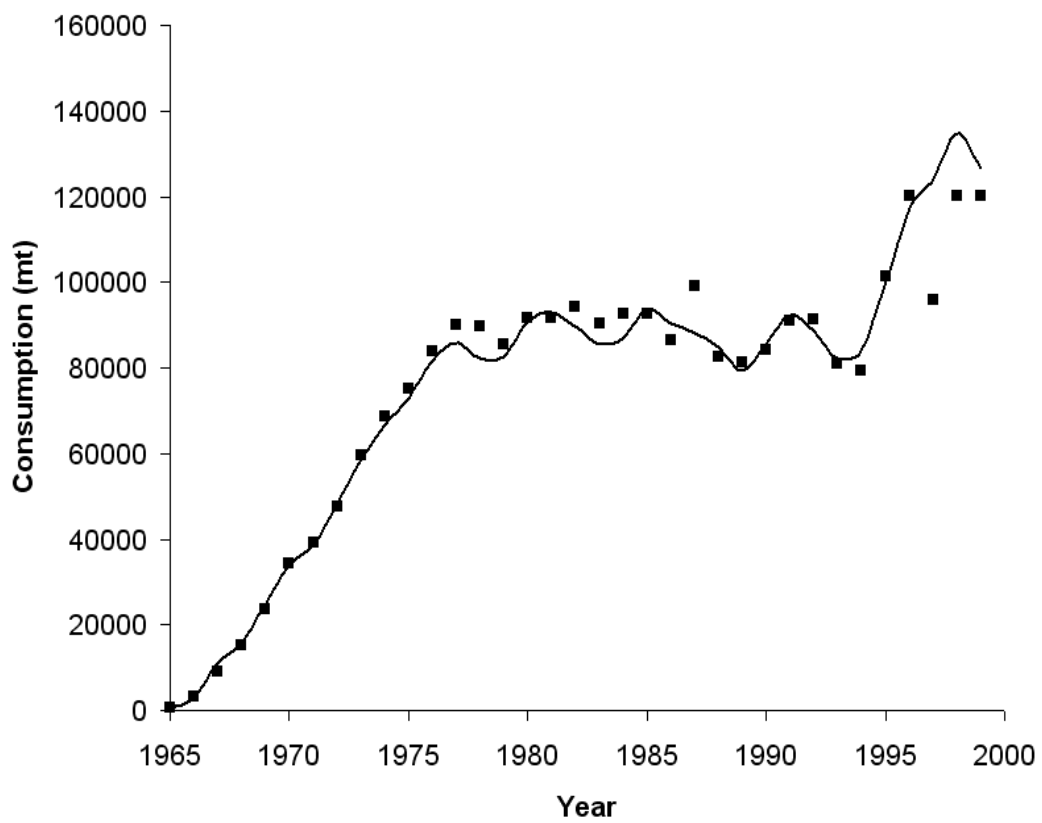
Figure 5. Observed (squares) and predicted (line) consumption of all prey types by all five salmonine species in Lake Michigan, 1965-1999.
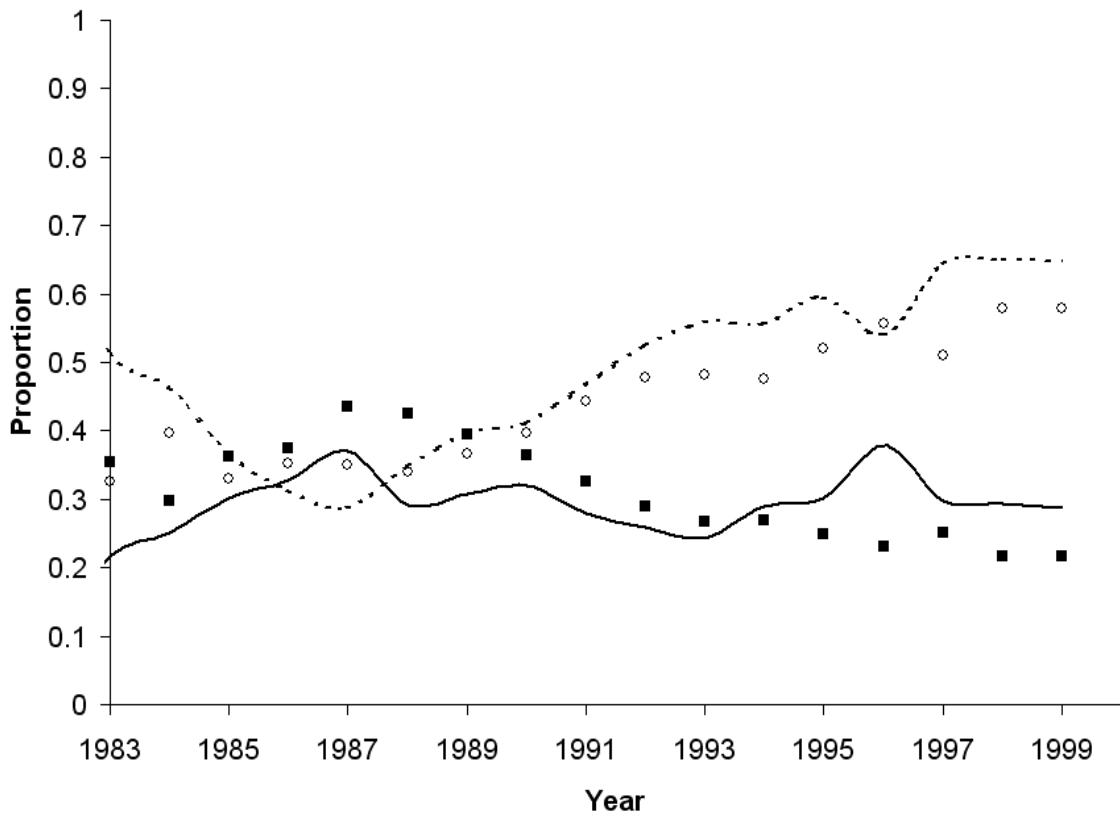
Figure 6. Observed (symbols) and predicted (lines) proportion of small alewife (squares, solid line) and large alewife (circles, dashed line) in the total consumption by all five salmonine species in Lake Michigan, 1965-1999.
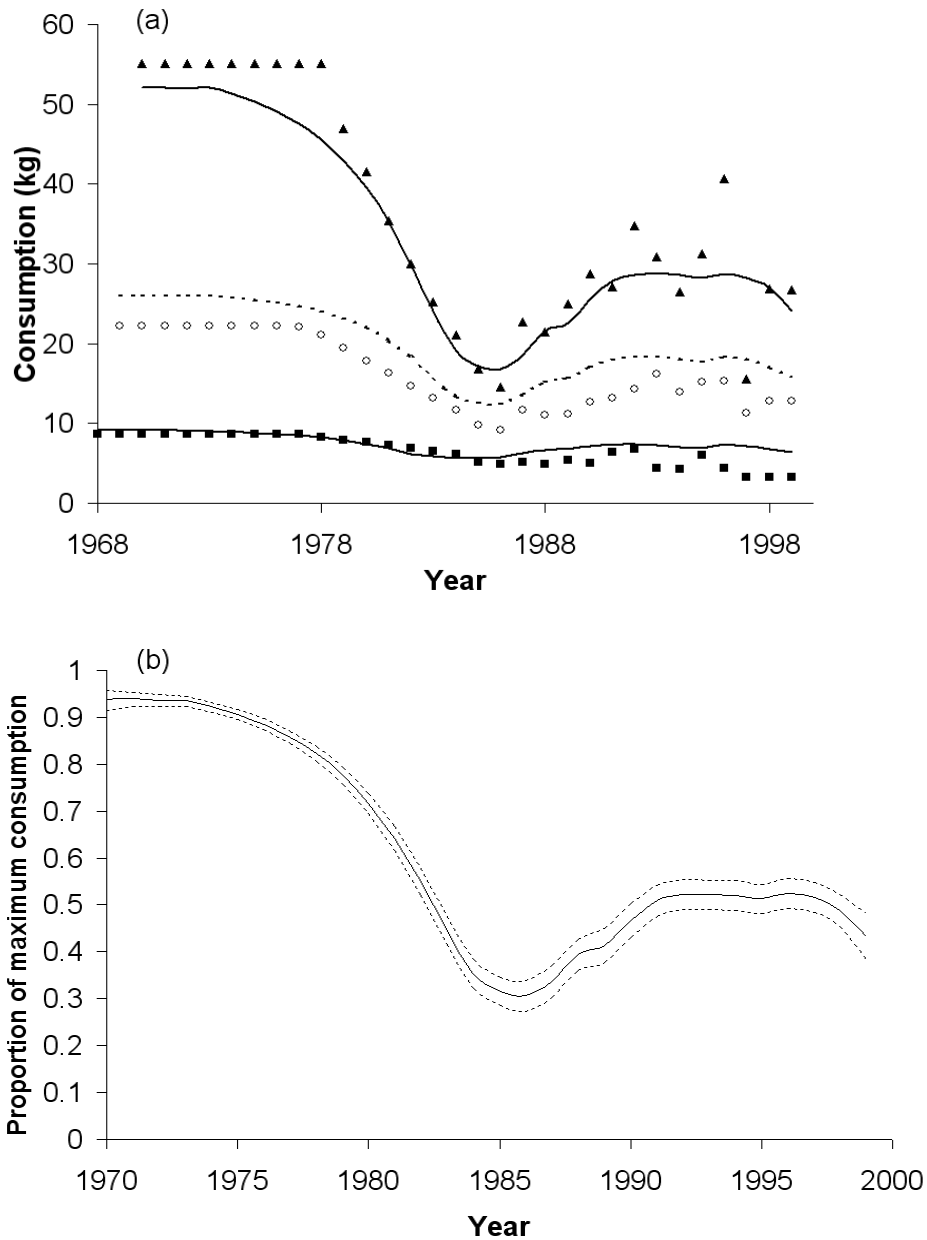
Figure 7. (a)

Observed (symbols) and predicted (lines) consumption per predator for age 1 (squares, solid line), age 2 (circles, dashed line), and age 3 (triangles, solid line), (b) predicted proportion of maximum consumption achieved (solid line) and 95% credibility intervals for age 3 chinook salmon in Lake Michigan, 1968-1999.
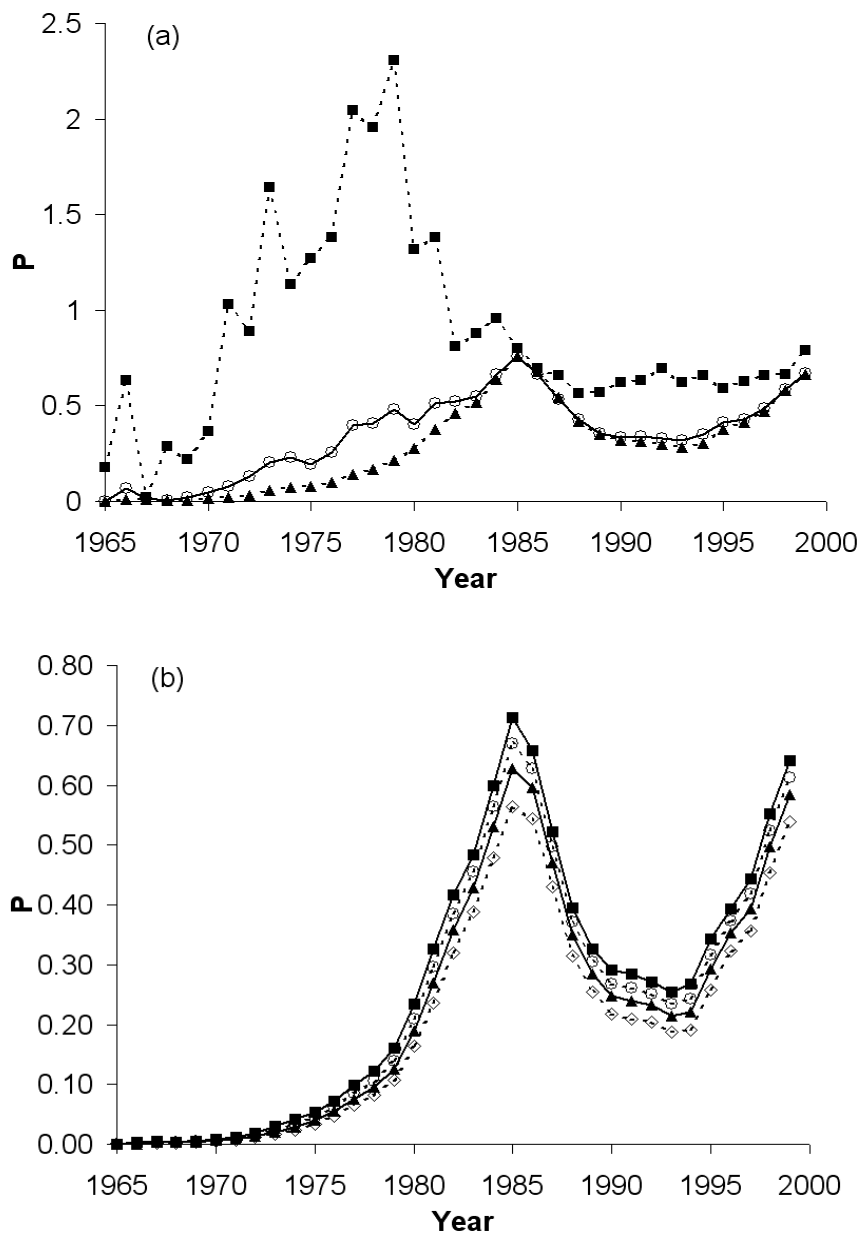
Figure 8.

Predicted instantaneous predation rates (P) on (a) age 0 (squares, dashed line), age 1 (circles, solid line), and age 2 (triangles, dashed line) and (b) age 3 (squares, solid line), age 4 (circles, dashed line), age 5 (triangles, solid line), and age 6+ (diamonds, dashed line) alewife in Lake Michigan, 1965-1999.
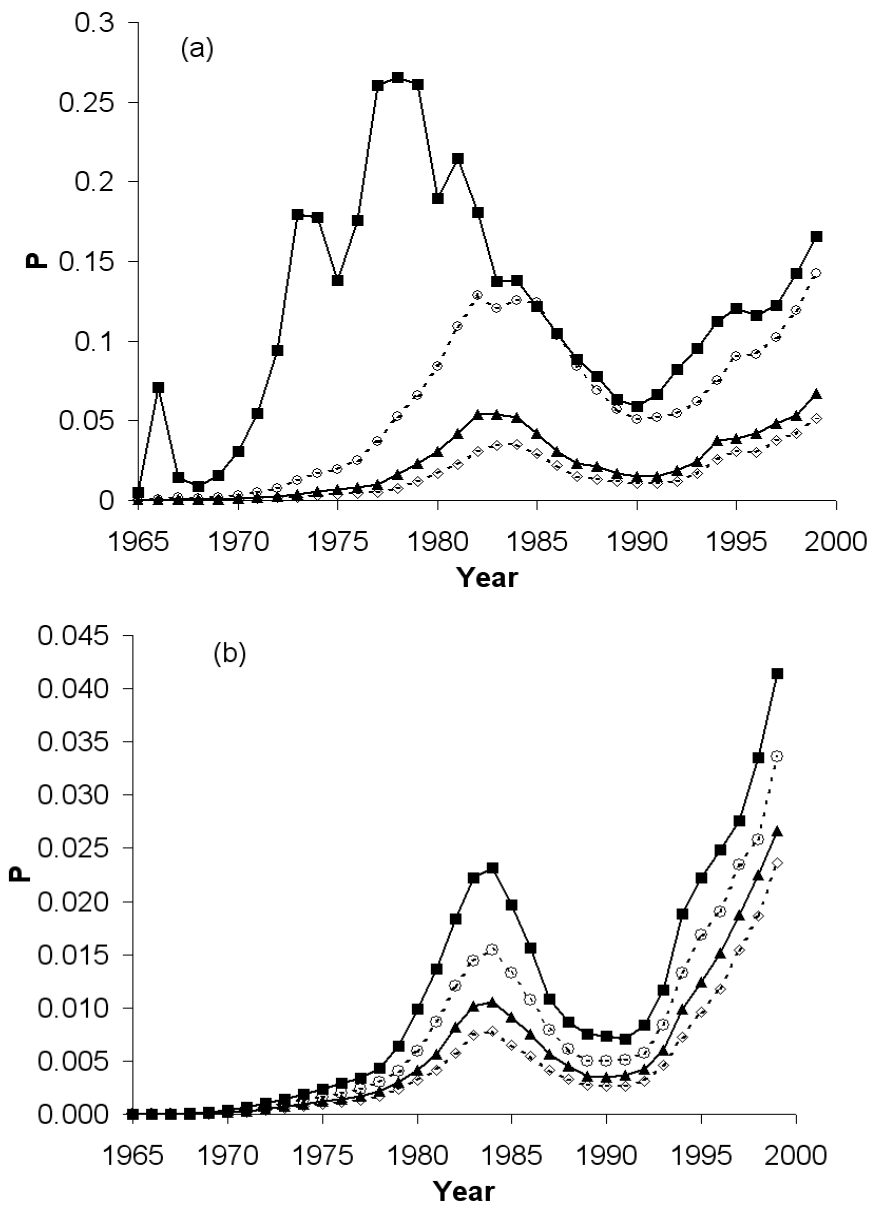
Figure 9. Predicted instantaneous predation rates (P) for (a) age 0 (squares, solid line),

age 1 (circles, dashed line), age 2 (triangles, solid line), and age 3 (diamonds, dashed

line), and (b) age 4 (squares, solid line), age 5 (circles, dashed line), age 6 (triangles,

solid line), and age 7+ (diamonds, dashed line) bloater in Lake Michigan, 1965-1999.
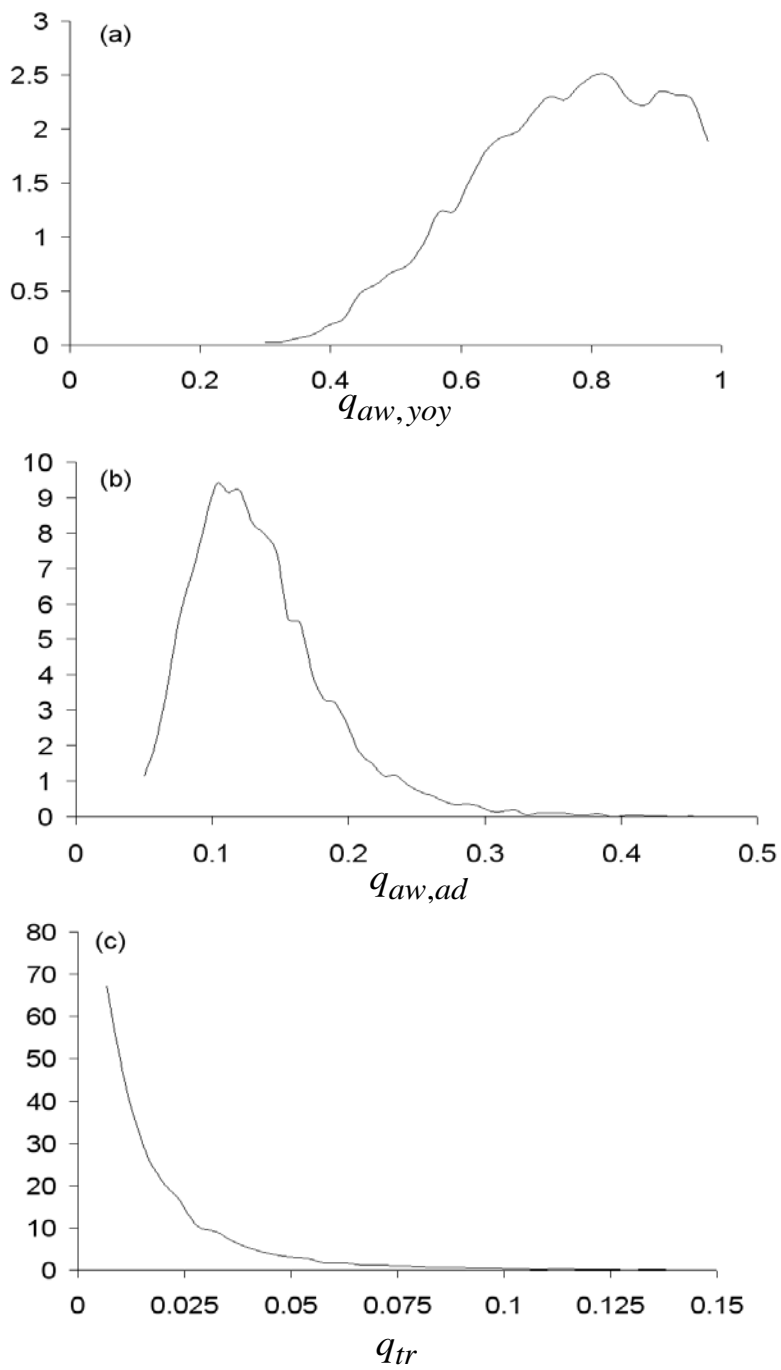
Figure 10. Posterior density functions of the catchability coefficients of (a) age 0 and (b) age 1+ alewife hydroacoustic survey in Lake Michigan, 1993-1996, and (c) age 0 alewife fall trawl survey in Lake Michigan, 1991-1999.
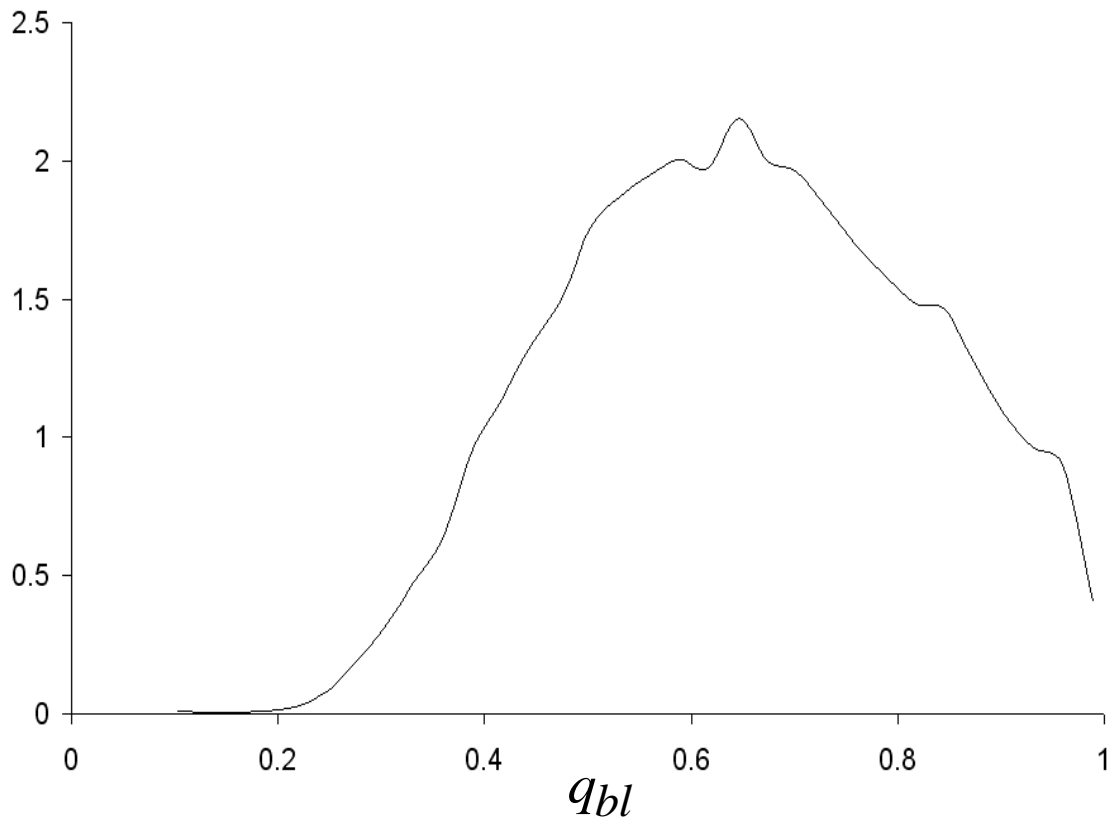
Figure 11. Posterior density function of the catchability coefficients of the bloater hydroacoustic survey in Lake Michigan, 1993-1996.
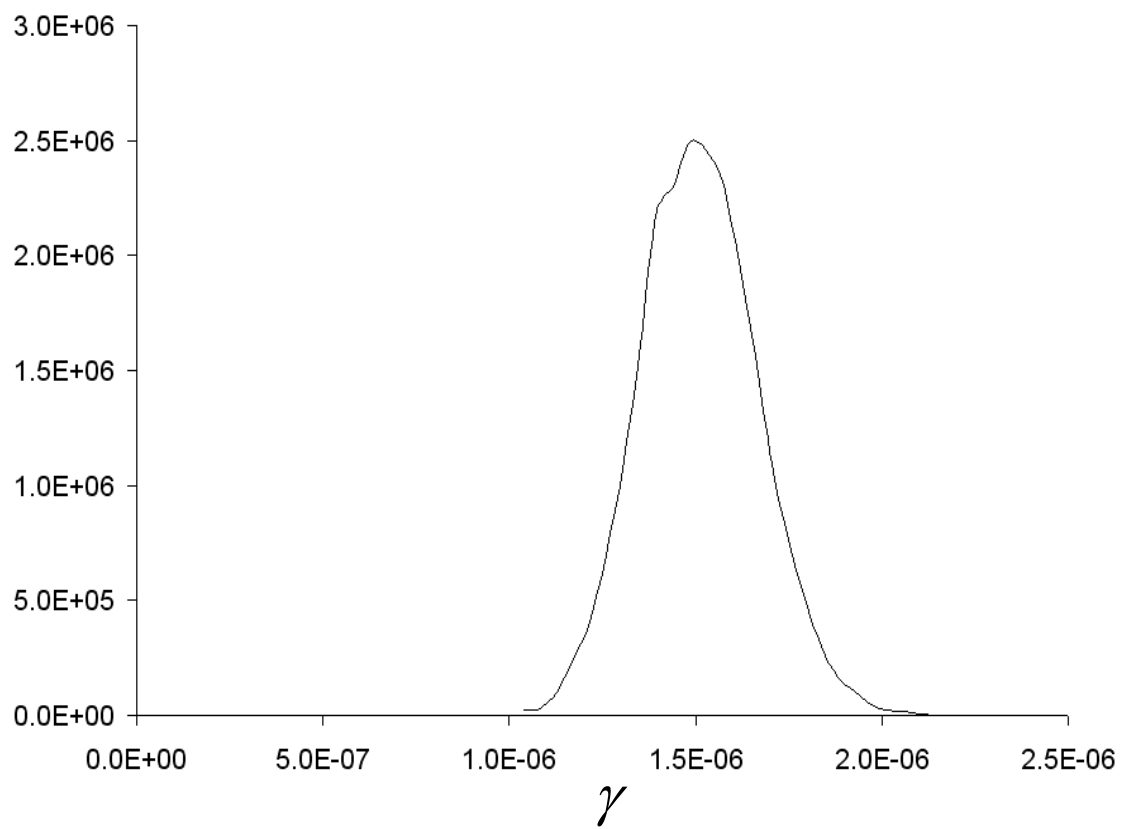
Figure 12. Posterior density function of the length-based scalar of the effective searching

efficiency on an optimal sized prey for salmonine predators in Lake Michigan.
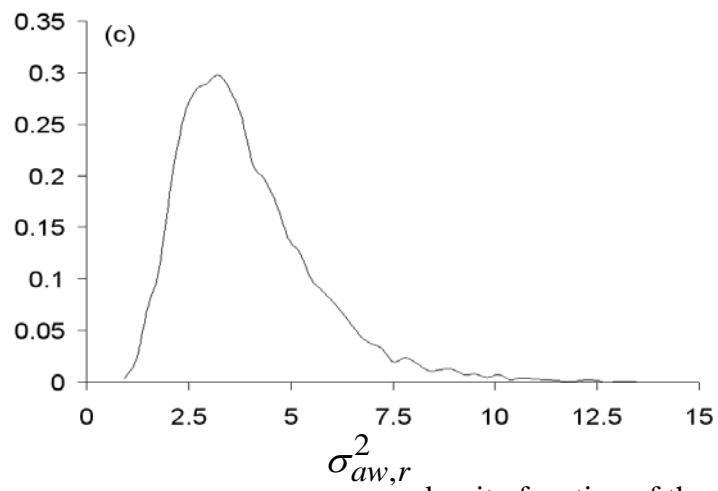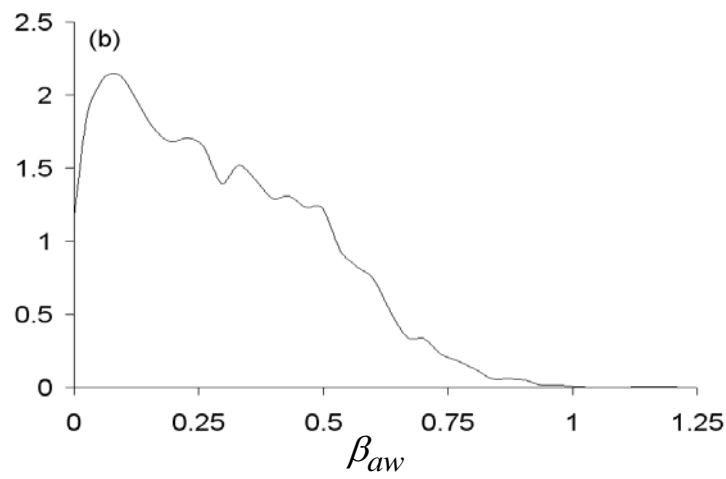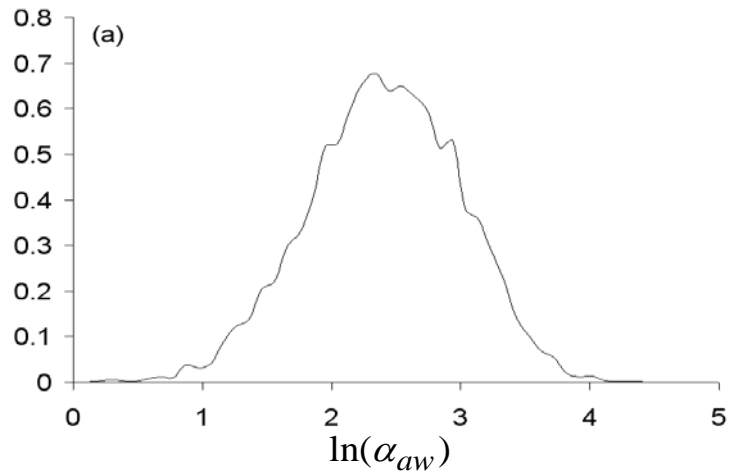
Figure 13. Posterior density function of the (a) $\ln(\alpha_{aw})$, (b) β_{aw}, and (c) $\sigma^2_{aw,r}$ parameter of the Ricker stock-recruitment function for alewife in Lake

Michigan.
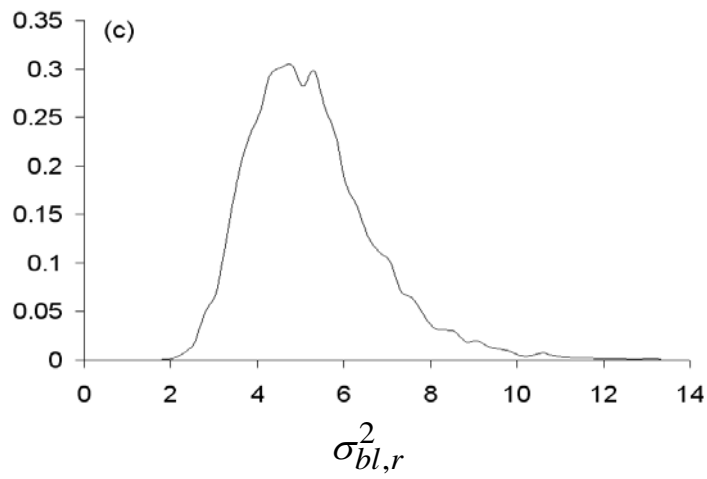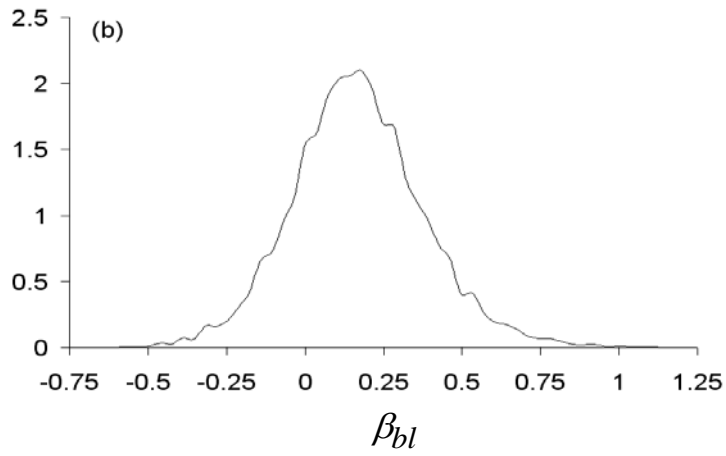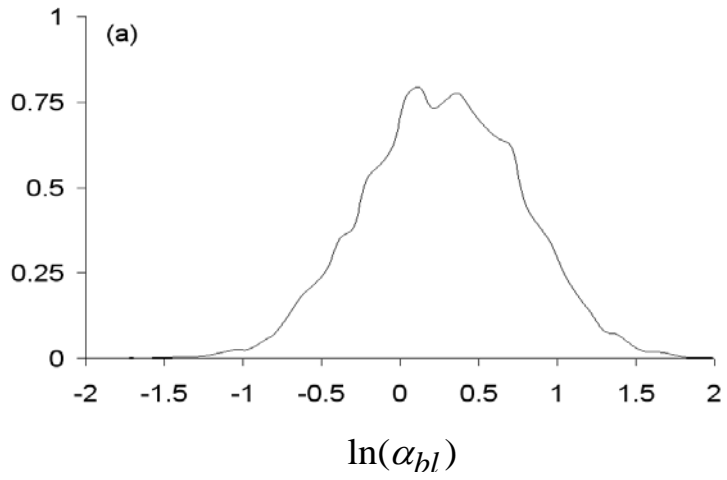
Figure 14. Posterior density functions of the (a) $\ln(\alpha_{bl})$, (b) β_{bl}, and (c) $\sigma_{bl,r}^2$ parameter of the Ricker stock-recruitment function for

bloater in Lake Michigan.
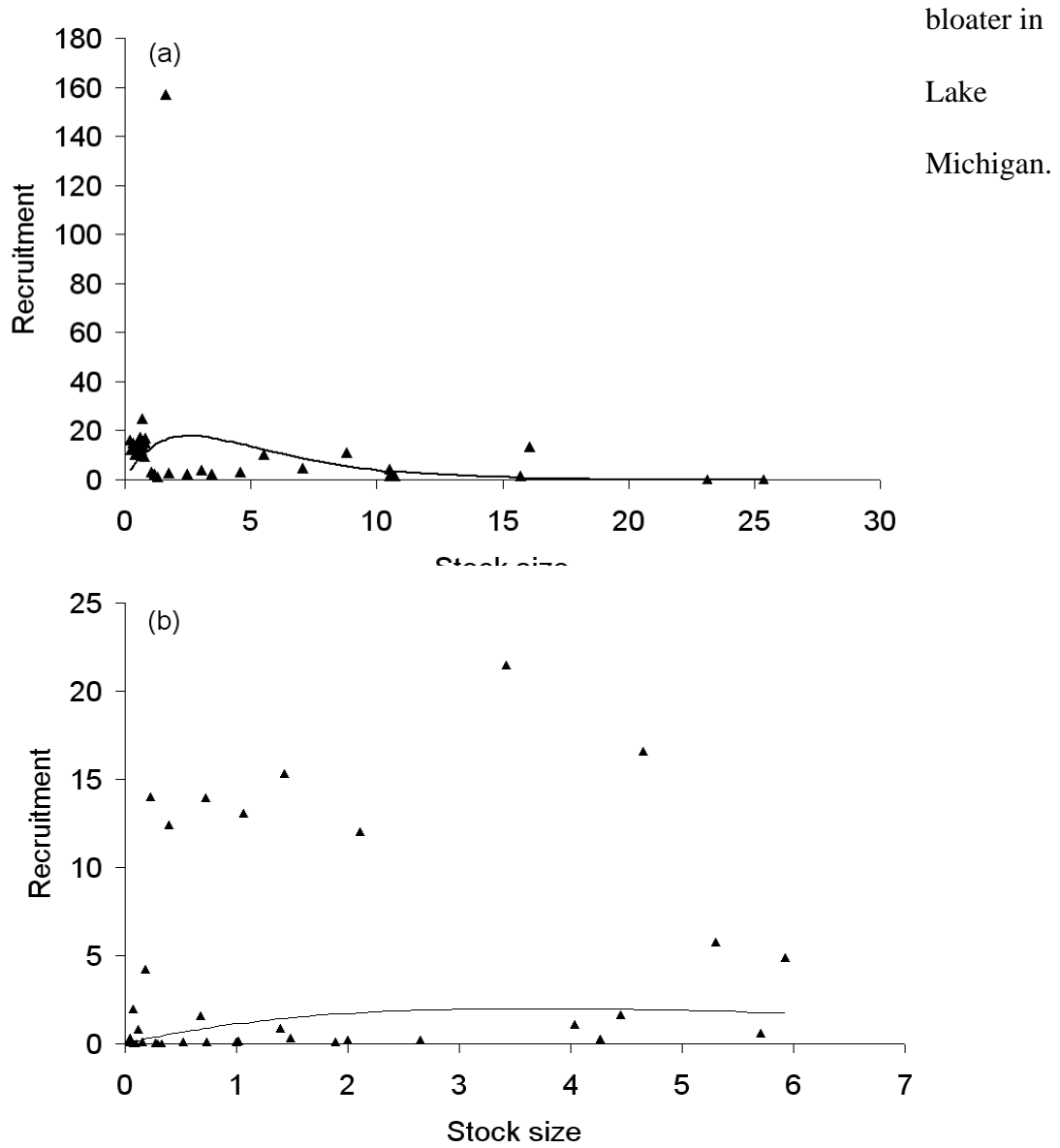
Figure 15. Maximum posterior estimates of the stock-recruitment relationships for (a)

alewife (Stock size is the number of age 2+ fish divided by $1x10^{10}$. Recruitment is the

number of age 0 fish divided by $1\text{x}10^9$), and (b) bloater (Stock size is the number of eggs

divided by $1\text{x}10^{13}$. Recruitment is the number of age 0 fish divided by $1\text{x}10^9$).
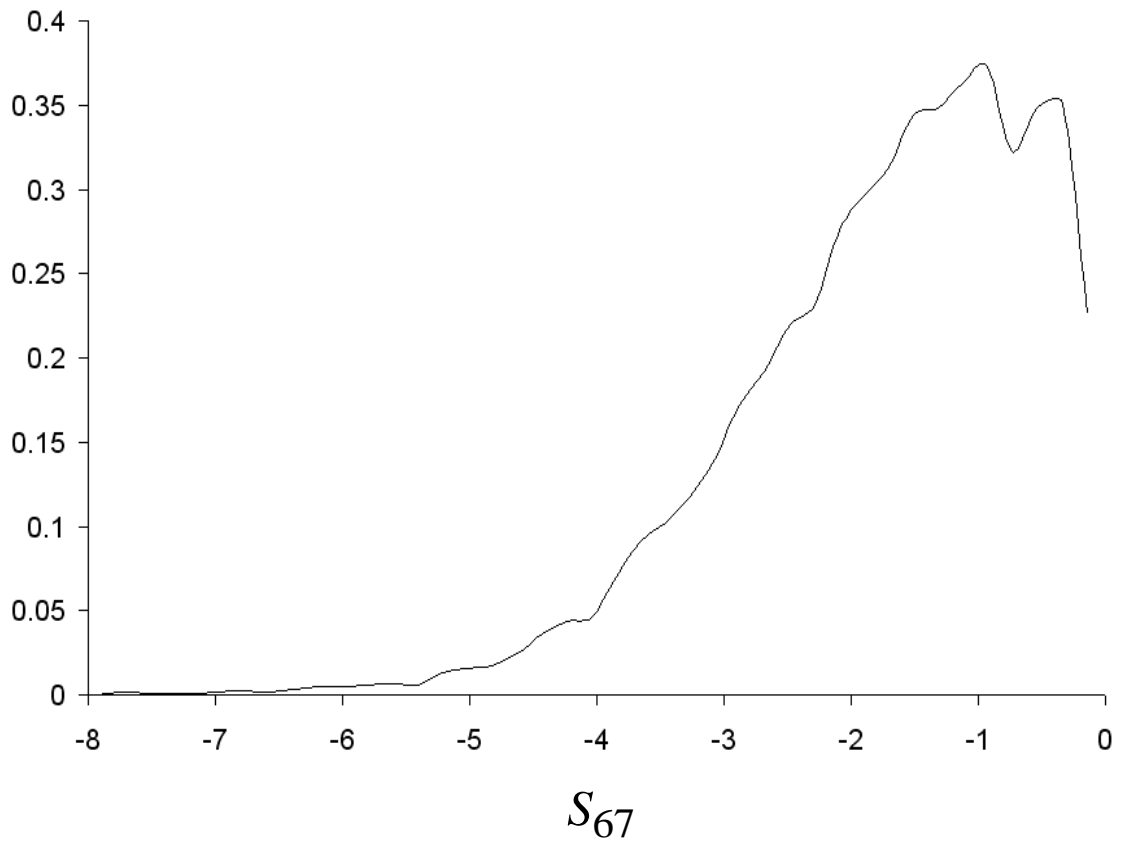
Figure 16. Posterior density function of the instantaneous mortality rate (S_{67}) on age

1+ alewife during the dieoff in 1967 in Lake Michigan.

CHAPTER 3

EVALUATION OF THE EFFECTS OF UNCERTAINTY IN ALEWIFE AND CHINOOK SALMON POPULATION DYNAMICS ON THE OUTCOMES OF STOCKING STRATEGIES IN LAKE MICHIGAN.

Introduction

Acknowledging uncertainty in the outcome of fisheries management requires managers and decision makers to formally and quantitatively incorporate uncertainty in the decision making process (Punt and Hilborn 1997; Varis and Kuikka 1999; Harwood 2000; Peterson and Evans 2003). In natural systems where our level of uncertainty is often quite high, the influence of this uncertainty on the outcomes of our management decisions may be substantial. Ludwig (1996a) and Ludwig (1996b) found that failure to incorporate uncertainty in the prediction of outcomes, by only utilizing point estimates in simulation models, leads to an overestimate of the resiliency of a stock to exploitation. Therefore, in an era where risk assessment and a precautionary approach to fisheries management are being advocated (Francis and Shotton 1997), acknowledging and incorporating uncertainty in fisheries management decisions has become paramount.

Bayesian decision analysis provides a framework to explicitly incorporate uncertainty into our predictions of the outcomes of different management actions and to choose between management actions based on the management objective specified (Raiffa 1968; Punt and Hilborn 1997). Additionally, it provides the tools to evaluate how reductions in different sources of uncertainty will affect the outcomes of management actions and provides a quantitative methodology for ranking the importance of reducing

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uncertainty from different sources (Raiffa 1968). The first step in decision analysis is the identification of the management objectives for the fishery and of potential management actions. Then, areas of key uncertainty are identified and quantified. A simulation model that incorporates these uncertainties is then built and the performance of each management action is assessed (Punt and Hilborn 1997). This simulation model can then also be used to address questions regarding the importance of different sources of uncertainty on the resulting decisions.

The application of decision analysis to fisheries management decisions has increased dramatically in recent times (e.g., Schnute et al. 2000; Peters and Marmorek 2001; Peterson and Evan 2003). However, most of these applications have focused on single-species management decisions and have not incorporated ecological interactions with other species. As the importance of the consideration of ecological interactions in fisheries management decisions increases and as we acknowledge our uncertainty about these interactions (Link 2002), the need for decision analyses for these types of decisions will grow. Here we present an attempt, using the techniques of decision analysis, to inform us of the effects of uncertainty on management outcomes for a predator-prey system, where the abundance of predators is primarily controlled through stocking. Due to the lack of a natural feedback mechanism between the abundance of predator and their prey, it is necessary, through management of stocking levels, to provide a balance between the desire for large predator populations to support a sport fishery and ability of the prey fish production to support the predatory consumption demand.

The history of the Lake Michigan fish community has mirrored the changes seen in the other Great Lakes during the last century with the virtual extirpation of the native piscivores, lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*), and chub species

(*Coregonus* spp.) and the invasion of the exotic planktivores alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*). Alewife, in particular, dominated the fish community in the early 1960s and caused severe economic damage, by littering beaches and clogging city water intake lines with dead fish, and ecological damage, through predation on native fish eggs and larval stages (Brown 1972; Brown et al. 1987). The need to reduce alewife stocks, the desire to establish a successful sport fishery, and the desire to re-establish the native lake trout population led to the stocking of lake trout along with chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), brown trout (*Salmo trutta*) and steelhead (*O. mykiss*) in the late 1960s (Tody and Tanner 1966). The numbers of stocked salmonines quickly increased from 1.3 million fish in 1965 to over 16.5 million fish in 1985 (Benjamin 1998; Bence and Benjamin in press b).

The stocking program in Lake Michigan was successful in establishing an economically important sport fishery and has dramatically reduced alewife abundance lakewide (Bence and Smith 1999; Madenjian et al. 2002; Chapter 2). The stocked salmonines feed primarily on alewife, but also consume the native coregonid bloater (*Coregonus hoyi*), the exotic rainbow smelt and lesser numbers of a variety of other species (Jude et al. 1987). Chinook salmon have dominated consumption in Lake Michigan due to their fast growth rates and large population sizes (Madenjian et al. 2002). Concern over a potential imbalance between the consumption demand by the predators and prey fish production arose after declining growth rates of chinook salmon and large mortality events, thought to be caused by bacterial kidney disease, were observed in the late 1980s (Holey et al. 1998; Stewart and Ibarra 1991).

The need to balance predatory demand with prey production led to a series of

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investigations of both the amount consumed by salmonine predators through bioenergetics modeling (Stewart et al. 1981; Stewart and Ibarra 1991) and the potential production of the alewife population (Eck and Brown 1985; Eck and Wells 1987). Jones et al. (1993) and Koonce and Jones (1994) recognized the need to develop dynamic models where both prey and predator populations responded to changes in stocking policies and developed the SIMPLE models for Lakes Michigan and Ontario. Jones et al. (1993) also noted substantial uncertainty about the ecological interactions between the salmonine predators and their prey fish and called for improved stock assessments to address these uncertainties. With the recent development of a statistical stock assessment of alewife and bloater populations in Lake Michigan (Chapter 2) and improved stock assessments for the salmonine predators, particularly chinook salmon (Appendix A), our ability to construct a dynamic stimulation model that acknowledges uncertainty in our understanding of the Lake Michigan salmonine community and their prey has substantially increased.

Here we present the development of such a model and evaluate its behavior in response to changes in stocking policy. We have explicitly incorporated both parameter and model structure uncertainty in three primary areas: the stock-recruitment relationship of alewife, the functional response of chinook salmon to their prey, and the potential for episodic mortality events in chinook salmon during periods of poor growth. These processes have been identified by Lake Michigan managers, decision makers, scientists and stakeholders as the key uncertainties affecting management decisions for chinook salmon stocking (Jones and Peterman 2000). We also examine the model's sensitivity to assumptions that are uncertain, but for which we lack sufficient data for quantitative analysis. The purpose of this project is not to determine the optimal stocking strategy for

stocking salmonines in Lake Michigan but rather to explore the importance of our

uncertainty on the outcomes of salmonine stocking decisions and explore the

performance of several potential stocking strategies in the face of these uncertainties.

Methods

We developed a suite of age-based stochastic population models to describe the interactions between salmonine predators and their prey in Lake Michigan following the example of Jones et al. (1993) and Koonce and Jones (1994). Predation between the salmonine predators and their prey was described using a Type II function response (Hollings 1959). The effects of different stocking policies were simulated for a 30 year time period. Several alterative forms of the model, called model scenarios, were also investigated for a more limited suite of stocking policies. The 30 year time series for each model scenario and stocking decision was simulated 1000 times (called trials) to incorporate the effects of stochastic variation and quantified uncertainty in model parameters. For parameters where posterior distributions describing our uncertainty were available, a new set of parameters (sample) was selected from the posterior distributions for each trial but the same set of samples were used for each scenario to eliminate variation among scenarios due solely to sampling variability. The parameters and symbols used in the model equation are defined in Table 8. The equations describing the dynamics of the model are in Tables 9 and 10 and the equations will be referenced in the text as *Tx.y* where *x* is the table number and *y* is the equation number within Table *x*.

Predator population models

Chinook salmon (ages 0-5), coho salmon (ages 1-2), lake trout (ages 1-9), brown trout (ages 1-4) and steelhead (ages 1-4), were included in the simulation model. For coho salmon, brown trout, and steelhead, size at age and mortality rates were assumed to be constant over time because there is little evidence of decreased growth rates or increased mortality rates with the declines in prey abundance in Lake Michigan (Appendix A). Mortality rates and length at age were based on the most current stock

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assessments for these predators (Appendix A). Because we assumed a constant stocking

rate over time for these species and a constant level of natural recruitment (for coho

salmon and steelhead), this leads to constant numbers at age over the thirty year

simulation period (Table 11).

For both chinook salmon and lake trout, we investigated several different stocking

policies (Table 12). The recruitment to the first age of lake trout (age 1) and chinook

(age 0) was calculated by eq. T9.1. Post-stocking mortality, H_s, was assumed to be 0.4

for both species. Natural recruitment was assumed to be constant over the 30 year

simulation period at zero for lake trout and 960,000 for chinook salmon (Appendix A).

Numbers at age for older ages in each year for both lake trout and chinook were

calculated by eq. T9.2. Maturation mortality was assumed to be zero for lake trout

(Appendix A). For chinook salmon, maturation mortality was assumed to be 1 for all

mature fish and the proportion of mature fish at age was predicted by a logistic function

of spawning weight (eq. T9.3, see Appendices A and C for more details). The proportion

mature at age was capped at a maximum of 15.8% for age 1 chinook, and 42.9% for age

2 chinook, regardless of size. Total instantaneous mortality rates for lake trout were the

sum of background natural mortality rates and fishing mortality rates (eq. T9.4b).

Background age-specific natural mortality rates from the most recent assessment were

used and were assumed to be constant over the simulation time period (Appendix A).

Fishing mortality was predicted as the product of age-specific vulnerability (Appendix A)

and effort (eq. T9.5). Effort was assumed constant over the simulation time period at 5.1

million angler hours. Lake trout growth rates were assumed to be constant over time and

mid-year length at age was set at the values used in Chapter 2.

Total instantaneous mortality rates for chinook salmon were the sum of three

components, background natural mortality rates, fishing mortality rates, and a time-varying natural mortality rate (eq. T 9.4a). Background mortality rates from the most recent assessment were used and were assumed to be constant over the simulation time period (Appendix A). As for lake trout, fishing mortality was predicted as the product of age-specific vulnerability (Appendix A) and effort (eq. T9.5). Harvest (in numbers) of chinook salmon was predicted using the Baranov catch equation (eq. T9.13). The final component, $D_{ch,a,y}$, was incorporated to allow for increased mortality on chinook salmon during periods of poor growth as was observed in the late 1980s (Holey et al. 1998; Bence and Benjamin in press a). Because only one incident of this increased mortality rate was observed in chinook salmon in Lake Michigan, there are several competing hypotheses of how this mortality rate is related to chinook salmon growth rates. We chose to represent several of these hypotheses in three different models describing the dependence of $D_{ch,a,y}$ on chinook salmon growth rates. For all models, $D_{ch,a,y}$ was decomposed into an age and age-year effect (Appendix C):

$$D_{chs,a,y} = \lambda_a \kappa_{a,y} \qquad (1).$$

In the first model (M1), the age-year effect ($\kappa_{a,y}$) was assumed equal for all ages as a year effect (κ_y) and was modeled on the log-scale using an autoregressive time series model. The year effect was a function of the year effect in the previous year, the weight achieved by an age 2 fish at then end of the current year and a year-specific process error term (for more details see Appendix C). A joint posterior distribution for all parameters was available and 1000 samples (one for each model trial) was drawn from it (see Appendix C for details). The second and third mortality models (M2 and M3,

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respectively) are based on stronger assumptions about the relationship between growth and mortality events. Both models are based on the assumption that there are two distinct mortality states, one with high levels of mortality and one with low levels of mortality. The transition probability between these states depends upon the current mean weight at age of chinook salmon. These two models differ in their description of how weight affects the transition between these two states.

For M2, each episode of high mortality was assumed to last at least five years. After being in a high mortality state for 5 years, the transition probability between high and low mortality rates was assumed to be logistic function of end of the year weight. The transition probability from a low mortality state to a high mortality state, was assumed to be the complement of a logistic function of end of the year weight. In the final mortality model (M3), the transition from a high mortality state to a low mortality state is assumed to be deterministic after the end of the year weight at age exceeded a threshold value. The transition probability from a low mortality state to a high mortality state, was assumed to be the complement of a logistic function of the end of the year weight. For both M2 and M3, the time-varying natural mortality was calculated using eq.1 with $\kappa_{a,y}$ equal to 1.27 for high mortality states and 5E-5 for low mortality states. During each trial, a mortality model (M1, M2, or M3) was chosen, with equal probabilities, and the chosen mortality model was used during the trial's 30 year simulation time period.

For both M2 and M3, the parameter values were chosen to reflect observed patterns in the mortality event of the late 1980s. With only one high mortality event in Lake Michigan, it was not possible to statistically estimate these parameters and therefore we have not quantitatively described uncertainty with regard to these parameters (for

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more details, see Appendix C).

For all three mortality models, it is still possible for chinook salmon to reach an unreasonably small size without the occurrence of a mortality event, particularly with M1. To prevent this situation, we included a logistic model that increases the probability of a mortality event with decreasing end of the year weight at age if a mortality event has not occurred. With this model, the probability of invoking a mortality event, if one is not occurring, for 4.9 kg age 3 chinook is close to zero but approaches 1 as weight of an age 3 chinook declines to 3.4 kg.

We modeled how chinook salmon's and the other predator's consumption responded to changes in the abundances of prey using a multi-species Type II functional response (eq. T9.6; Holling 1959). For all predators, we followed the general approach used for chinook salmon in Chapter 2. The instantaneous attack rate of all predators on all prey types was assumed to be the product of four components (eq. T9.7): the predator's mid-year length, the size preference function, the habitat overlap between each predator and prey type and the length-based scalar for a predators effective search rate on an optimal prey. The habitat overlaps between the salmonine predators and the prey types were as in Chapter 2. As in Chapter 2, the size preference function (eq.T9.8) is a bell shaped function with the optimal prey length of 25% of the predator's length. A posterior density for the length-based scalar for a chinook salmon's effective search rate on an optimal prey, γ_{chs}, was estimated in Chapter 2 and a value was sampled from this distribution for each simulation trial to account for the uncertainty in this parameter.

Search rates for the other predators were not statistically estimated because their growth rates have not varied with changes in prey abundance (Appendix A). Instead, we assumed that all other predators had the same effective search rate (γ_j) and that this

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effective search rate was 1.5 times as large as γ_{chs}. Using the maximum posterior

parameter estimates from Chapter 2, this was the lowest effective search rate that leads to

lake trout consumption at age being at least 75% of $C_{\max,lt,a}$ for all ages in 1986, the year

with the lowest alewife abundance. We felt that if the actual value of the effective search

rate was lower than this value, a relationship between lake trout growth rates and prey

abundance would have been evident.

The approximate mid-year abundance at age, $\tilde{N}_{i,y}$, for all predators except

chinook salmon was calculated as the geometric mean abundance at age by projecting the

end of year abundance using the instantaneous mortality rates (Appendix A). For

chinook salmon, the total instantaneous mortality rate depends in part on the

consumption of chinook salmon through $D_{ch,a,y}$ (eq. T9.4a). Therefore, the geometric

mean abundance at age could not be calculated prior to calculating chinook salmon

consumption. To approximate mean abundance, we assumed that $D_{ch,a,y}$ would be the

same as $D_{ch,a,y-1}$ and used this approximate total instantaneous mortality rate at age to

calculate to the geometric average abundance at age.

To allow for competition among predators for prey, consumption per predator at

age for chinook salmon was predicted for each prey type using the Baranov catch

equation (eq. T9.9) and summed across all prey types. The proportion of $C_{\max,chs,a}$ was

calculated (eq. T9.10) and a bioenergetics model (Appendix A) using this proportion as

the proportion of maximum ration and the current weight at age at annulus formation (or

$W_{ch,a-1,y-1}^{end}$) was used to predict the amount of growth achieved during the year, $G_{a,y}^{chs}$.

Current end of the year weight, $W_{ch,a,y}^{end}$, and spawning weight at age, $W_{ch,a,y}^{sp}$, were

predicted using eqs. T9.11 and T9.12. Similar calculations were not done for the other

predators which were assumed to have a constant size at age schedule.

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Prey population models

Alewife dynamics are strongly influenced by the predatory demand of the salmonine predators in Lake Michigan and chinook salmon population dynamics appear to be strongly influenced by the abundance of alewife (Madenjian et al. 2002; Chapter 2). However, the influence of the other main prey species, bloater and rainbow smelt, on chinook salmon appears to be limited (Madenjian et al. 2002). Therefore, we chose only to model alewife dynamically and bloater and rainbow smelt abundance was assumed to be independent of predator abundance and constant for the 30 year simulation period. The abundance of age 1 through 7+ bloater and both small (< 120 mm) and large rainbow smelt was set at the average abundance from 1995 to 1997 from Chapter 2, as was the mid year length at age. The approximate mid-year abundance ($\tilde{N}_{i,y}$) of bloater and rainbow smelt was assumed to be equal to the beginning of the year abundance. To calculate consumption of these prey species for chinook salmon (eq. T9.9), total instantaneous mortality rates were assumed to be equal to the instantaneous predation rates (eq. T10.5) with no background mortality rates.

Alewife (ages 0 to 6+) numbers at age were modeled dynamically to respond to changes in the demand of salmonine predators. Recruitment of alewife was predicted using a Ricker stock-recruitment function where stock size was defined as the number of age 2+ alewife (eq. T10.1). The year-specific random errors, ε_y, were assumed to be independent and identically distributed as a normal distribution with a mean of zero and a variance of σ_r^2. A sample of parameters was selected for each simulation trial from the joint posterior distribution of α_{aw}, β_{aw}, and σ_r^2 estimated in Chapter 2. The ε_y were then drawn randomly from a normal distribution with mean zero and variance equal to the value of σ_r^2 selected from the joint posterior distribution. Numbers at age for each

year were then calculated using eq T10.2. Numbers at age 6+ were the sum of numbers

surviving from age 5 and the numbers of age 6+ surviving from the previous year (eq.

T10.3). For alewife, the total instantaneous mortality rates were the sum of background

natural mortality rates and instantaneous predation rates (eqs. T10.4, T10.5). To

calculate the approximate mid-year abundance ($\tilde{N}_{i,y}$) of alewife used in the functional

response (eq. T9.6), the iterative method proposed in Chapter 2 was used. The following

steps were repeated until total consumption in biomass of alewife changed by less than

1% of the total consumption calculated in the previous iteration :

    1. Instantaneous predation rates were predicted using "average" abundance for

    alewife (beginning of the year abundance in the first iteration)

    2. The instantaneous predation rates were used to calculate the end of the year

    abundance of alewife along with the total consumption of alewife.

    3. The geometric mean abundance of alewife was used as the new "average"

    abundance in step 1.

    A large dieoff in the alewife population occurred in 1967 and this dieoff was

thought to be caused, in part, by the high abundance of alewife in the mid-1960s (Smith

1972). We attempted to capture this behavior by incorporating a stochastic dieoff

mortality model for alewife. The probability of an alewife dieoff occurring was assumed

to follow a logistic function of the stock size (eq T10.6). Because only one major dieoff

of alewife has occurred in Lake Michigan, the parameters of this model could not be

estimated statistically. Rather, the parameters were chosen such that the probability of a

dieoff occurring at a stock size of approximately 4×10^{12} (the estimated stock size in

1966 and 1967; Chapter 2) was 50%, since a dieoff occurred in 1967 but not in 1966.

Additionally, the slope parameter was adjusted so that the probability of a dieoff

occurring at stock sizes less than 2 x 10^{12} was small (< 0.1) since a dieoff did not occur in the early 1960s or early 1970s when alewife stock sizes were estimated to be approximately 2 x 10^{12} (Chapter 2). The dieoff affected age 2+ alewife only and the proportion of alewife surviving the dieoff (S_{die}) was 0.65 , the maximum posterior estimate of the survival of the 1967 dieoff from Chapter 2, if a dieoff occurred and 1 otherwise.

Model scenarios and stocking strategies

The outcomes of different model scenarios and different stocking policies were evaluated using system variables that relate to the major objectives of Lake Michigan salmonine management. In particular, we looked at total cumulative harvest (in numbers) of chinook salmon over the 30 year simulation time period to assess effects on the chinook salmon fishery. We also looked at the frequency and duration of chinook salmon dieoffs ($D_{ch,2,y} > 1.25$) along with the average spawning weight of an age 3 chinook salmon during the 30 year simulation time period to determine the health of the chinook salmon population. Finally, we measured the frequency of alewife biomass in each of three categories, low ($< 100,000$ metric tons), moderate (100,000 - 2.5 million metric tons), and high (over 2.5 million metric tons), over the 30 year time period. These categories were chosen to approximate the three general states of the alewife population during the late 1980s (low), the mid 1970s (moderate) and late 1960s (high).

To assess the sensitivity of the decision model to assumptions made during model construction, we tested its performance with alternative values for some model parameters that were not statistically estimated (Table 12). In the baseline scenario, the values of all of the parameters that were not statistically estimated were set at our best guesses and all three chinook mortality models were used with equal probabilities. We

assessed the effect of the search rate of predators other than chinook by increasing their

relative search rates, so that they are 3 times more efficient predators than chinook

salmon of the same size at low prey abundance and by decreasing their relative search

rates, so that they search with the same efficiency as chinook salmon of the same size.

Additionally, we tested the model's sensitivity to the occurrence of alewife dieoffs by

altering the parameters of the logistic model to make dieoffs both more likely and less

likely at lower alewife abundances (Figure 17). We also evaluated the performance of

the decision model when the uncertainty in key parameters representing the chinook

functional response, the alewife stock-recruitment relationship and the chinook mortality

model, was ignored by setting the parameters of interest to the value with maximum

density in the posterior distribution.

A total of eight stocking strategies were evaluated to determine the differences in

the outcomes of the model caused by stocking strategy (Table 13). We evaluated two

main types of stocking strategies, a fixed stocking strategy where the number of chinook

salmon and lake trout stocked are constant and does not respond to changes in the state of

the system and a feedback stocking policy, where the number of chinook salmon stocked

respond to a measure of the current state of the system. The four fixed stocking strategies

included the current status quo stocking rates (SQ), a reduction in chinook stocking by

25%, a reduction of chinook stocking by 50%, and status quo stocking of chinook salmon

with a doubling of lake trout stocking rates (Table 13).

Two general classes of feedback policies were used, both with status quo or

increased stocking of lake trout. Both feedback policies responded to changes in chinook

salmon end of the year weight at age 3. When end of the year weight at age 3 fell below

a critical point (7 kg), stocking of chinook salmon was decreased by 50% from the status

quo level. When chinook salmon end of the year weight at age 3 increased above 7 kg, stocking rate was returned to the status quo level. The difference between the two strategies was the lag time between the measurement of the state of the system and the implementation of the stocking increase or decrease. In the first set of feedback stocking strategies (F1 and F1LT), the response in stocking rate to the state of the system had no delay. That is, when end of the year weight of an age 3 chinook salmon reached the critical level, the appropriate change in stocking was implemented in the following year. In the second set of feedback stocking strategies (F3, F3LT), we included a delay of three years to occur between the measurement of the system and the implementation of a new stocking rate to simulate practical constraints associated with substantial changes in stocking levels.

We also constructed a simplified decision model where only alewife and chinook salmon population dynamics were included and alternative prey and the stocking of all other salmonines was excluded to determine if the behavior of our decision model was sensitive to the inclusion of these other species. We evaluated the performance of this simplified model for five different stocking strategies (the strategies with changes in lake trout stocking were excluded).

Results

Harvest

The average cumulative harvest in the baseline scenario is highest for the

feedback policy with a one year lag (F1, Table 14), however, average cumulative harvest

for both status quo stocking and the feedback policy with a three year lag were within 2%

of this level. The feedback policy with a one year lag reduces the occurrence of low

harvests, in comparison with status quo stocking, however the distributions of potential

cumulative harvests for both policies were wide and flat (Figure 18). A 25 % reduction

in chinook stocking (R25) led to a 13% decrease in average cumulative harvest and a

50% reduction led to a 26 % reduction in average cumulative harvest relative to status

quo stocking. Doubling the number of lake trout stocked without reducing chinook

salmon stocking (DLT) leads to a decline of approximately 14% in average cumulative

harvest of chinook salmon relative to status quo stocking (Table 14). When combined

with a feedback policy, doubling lake trout stocking reduces average cumulative harvest

of chinook salmon by 12 % and 10% for the 1 and 3 year lag.

The effects of alternative assumptions for the search rate of lake trout, coho

salmon, brown trout, and steelhead on average cumulative harvest are substantial. By

assuming that these predators are only as efficient as chinook salmon of the same size at

low prey abundance (FL), the average cumulative harvest increases for all stocking

strategies between 12 and 14 % (Table 14). If the search rate of lake trout, coho salmon,

brown trout, and steelhead is assumed to be three times more efficient than chinook

salmon of the same size, the average cumulative harvest decreases for all stocking

strategies by 12 to 15% (Table 14).

The effect of changes in the probability of an alewife dieoff was less pronounced.

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If the probability of an alewife dieoff occurring at lower alewife abundances was increased (DB, DD) relative to the baseline scenario, then the average cumulative harvest decreased for all stocking strategies and the feedback policy with a one year lag increases harvest by 3.4 % (DD) or 2.1 % (DB) relative to status quo stocking. When the probability of an alewife dieoff occurring at lower abundances is decreased, the status quo stocking policy has a higher average cumulative harvest than the feedback policy with one year lag (Table 14).

To assess the effects of including uncertainty on the cumulative harvest of chinook salmon, we ignored the uncertainty in both the effective search rate of chinook salmon and the stock-recruitment parameters of alewife. If we ignored the uncertainty in the stock-recruitment parameters of alewife and the maximum posterior estimates were assumed to be the true values, the status quo stocking policy rather than the feedback policy with a one year lag provided the highest average cumulative harvest (Table 15). Using a feedback policy with a lag of one year, the distribution of cumulative harvests ignoring the uncertainty in the stock-recruitment parameters is more sharply peaked and the probability of extreme harvests are reduced when compared to the baseline scenario (Figures 18b, 19b). Not including uncertainty in the effective search rate of chinook salmon and assuming the maximum posterior estimate is the true value leads to a significantly lower average cumulative harvest (Table 15). The distribution of harvests with F1 stocking remains wide with a slightly higher occurrence of low harvests than the baseline scenario (Figures 18b, 19a).

The different models for chinook salmon mortality also have large effects on the average cumulative harvest predicted by the decision model. The first mortality model (M1) is characterized by much lower levels of harvest then either of the other two models

(Table 15). The other mortality models (M2 and M3) predict similar levels of cumulative

harvest with M3 providing slightly higher average cumulative harvest (Table 15). The

differences in the three mortality models are also reflected in the distributions of

cumulative harvest, however all three mortality models still result in a wide distribution

of potential harvests (Figure 20). For all three mortality models, stocking policy F1

provides the highest average cumulative harvest (Table 15).

In the simplified decision model with only chinook salmon and alewife, the

average cumulative harvests for all five stocking policies were larger than in the full

decision model (Tables 15 and 16). The status quo stocking policy produced the largest

average harvest in all model scenarios (Table 16). The distribution of cumulative

harvests for the simplified model were more sharply peaked than their counterparts in the

full decision model (Figures 21 ,22) and the effect of removing uncertainty from the

stock-recruitment parameters on the distribution of harvests was not as large as in the full

model (Figure 21).

Alewife biomass

In the baseline scenario, the percentage of occurrences with alewife in either the

low or high abundance category was approximately 45% for the status quo stocking

policy and slightly lower (41%) for the F1 policy (Table 17). Alternative assumptions

about the alewife dieoff model affected the distribution of alewife biomass as expected

with scenarios with a decreased chance of dieoffs at low abundances having less

occurrences of low biomass and more occurrences of high biomass relative to the

baseline scenario (Table 17). The effects of the effective search rate of lake trout, brown

trout, steelhead and coho salmon were large with the higher search efficiencies leading to

more occurrences of low alewife biomass (Table 17). The functional form of the chinook

mortality model used had very little effect on the distribution of alewife abundances. Ignoring the uncertainty in the chinook salmon effective search rate slightly increased the occurrence of low alewife biomass. Ignoring the uncertainty in alewife stock-recruitment parameters had the largest effect on alewife biomass distribution with the occurrence of low alewife biomass declining by over one half from the baseline scenario with F1 stocking.

Chinook mean size at age and mortality events

The distribution of average spawning weight for an age 3 chinook salmon was wide for all model scenarios with both status quo stocking and F1 stocking, ranging from less than 4 kg to over 16 kg (Figures 23-27). The percentage of simulations with average weight at age 3 less than 4 kg was smaller with F1 stocking than status quo stocking for the baseline scenario (Figures 23a, 26a). Not surprisingly, as the searching efficiency of other salmonines, relative to chinook salmon, is increased (Figure 23), or as the probability of an alewife dieoff at lower abundances increased (Figures 24, 25), the occurrence of small chinook salmon also increased.

Ignoring the uncertainty in chinook salmon's effective search rate slightly increases the occurrence of small chinook salmon with F1 stocking while ignoring the uncertainty in alewife's stock-recruitment parameters had a large effect, reducing the occurrence of small (< 4 kg) chinook from 20% to 7% (Figure 26). The effect of the form of the chinook mortality model on the distribution of the average spawning weight of an age 3 chinook salmon was slight (Figure 27).

The frequency of chinook salmon mortality events in the baseline scenario was similar for both status quo stocking and F1 stocking with over 90% of all simulation trials having at least one mortality event during the 30 year simulation period and over

half having one or two events (Figure 28). The functional form of the mortality model had a substantial effect on the distribution of the number of mortality events with model scenario M1 producing a higher occurrence of multiple (3 or more) mortality events in a 30 year simulation period (Figure 29).

The average duration of the mortality events ranged from 5.63 to 13.33 years but in all scenarios, the durations were highly variable (Table 18). A feedback stocking policy (F1) appeared to reduce the average duration of mortality events in the baseline scenario slightly but both stocking strategies had outcomes with prolonged (> 20 years) mortality events. Any model scenario that increased the occurrence of low alewife biomass (DB, DD, FH) also increased the average duration of mortality events (Table 18). Ignoring the uncertainty in alewife's stock-recruitment parameters had the largest effect reducing the average duration of an event to 5.6 years and reducing the variability in duration time (Table 18). Model scenario M2 produced slightly longer duration times due to its assumption of a minimum duration of 5 years.

Discussion

The management of predatory demand in Lake Michigan through the stocking of five species of salmonines poses an interesting challenge to decision makers. The original goals of the salmonine stocking program to support a successful salmonine sport fishery and to control the exotic alewife abundance have been achieved (Madenjian et al. 2002) and managers are faced with a objective of maintaining the valuable sport fishery while controlling the predatory demand to maintain moderate levels of alewife abundance (Eshenroder et al. 1995). This objective requires the understanding of the dynamics of the alewife population along with an understanding of the dynamic link between salmonine predators and their prey (Jones et al. 1993). Recent advances in the quantitative stock assessments of both the salmonine predators and alewife has led to an increased understanding of the systems dynamics along with a quantitative evaluation of our uncertainty in key parameters, such as the alewife stock-recruitment parameters, and the effective search rate of chinook salmon. By incorporating these uncertainties in a stochastic decision model, we were able to evaluate the effects of these uncertainties on system dynamics and investigate which stocking strategies may hold the most potential for achieving the management objective in the future.

Perhaps the most important outcome of our analysis is that all model scenarios and stocking strategies investigated in the full decision model result in a wide range of potential system states in the future. All model scenarios and stocking strategies we investigated had a non-trivial chance of producing a future state of the system where alewife abundance and chinook harvest were low, chinook mortality events were either frequent or prolonged and the average spawning weight at age of an age 3 chinook was unacceptably low (< 4kg). Additionally, a non-trivial chance of a future state of the

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system where alewife abundance is unacceptably high for these same scenarios and stocking strategies was predicted. This suggests, given our current understanding of the system, that management of the system through the stocking of salmonines may not be able to meet all of our management objectives without accepting a level of risk for undesirable future outcomes. Effective communication of this outcome to stakeholder groups and decision makers so that the economic and social costs of these risks can be incorporated in the decision making process may be vital (Hilborn and Walters 1997; Krueger and Decker 1999).

Our analysis also reveals the importance of lake trout, brown trout, steelhead, and coho salmon in predicting the future dynamics of the system. The response of these predators to low alewife abundance remains a significant uncertainty regarding the dynamics of predator-prey interactions in Lake Michigan and the assumptions made about the relative search efficiency of these predators has a large impact in the potential outcomes of management actions. While chinook salmon is the dominant consumer in Lake Michigan (Madenjian et al. 2002), the effect of these other predators on alewife dynamics, should alewife abundance become low, appears to be important, with increased searching efficiency of these predators increasing the chance of undesirable outcomes. Additionally, the results of our simplified chinook-alewife model show that the chance of low cumulative harvests is substantially underestimated if the effects of the other salmonine predators are ignored. This implies that the suite of salmonine predators must be managed in concert and changes in the management of one species, e.g. lake trout, may have important effects on the chinook salmon fishery.

Our examination of the importance of different sources of uncertainty on the outcomes of management actions revealed that ignoring the uncertainty in alewife stock-

recruitment parameters leads to an overly optimistic prediction of the outcomes of future

stocking decisions. Ignoring our uncertainty in the stock-recruitment parameters of

alewife also suggested that the status quo stocking policy would provide higher average

cumulative harvests of chinook salmon than a feedback policy. This results suggests that

the failure to include our uncertainty, as in Ludwig (1996a) and Ludwig (1996b),

camouflages the true level of risk in management decisions.

Additionally, the chance of an alewife dieoff occurring in the future similar to the

dieoff that occurred in 1967 also has noticeable effects on the outcomes of management

actions. Any scenario where there is an increased chance of dieoffs occurring at lower

population abundances leads to an increased frequency of undesirable outcomes. These

results strongly suggest that understanding the dynamics of the alewife population is key

to managing the Lake Michigan salmonine community. The need for future research that

further investigates both the stock-recruitment dynamics and potentially the mechanisms

triggering large alewife dieoffs is paramount.

However, the dominance of the importance of the dynamics of alewife in the

performance of management objectives suggests that our ability to control the system

through the stocking of salmonine predators may be limited by stochastic variation in

alewife recruitment that is not predictable. An additional concern for future management

is the profound changes in the lower trophic levels of Lake Michigan with the invasion of

zebra mussels (*Dreissena polymorpha*) and the disappearance of *Diporeia* (Madenjian et

al. 2002). Recently, declines in the growth and condition of alewife in Lake Michigan

have been noted (Madenjian et al. in press) and the impact of these declines on alewife

population dynamics remains unknown.

Given the large sources of uncontrollable variability, focusing on stocking

strategies that optimize cumulative chinook salmon harvests over time using a risk neutral utility function may not address the needs and concerns of all stakeholder groups. Rather, policies that provide lower chances of certain unfavorable outcomes (e.g. low chinook salmon size at age) or that minimize the interannual variability in the state of certain system variables may be preferred (Quinn and Deriso 1999). Choosing an objective function that minimizes variability in annual chinook salmon harvests (e.g, Quinn et al. 1990) or incorporates a risk-averse utility function (e.g., Mendelssohn 1982) could provide a quantitative technique for incorporating these objectives.

In this analysis, we chose to investigate the performance of two classes of stocking strategies, a static stocking strategy and a responsive stocking strategy. We initially believed that a stocking strategy that responds to the state of the system would provide some feedback to stabilize the predator-prey interaction as in a natural system. We chose chinook weight at age as a trigger for changes in the stocking policy because we felt weight at age integrated the overall state of the system and would be easily measured and interpreted by managers and decision makers. The results of our decision model suggest, that while a feedback policy does impart some benefit in the baseline scenario, the gains are often slight and are not robust to changes in model assumptions. There are several potential explanations for the unexpected poor performance of our feedback stocking policies. One is that weight at age 3 does not respond quickly enough and that previous years of good growth can mask changes in growth rates making the feedback trigger too slow to stabilize the system. Using a more responsive trigger such as the proportion of maximum ration consumed by chinook salmon may allow managers to respond more quickly to changes in the system. Additionally, triggers related to the alewife population rather than the chinook salmon populations may allow managers to

anticipate future changes in the chinook salmon population and be pro-active in management actions. However, the use of more responsive triggers may be hindered by the difficulty in obtaining measurements of these quantities that are precise and accurate. Clearly, a more thorough investigation of potential triggers for a responsive stocking policy is warranted.

While our investigation has incorporated some of the key uncertainties in the salmonine predator-prey system in Lake Michigan, there are many uncertainties that were not be included in our analysis. As discussed in Chapter 2, the form of the functional response of chinook salmon remains a key uncertainty. In historical reconstructions of the Lake Michigan salmonine predator-prey system, the Type II functional response tended to underestimate the contribution of alewife to salmonine consumption at low alewife abundances. Given the importance of the response of chinook salmon to low alewife abundances in predicting future outcomes, these deviations from the Type II functional response could have profound effects on future outcomes.

Secondly, the link between consumption, energy density and chinook salmon growth rates remains an area of uncertainty. Current investigations into the energy density of chinook salmon in Lake Michigan suggest that energy density can vary from year to year and has been low enough in the recent past to be a potential concern for fish health (A. Peters, Michigan State University, personal communication). Given the importance of energy status on fish health and population dynamics (Adams 1999), these changes in energy density may have implications for the response of the chinook salmon population to changes in stocking rates and alewife abundance. A greater understanding of the link between consumption, energy density and chinook salmon population dynamics may be necessary to improve our ability to forecast the response of the system

to changes in stocking rates.

While significant uncertainties about the Lake Michigan salmonine community remain, the decision model presented here provides managers and decision makers with the opportunity to explore potential stocking strategies and when used in concert with other analyses may provide a useful vehicle for exploring the future management of Lake Michigan salmonines. Acknowledgment of uncertainty in some key parameters has revealed areas for future investigation and led to recognition of the difficulty in prescribing one management policy that meets all management objectives.

Table 8. List of variables and parameters used in the simulation model (*a:* age, *y:* year).

$N_{s,a,y}$	Beginning of the year numbers at age of species s
$R_{s,y}$	Natural recruitment of predator species s
$S_{s,y}$	Annual stocking (numbers) for predator species s
$M_{st,s}$	Post-stocking mortality for predator species s
$Z_{s,a,y}$	Total instantaneous mortality rate for species s (y^{-1})
$M_{s,a}$	Background instantaneous natural mortality rate for species s (y^{-1})
$D_{ch,a,y}$	Time-varying instantaneous mortality rate for chinook salmon (y^{-1})
$F_{s,a,y}$	Instantaneous fishing mortality rate for predator species s (y^{-1})
$P_{s,a,y}^{mat}$	Proportion of predator species s dying due to maturation
$P_{s,a,y}$	Instantaneous total predation mortality rate for prey species s (y^{-1})
S_{die}	Proportion of alewife age 2+ surviving a dieoff
$C_{max,j}$	Maximum annual consumption rate (kg y^{-1}) per predator by predator type j
$A_{i,j,y}$	Instantaneous consumption rate (in numbers) per predator of predator type j on prey type i
$A_{a,i,y}^{chs}$	Instantaneous consumption rate (in numbers) per chinook salmon predator on prey type i
$A_{s,a,j,y}$	Instantaneous consumption rate (in numbers) per predator of predator type j on prey species s
$w_{s,a,y}$	Mid-year weight (kg) of species s
w_i	Mid-year weight (kg) of prey type i
$W_{ch,a,y}^{end}$	End of the year weight (kg) for chinook salmon
$W_{ch,a,y}^{sp}$	Spawning weight (kg) of chinook salmon
$\alpha_{i,j}$	Instantaneous attack rate of predator type j on prey type i
$\tilde{N}_{i,y}$	Approximate mid-year abundance of prey or predator type i
γ_j	Length-based scalar for a predator j's effective search area (cm^{-1})
$\ell_{i,j}$	Length ratio between prey type i and predator type j
l_j	Mid-year length of predator type j (cm)
$\theta_{i,j}$	Size preference of predator type j for prey type i

Table 8, cont.

$HO_{i,j}$	Habitat overlap of predator type j and prey type i
ℓ_{opt}	Optimal predator-prey length ratio
ϖ	Parameter controlling the width of the size preference function
α_{aw}	Parameter for alewife Ricker stock-recruitment function
β_{aw}	Compensation parameter for alewife Ricker stock-recruitment function
σ_r^2	Alewife recruitment variability unexplained by stock size
ε_y	Process error for alewife Ricker stock-recruitment function
$\upsilon_{s,a}$	Vulnerability of predator species s to fishing
E_y	Fishing effort
$C_{a,y}^{chs}$	Consumption per predator (kg) of chinook salmon
$\Re_{a,y}^{chs}$	Proportion of maximum consumption ration consumed by chinook salmon
$G_{a,y}^{chs}$	Annual change in weight (kg) by chinook salmon
H_y^{chs}	Annual harvest (numbers) of chinook salmon
η_a	Inflection point for the chinook salmon maturation model
ω_a	Slope for the chinook salmon maturation model
$P_{die,y}$	Probability of an alewife dieoff occurring
d_1	Slope of the alewife logistic dieoff model
d_2	Inflection point of the alewife logistic dieoff model
$\rho_{\gamma j}$	Proportionality constant for γ for lake trout, brown trout, coho salmon and steelhead (*i.e.* $\gamma_j = \rho_j \gamma_{chs}$)

Table 9. Model equations describing the population dynamics of chinook salmon and lake trout in the simulation model.

$$N_{s,i,y} = R_{s,y} + S_{s,y} e^{-M_{st,s}} \quad i = 0 \text{ or } 1 \tag{T9.1}$$

$$N_{s,a+1,y+1} = N_{s,a,y} e^{-Z_{s,a,y}} (1 - P_{s,a,y}^{mat}) \tag{T9.2}$$

$$P_{ch,a,y}^{mat} = \frac{1}{1 + \exp(-(\eta_a + \omega_a * W_{ch,a,y}^{sp}))} \tag{T9.3}$$

$$Z_{chs,a,y} = M_{chs,a} + F_{chs,a,y} + D_{chs,a,y} \tag{T9.4a}$$

$$Z_{lt,a,y} = M_{lt,a} + F_{lt,a,y} \tag{T9.4b}$$

$$F_{s,a,y} = \upsilon_{s,a} * E_y \tag{T9.5}$$

$$A_{i,j,y} = \frac{\alpha_{i,j} \tilde{N}_{i,y}}{1 + \sum_i \left(\alpha_{i,j} \tilde{N}_{i,y} w_{i,y} \middle/ C_{max,i} \right)} \tag{T9.6}$$

$$\alpha_{i,j} = \gamma_j * l_j * \theta_{i,j} * HO_{i,j} \tag{T9.7}$$

$$\theta_{i,j} = \exp(\frac{(l_{i,j} - l_{opt})^2}{\varpi}) \tag{T9.8}$$

$$C_{a,y}^{chs} = \sum_i \frac{A_{a,i,y}^{chs}}{Z_{i,y}} N_{i,y} (1 - e^{-Z_{i,y}}) * w_i \tag{T9.9}$$

$$\Re_{a,y}^{chs} = \frac{C_{a,y}^{chs}}{C_{max,chs,a}} \tag{T9.10}$$

$$W_{chs,a,y}^{end} = W_{chs,a-1,y-1}^{end} + G_{a,y}^{chs} \tag{T9.11}$$

$$W_{chs,a,y}^{sp} = W_{chs,a,y}^{end} - (1 - P_{G,fall}^{chs}) * G_{a,y}^{chs} \tag{T9.12}$$

$$H_y^{chs} = \sum_a \frac{F_{chs,a,y}}{Z_{chs,a,y}} N_{chs,a,y} * (1 - e^{-Z_{chs,a,y}}) \tag{T9.13}$$

Table 10. Model equations governing prey species dynamics in the simulation model (s: species, a: age, y: year).

$$N_{aw,0,y+1} = \alpha_{aw}\exp[-\beta_{aw} * S_{aw,y} + \varepsilon_y]$$ (T10.1)

$$N_{aw,a+1,y+1} = N_{aw,a,y}e^{-Z_{aw,a,y}} * S_{die}$$ (T10.2)

$$N_{aw,l,y+1} = (N_{aw,l-1,y}e^{-Z_{aw,l-1,y}} + N_{aw,l,y}e^{-Z_{aw,l,y}}) * S_{die}$$ (T10.3)

$$Z_{aw,a,y} = M_{aw,a} + P_{aw,a,y}$$ (T10.4)

$$P_{s,a,y} = \frac{1}{N_{s,a,y}}\sum_j A_{s,a,j,y}\tilde{N}_{j,y}$$ (T10.5)

$$P_{die,y} = \frac{1}{1 + \exp(-d_1(S_{aw,y} - d_2))}$$ (T10.6)

Table 11. Numbers at age (in thousands) and length at age (mm) of coho salmon, brown trout and steelhead in the simulation model.

Numbers at age			
Coho salmon			
1	2		
818.2	672.7		
Steelhead			
1	2	3	4
925.5	853.9	588.4	293.7
Brown trout			
1	2	3	4
966.7	547.6	200.7	51.6
Length at age			
Coho Salmon			
1	2		
280.2	546.2		
Steelhead			
1	2	3	4
162.4	506.4	694.1	800.6
Brown trout			
1	2	3	4
277.0	445.5	600.0	658.2

Table 12. Model scenarios

BL	baseline scenario
DA	d_1 increased 25 %
DB	d_1 decreased 25 %
DC	d_2 increased 50 %
DD	d_2 decreased 50 %
FL	$\rho_\gamma = 1$
FH	$\rho_\gamma = 3$
M1	chinook mortality model 1
M2	chinook mortality model 2
M3	chinook mortality model 3
FR	no uncertainty in γ_{chs}
SR	no uncertainty in α_{aw}, β_{aw}, and σ_r^2

Table 13. Stocking (millions) policies for lake trout and chinook salmon.

Policy		Chinook		Lake trout
Status Quo (SQ)		5.5		2.5
25% Chinook Reduction (R25)		4.125		2.5
50% Chinook Reduction (R50)		2.75		2.5
Doubling Lake Trout (DLT)		5.5		5.0
Feedback policies				
	Lag	$W^{end}_{chs,3,y} < 7.0$	$W^{end}_{chs,3,y} > 7.0$	
F1	1	2.75	5.5	2.5
F3	3	2.75	5.5	2.5
F1LT	1	2.75	5.5	5.0
F3LT	3	2.75	5.5	5.0

Table 14. Average cumulative harvest (numbers in thousands) of chinook salmon in 30 years under eight different stocking policies for different model scenarios. Stocking policies with the highest average cumulative harvest are in bold.

	SQ	R25	R50	DLT	F1	F3	F1LT	F3LT
BL	5,574.6	4,851.7	4,112.4	4,798.0	**5,604.1**	5,517.0	4,958.4	4,914.7
FL	6,302.9	5,546.8	4,667.1	5,833.0	**6,310.2**	6,122.2	5,912.4	5,677.4
FH	**4,789.8**	4,128.0	3,588.0	3,856.6	4,610.5	4,618.1	3,774.7	3,828.8
DA	**5,829.8**	5,144.6	4,344.3	5,098.6	5,778.4	5,641.5	5,107.0	5,006.0
DB	4,889.0	4,323.4	3,740.2	4,241.4	**4,991.7**	4,922.0	4,304.9	4,361.6
DC	**5,131.4**	4,567.1	3,870.3	4,583.1	5,073.2	5,035.1	4,555.6	4,571.1
DD	3,917.4	3,620.4	3,125.0	3,300.4	**4,051.6**	3,986.2	3,474.7	3,344.8

Table 15. Average cumulative harvest (numbers in thousands) of chinook salmon in 30 years under eight different stocking policies when uncertainty is ignored in key parameters. Stocking policies with the highest average cumulative harvest are in bold.

	SQ	R25	R50	LT	F1	F3	F1LT	F3LT
BL	5,574.6	4,851.7	4,112.4	4,798.0	**5,604.1**	5,517.0	4,958.4	4,914.7
SR	**6,204.4**	5,450.1	4,745.7	5,033.7	5,331.9	5,170.1	4,513.0	4,454.8
FR	4,706.1	4,213.2	3,639.9	4,132.5	4,703.5	**4,729.6**	4,163.2	4,196.7
M1	4,720.1	4,723.8	3,595.9	4,188.5	**4,816.2**	4,743.7	4,289.0	4,242.2
M2	5,814.5	5,180.8	4,371.2	5,040.9	**5,910.3**	5,695.6	5,138.4	5,043.0
M3	5,950.2	5,269.5	4,478.6	5,158.7	**6,026.1**	5,875.8	5,316.1	5,204.8

Table 16. Average cumulative harvest (metric tons) of chinook salmon in 30 years under five different stocking policies when uncertainty is ignored in key parameters for the simplified chinook-alewife model. Stocking policies with the highest average cumulative harvest are in bold.

	SQ	R25	R50	F1	F3
BL	**7,460.4**	6,417.2	5,351.4	7,381.2	7,237.5
SR	**8,188.5**	6,924.8	5,596.3	7,921.1	7,855.0
FR	**7,553.3**	6,453.0	5,311.5	7,314.3	7,299.3
M1	**6,587.6**	5,615.1	4,614.6	6,321.2	6,245.2
M2	**7,964.1**	6,827.6	5,561.7	7,797.3	7,725.9
M3	**8,133.4**	7,000.9	5,702.9	8,009.3	7,863.4

Table 17. Percentage of simulations years that fall alewife biomass (mt) was in each category for different model scenarios and stocking strategies.

Model Scenario	< 100,000	100,000 - 2,500,000	> 2,500,000
		Status Quo Stocking	
BL	23.18	55.04	21.78
DA	21.38	54.53	24.09
DB	29.83	53.65	16.52
DC	18.98	53.33	27.68
DD	40.62	49.40	9.98
FL	14.51	61.18	24.31
FH	33.55	48.34	18.11
		Feedback stocking with 1 year lag	
BL	17.95	59.32	22.73
M1	18.89	57.37	23.74
M2	18.07	58.64	23.29
M3	18.97	57.55	23.48
FR	23.10	55.10	21.81
SR	7.30	86.88	5.82

Table 18. Mean, standard deviation, 0.10, and 0.90 quantiles for the duration (years) of chinook salmon mortality episodes under different model scenarios and stocking strategies.

Model Scenario	Mean	Standard Deviation	Quantiles
		Status Quo Stocking	
BL	9.62	8.60	(1.5, 27)
DA	9.44	8.68	(1.5, 27)
DB	10.84	9.23	(2, 27)
DC	8.20	8.45	(1.5, 27)
DD	13.33	10.06	(3, 29)
FL	7.87	7.34	(1.5, 21)
FH	12.14	9.95	(2, 28)
		Feedback stocking with 1 year lag	
BL	8.51	8.32	(1.4, 26)
M1	8.24	8.60	(1.33, 26)
M2	10.03	7.88	(5, 27)
M3	8.25	8.34	(1, 27)
FR	9.18	9.11	(1.5, 27)
SR	5.63	5.81	(1.5, 12)
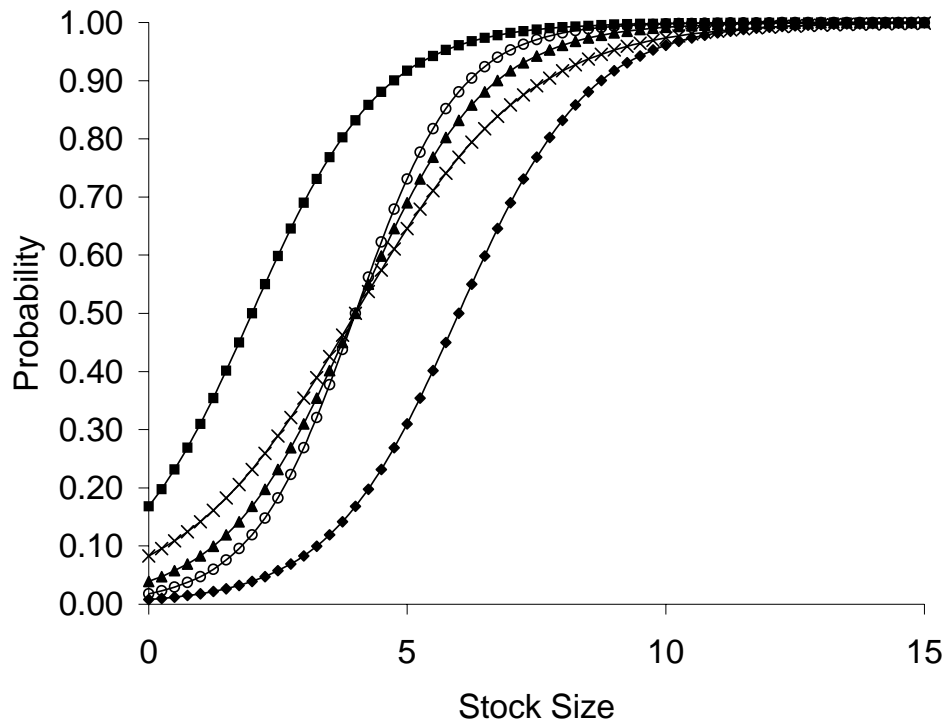
Figure 17. The probability of an alewife dieoff as a function of stock size (numbers times 10^{11}) for model scenarios: baseline (solid triangle), DA (open circles), DB (x's), DC (solid diamonds), and DD (solid squares).
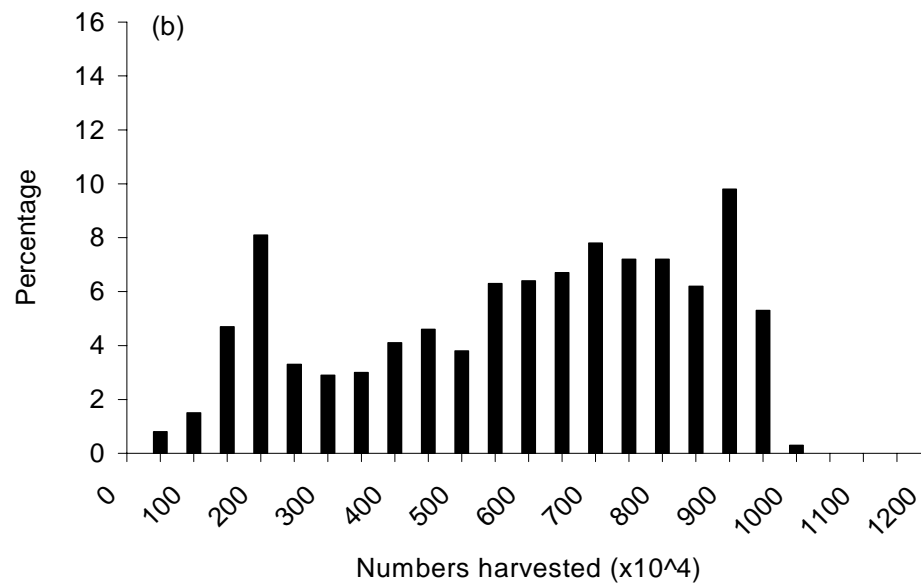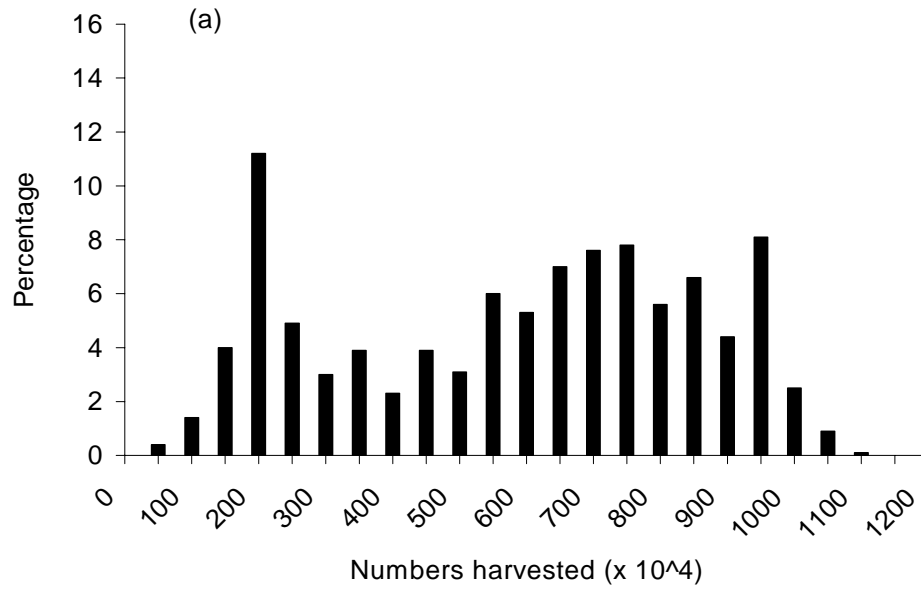
Figure 18. Distribution of the numbers of chinook salmon harvested in 1000 simulations for the baseline scenario with the (a) status quo stocking policy and (b) feedback stocking policy with one year lag.
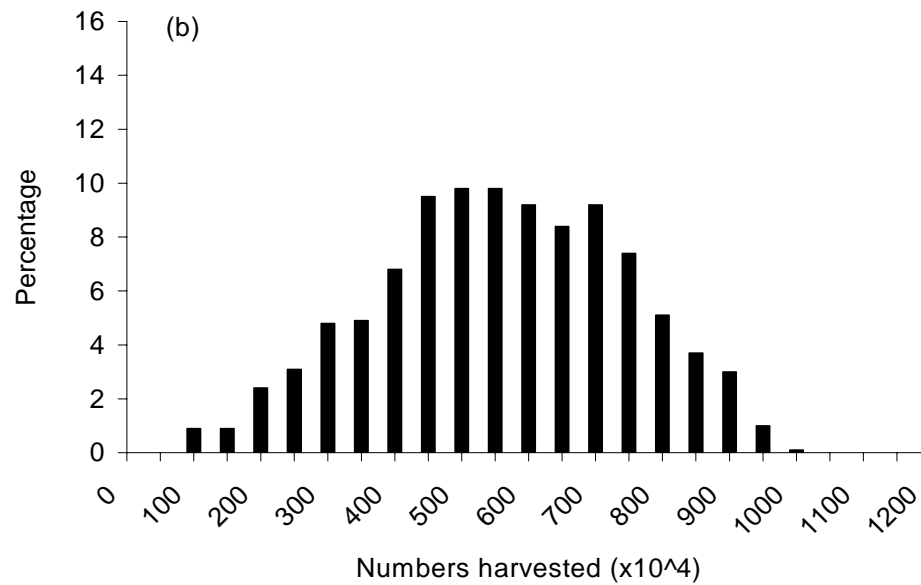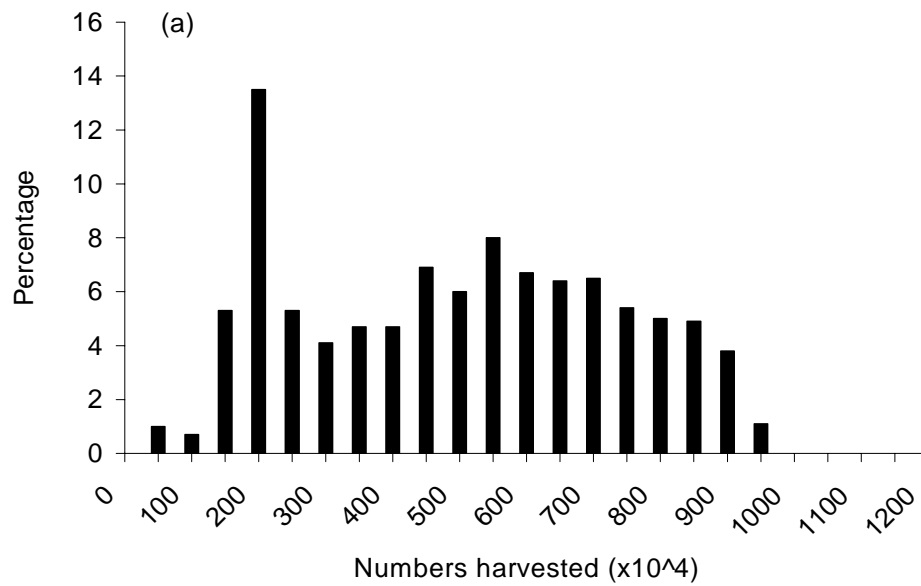
Figure 19. Distribution of cumulative harvest for 1000 simulations with a feedback stocking policy with a one year lag for model scenarios (a) FR and (b) SR.
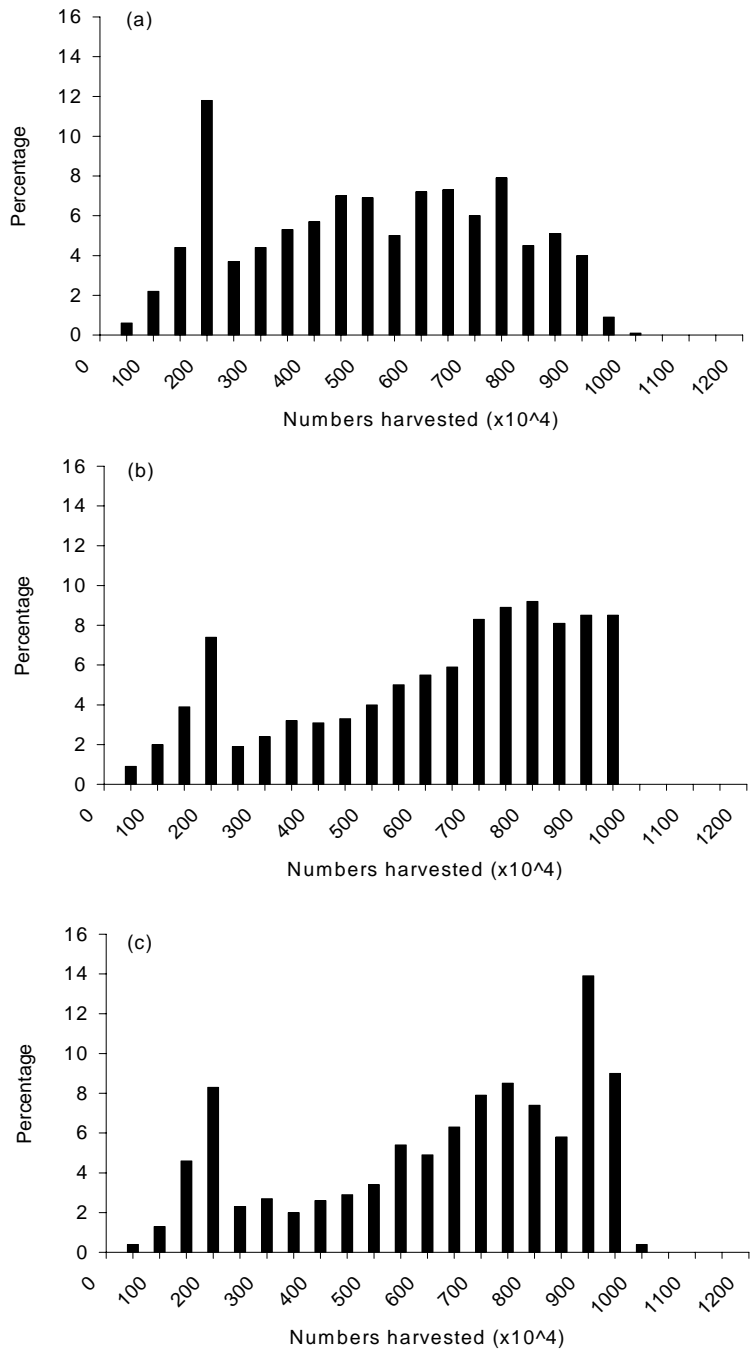
Figure 20. Distribution of cumulative harvest for 1000 simulations with a feedback stocking policy with a one year lag for model scenarios (a) M1, (b) M2, and (c) M3.
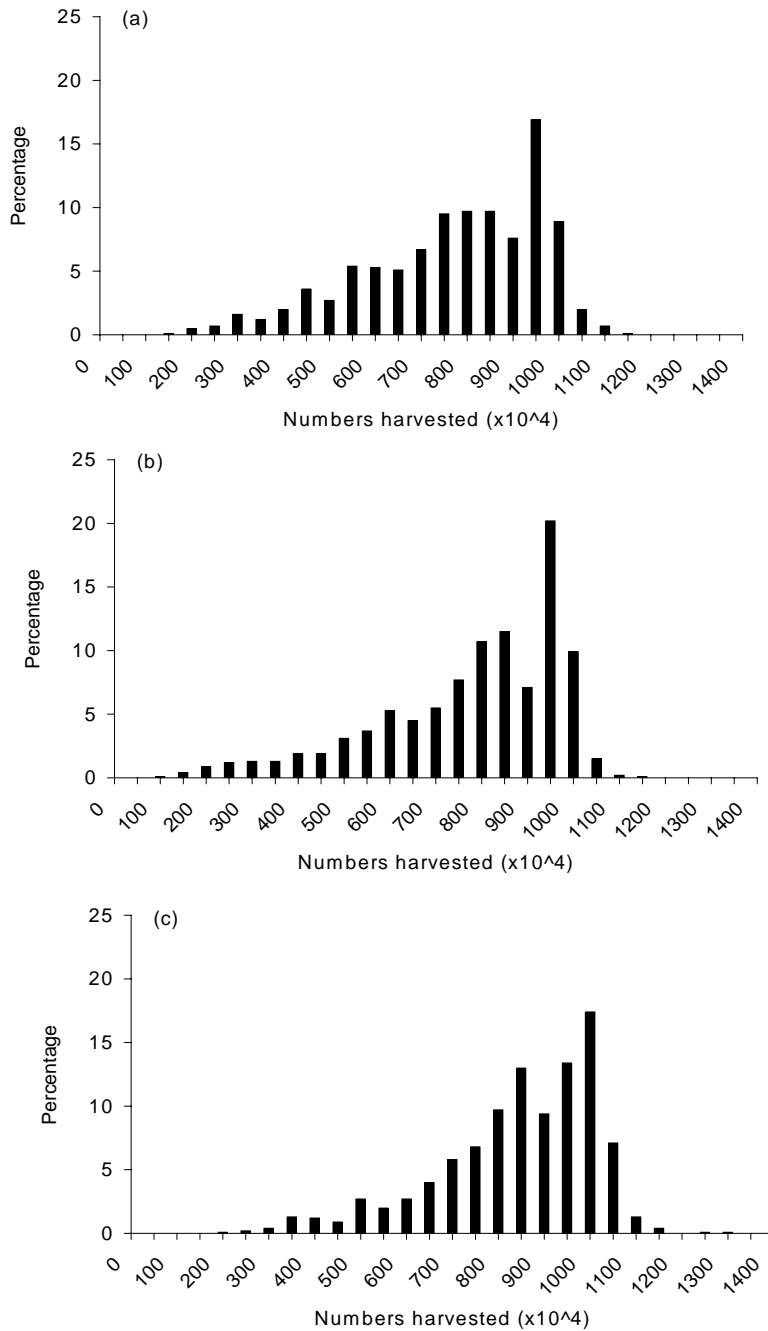
Figure 21. Distribution of cumulative harvest for 1000 simulations of the simplified
decision model with status quo stocking for model scenarios (a) baseline, (b) FR, and (c)
SR.
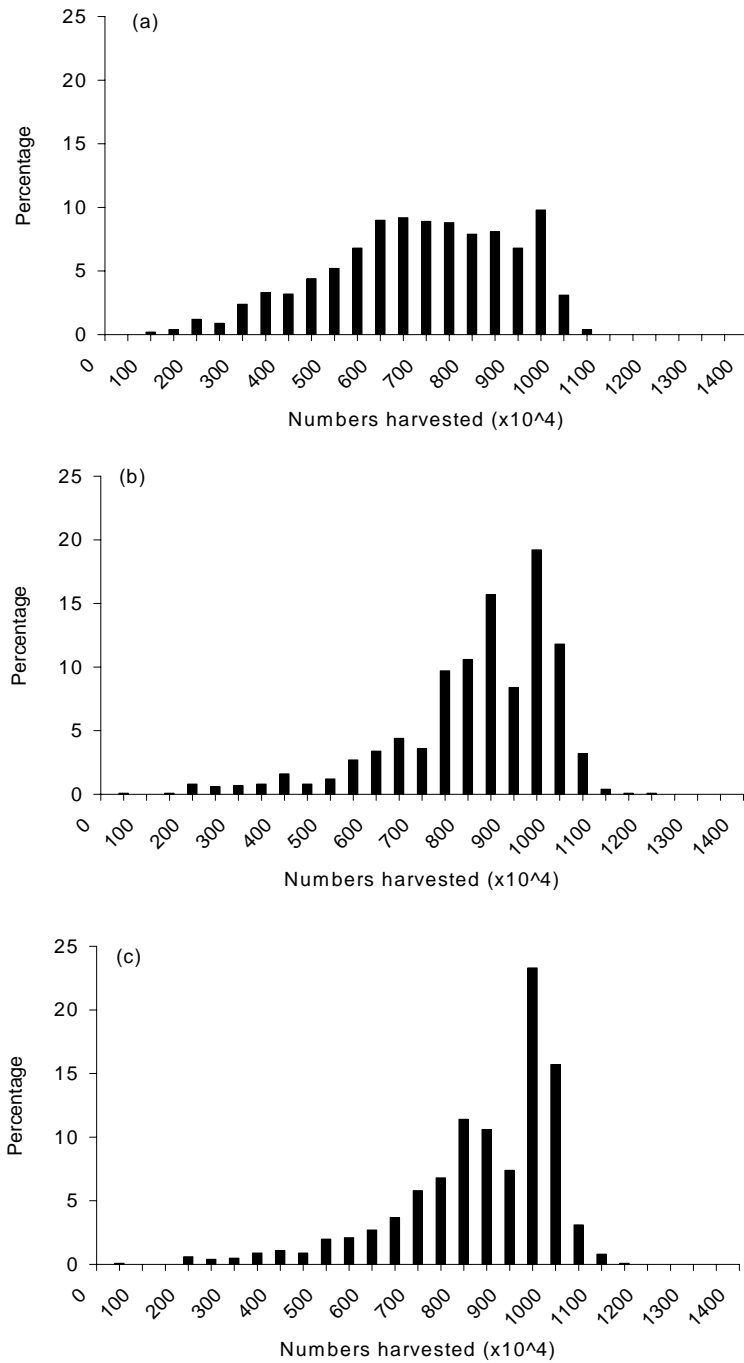
Figure 22. Distribution of cumulative harvest for 1000 simulations of the simplified decision model with status quo stocking for model scenarios (a) M1, (b) M2, and (c) M3.
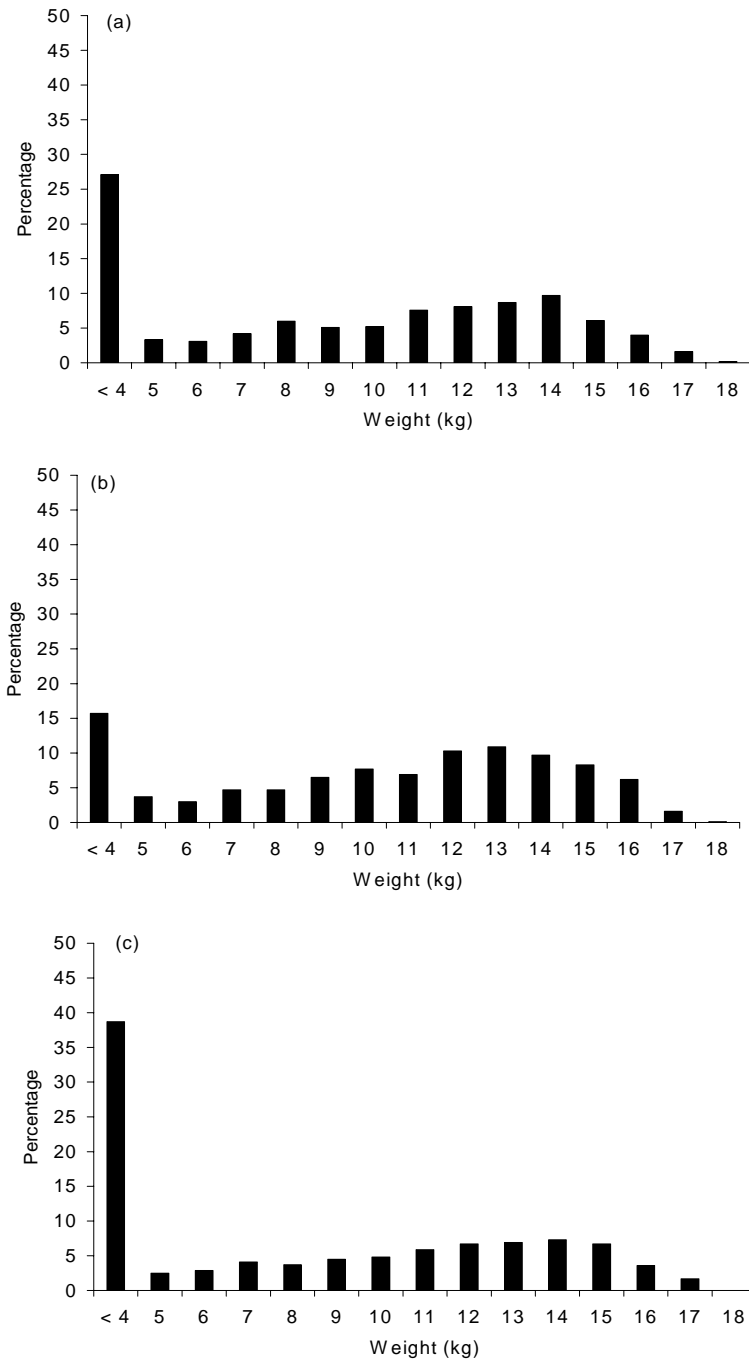
Figure 23. Chinook salmon average spawning weight at age 3 with status quo stocking for model scenarios (a) baseline, (b) FL, and (c) FH.
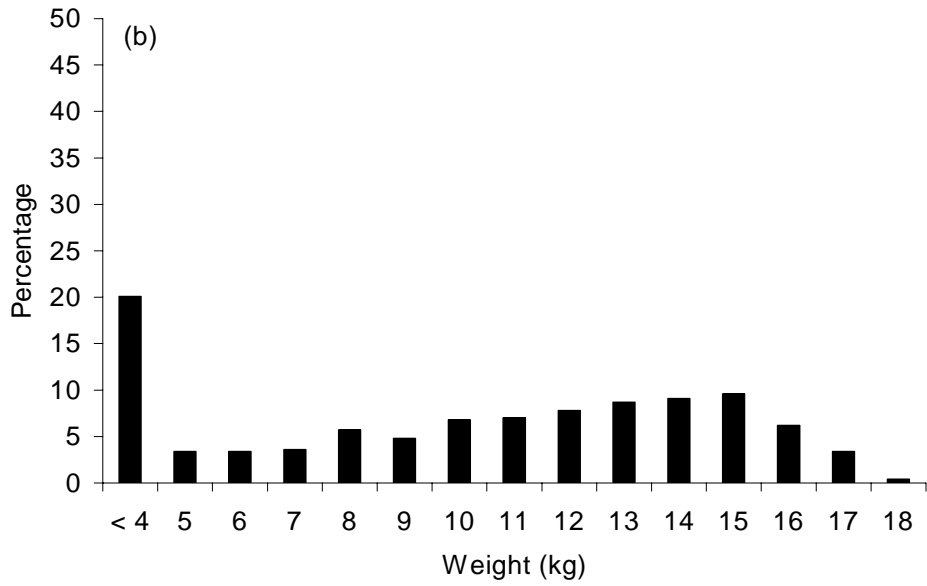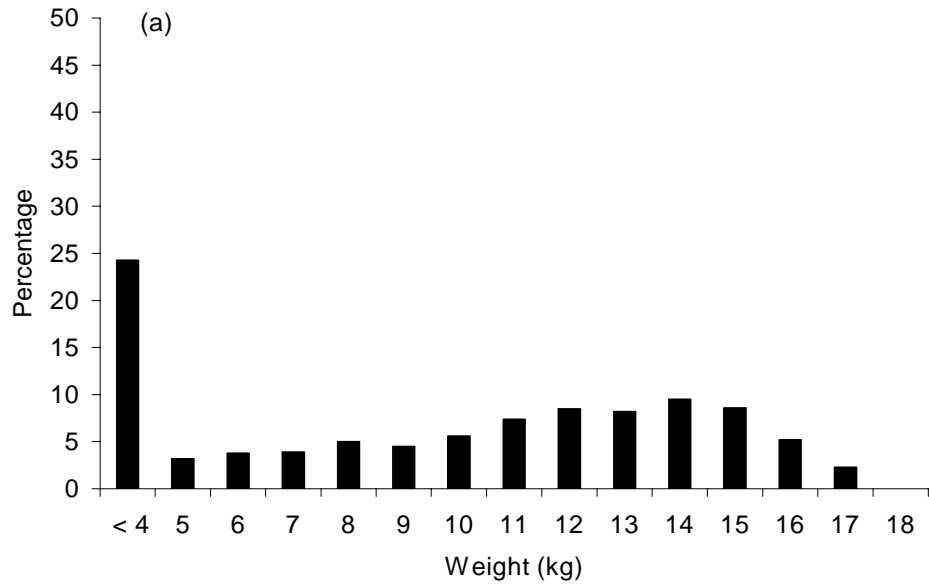
Figure 24. Chinook salmon average spawning weight at age 3 with status quo stocking for model scenarios (a) DA, and (b) DC.
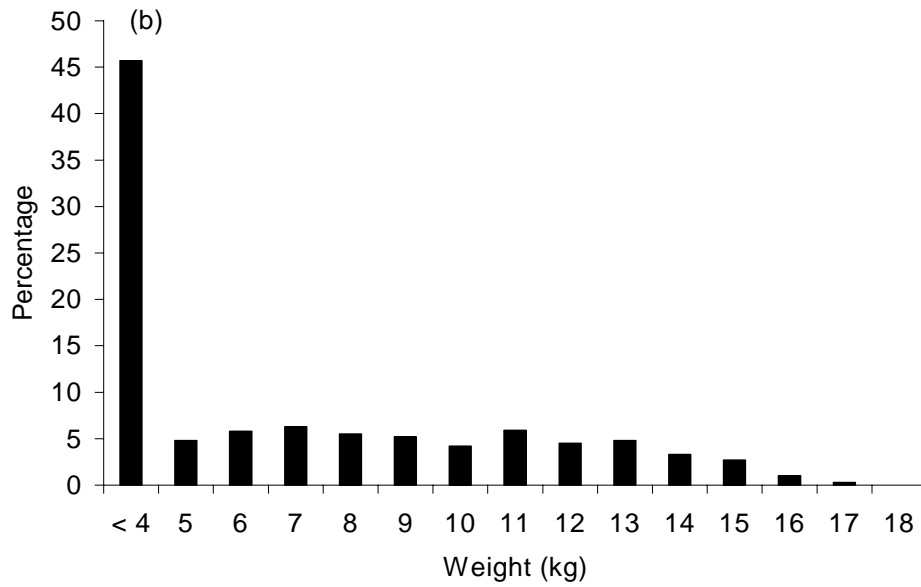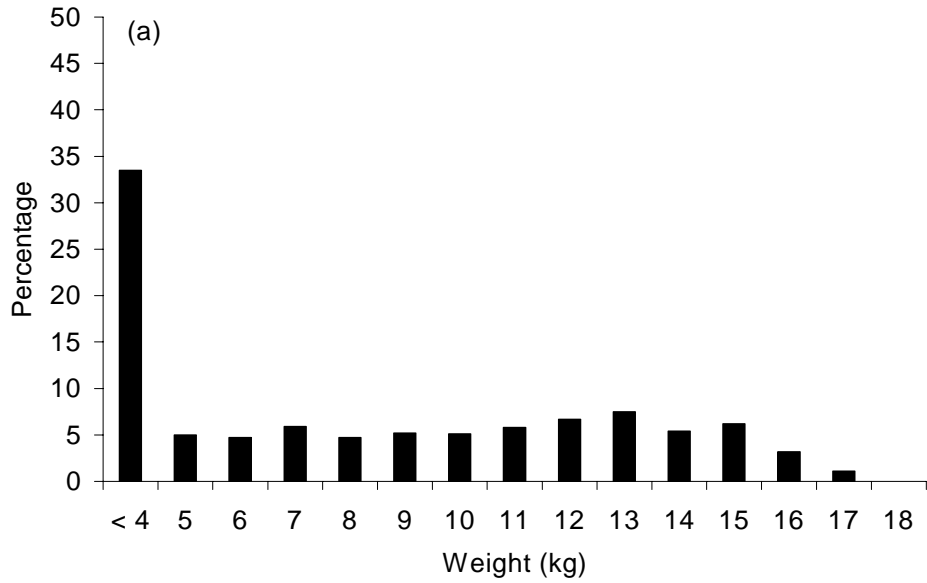
Figure 25. Chinook salmon average spawning weight at age 3 with status quo stocking for model scenarios (a) DB, and (b) DD.
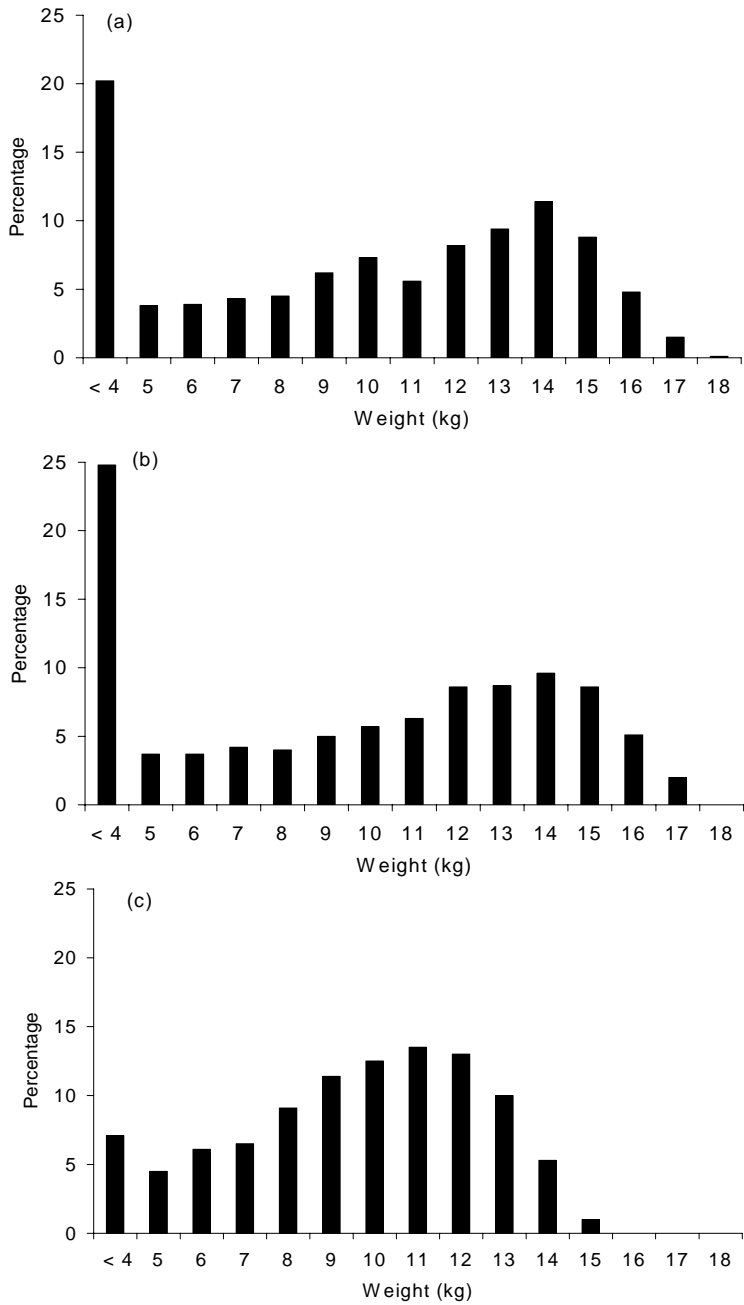
Figure 26. Chinook salmon average spawning weight at age 3 with a feedback stocking policy with one year lag for model scenarios (a) baseline, (b) FR, and (c) SR.
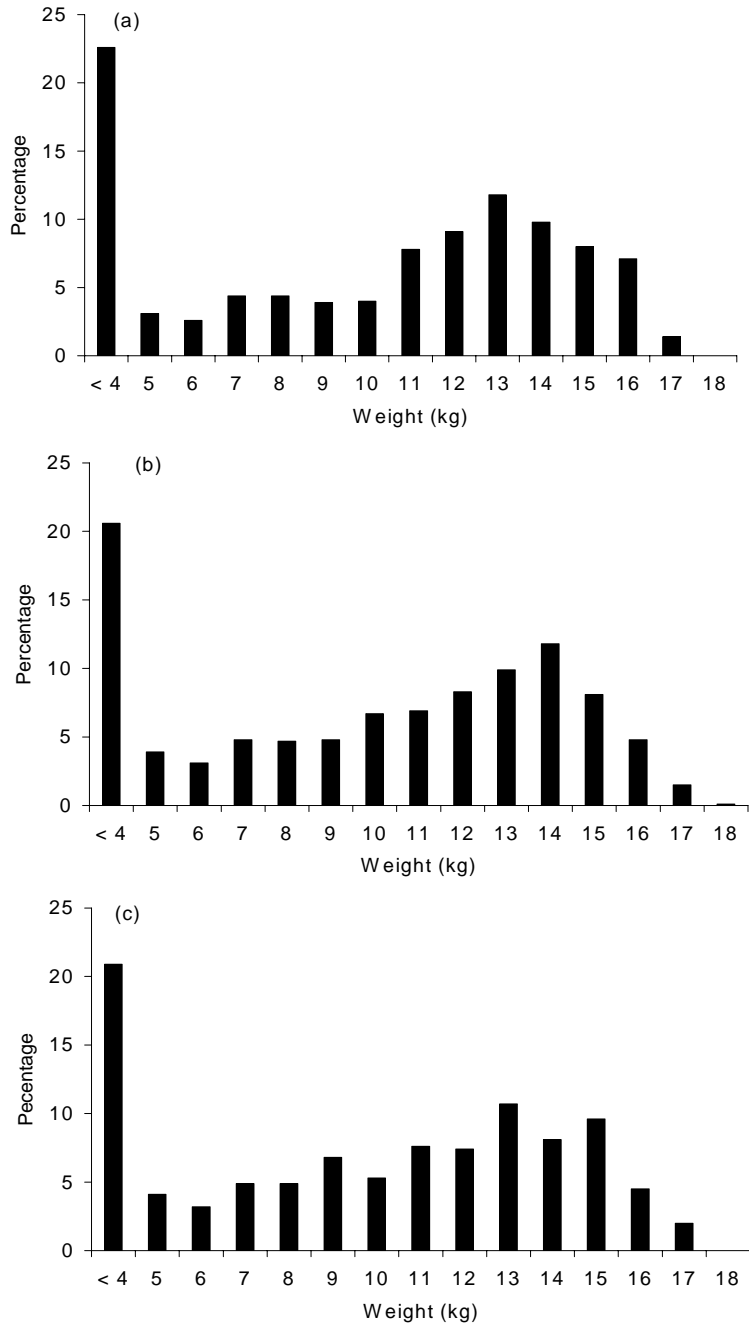
Figure 27. Chinook salmon average spawning weight at age 3 with a feedback stocking policy with one year lag for model scenarios (a) M1, (b) M2, and (c) M3.
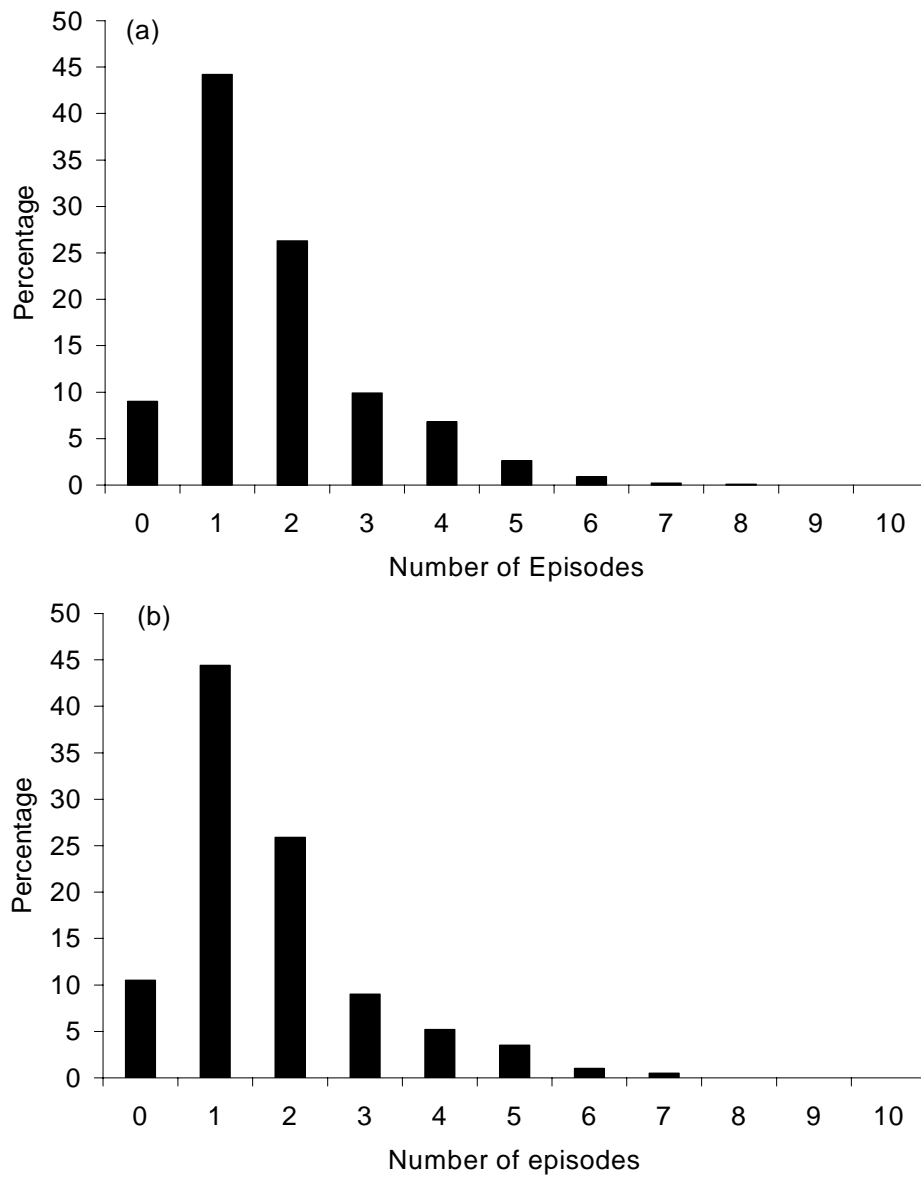
Figure 28.

Distribution of the number of mortality events in each 30 year simulation time period for the baseline scenario with (a) status quo stocking, and (b) feedback stocking with a one year lag.
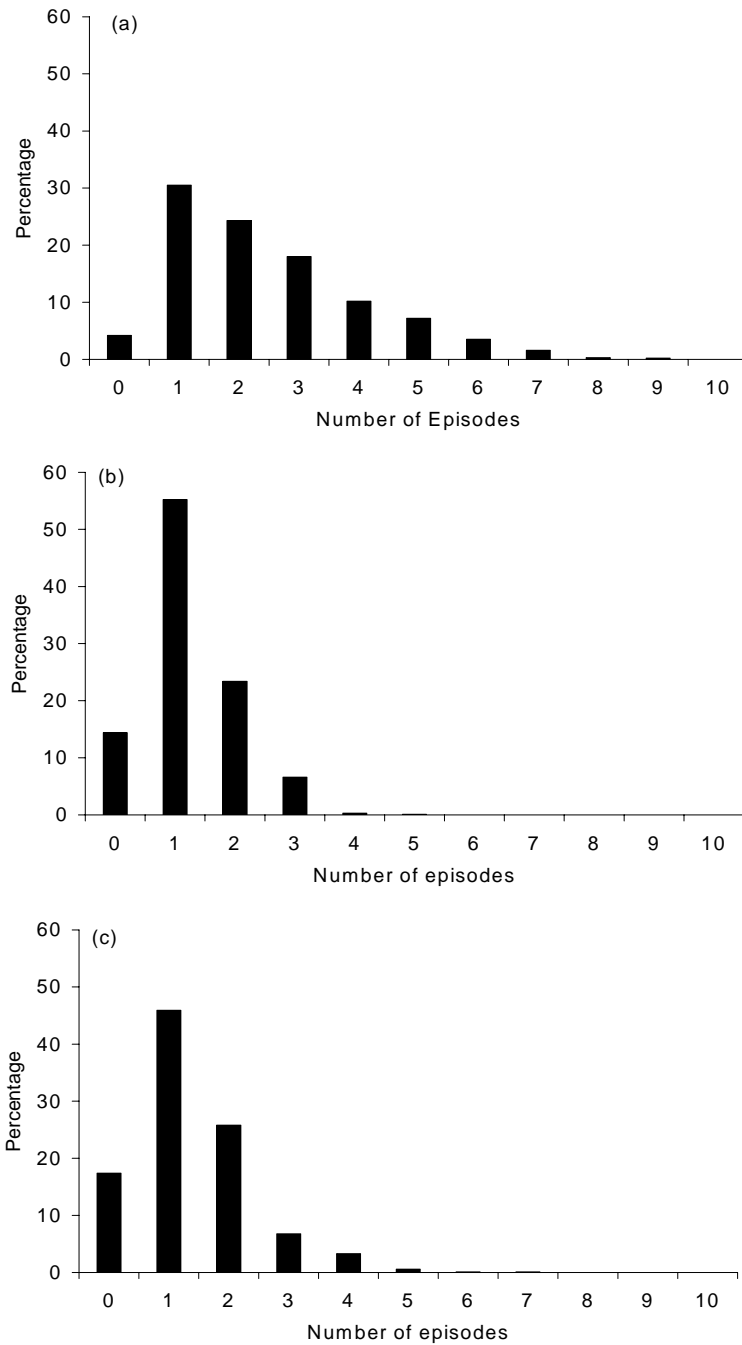
Figure 29. Distribution of the number of mortality events in each 30 year simulation time period with feedback stocking with a one year lag for model scenarios (a) M1, (b) M2, and (c) M3.

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Appendix A

Here I provide more detail on methods used to produce estimates of salmonine

dynamics, including biomass, production and consumption, which were reported by

Madenjian et al. (2002), and used to construct the prey fish population estimation model

reported in Chapter 2 and construct the simulation model presented in Chapter 3.

Overview of methods

We estimated biomass, production and consumption of the five major salmonine

species (lake trout, chinook salmon, coho salmon, steelhead, and brown trout). Age-

specific population models were parameterized and track abundance at age over time.

Together with mortality and growth rates, we used these abundance estimates to calculate

gross production over time for each species. Using estimates of gross conversion

efficiencies (GCE) from bioenergetics modeling, total consumption was calculated using

the production-conversion efficiency method (Ney 1990,1993) where the gross

production is divided by the GCE to obtain consumption estimates.

Population models

For all species except chinook salmon, we used structure of the population models

currently implemented in SIMPLE (Koonce and Jones 1994) for Lake Michigan. We

updated the parameter values in these models to incorporate the most recent information

available for each species. These population models operate on annual time steps.

Numbers at age in each year for each species except chinook salmon were calculated

from estimates of recruitment to age 1 in each year using eq. 1:

$$N_{a+1,y+1} = N_{a,y} e^{-Z_{a,y}} (1 - P_{m,a}) \qquad (1)$$

where $Z_{a,y}$ is the instantaneous mortality rate for a given age and year and $P_{m,a}$ is an age specific pulse of maturation mortality at the end of the year. Maturation mortality was assumed to be zero for all ages of lake trout. The instantaneous mortality rate was broken into mortality sources by eq. 2:

$$Z_{a,y} = M_a + L_{a,y} + F_{a,y} \tag{2}$$

where M_a is the age-specific instantaneous natural mortality rate, $L_{a,y}$ is the instantaneous sea lamprey mortality rate in a given age and year and $F_{a,y}$ is the instantaneous fishing mortality in a given age and year. Sea lamprey mortality was assumed zero for all ages and years for all species except lake trout. The details on how mortality over time was parameterized and estimated are described below.

For chinook salmon, the population was modeled in the stock assessment with two time periods within the year with a pulse fishery and a pulse of maturation mortality occurring in month seven (see Benjamin and Bence in press a). Note, this differs from the models presented in Chapters 2 and 3, where fishing mortality is assumed to occur throughout the year and maturation mortality is assumed occurs as a pulse of mortality at the end of the year. Numbers at age at the beginning of the year in the stock assessment are calculated using eq.3:

$$N_{a+1,y+1} = N_{a,y}e^{-M_{a,y}}(1 - P_{F,a,y})(1 - P_{m,a,y}) \tag{3}$$

where $P_{F,a,,y}$ and $P_{m,a,y}$ are the proportions of fish that die due to fishing or spawning. Natural mortality rates were allowed to vary over time with

$$M_{a,y} = M_a + M_{TVM,a,y} \tag{4}$$

where M_a is the baseline mortality rates and $M_{TVM,\,a,y}$ is age- and year-specific stress related mortality. The number at age at the end of the first period and at the end of the second time period, which are needed in calculations of gross production, are given by eqs. 5 and 6:

$$N_{a,y,1}^{+} = N_{a,y}e^{-7/12\,M_{a,y}} \tag{5}$$

$$N_{a,y,2} = N_{a,y,1}^{+}(1 - P_{Fa,y})(1 - P_{ma,y}) \tag{6}$$

where $N_{a,y,i}$ indicates the numbers for period i and the plus indicates the numbers are for the end rather than the beginning of the period. Maturation mortality was modeled to occur immediately after fishing mortality and before additional natural mortality. Details on how chinook salmon mortality was parameterized are described below.

The geometric average abundance at age during the year for each species for use in the estimation model presented in Chapter 2 was calculated as follows from the stock assessment estimates. For all predators except chinook salmon, the geometric mean abundance for predator j was calculated as

$$\overline{N}_{j,a,y} = \sqrt{N_{j,a,y} * N_{j,a,y}e^{-Z_{j,a,y}}} \tag{7}$$

where $N_{j,a,y}$ is the beginning of the year abundance and $Z_{j,a,y}$ is the total instantaneous mortality rate at age a in year y. For chinook salmon, fishing and

maturation mortality were modeled in the stock assessment to occur as a pulse at the end of July. Therefore, the average abundance used in the model presented in Chapter 2 was calculated as a weighted average of geometric mean abundances for the time periods before and after fishing and maturation mortality occurred.

Mortality Estimates

Lake trout

Lakewide age-specific natural mortality rates and age-and year-specific sea lamprey mortality rates were estimated from the catch-at-age models (CAA) constructed as part of the stock assessments in the 1836 treaty ceded waters, generally following methods similar to those used by Sitar (1999) and Bence and Ebener (2002). These models were management unit specific models for the Michigan waters of Lake Michigan, so the mortality rates in each area had to be combined to produce a lakewide rate. Additionally, the number of ages used in these models (15) was larger than the number of ages employed here (10), so a composite mortality rate for age 10+ lake trout was needed. First, within each area the age 10+ natural and sea lamprey mortality rate were estimated for each year by weighting the CAA model mortality estimates by the number of fish in each age class. This produced a year specific age 10+ natural and sea lamprey mortality rate in each area. Then lakewide age- and year-specific natural and sea lamprey mortality rates were estimated by taking a weighted average with each mortality rate weighted by the number of fish in that age class in each area. For sea lamprey mortality rates, these estimates represented the age- and year-specific mortality rates used in modeling lake trout abundance and consumption. For sea lamprey mortality rates prior to 1981 (the first year included in the CAA models), an average of the 1981-1983 rate was used. To estimate a lakewide average age-specific natural mortality rate,

each lakewide age- and year-specific natural mortality rate was averaged by weighting by the total number of lake trout in each age class for each year.

Using the lakewide natural and sea lamprey mortality rates, a lakewide fishery vulnerability function was estimated from the parameter estimates of the CAA models. First, the predicted catch at age for ages 1-10+ in each area in 1998 (the last year modeled in the lake assessment models used here) was calculated using the Baranov catch equation with the area specific natural mortality rates and sea lamprey mortality rates. These catches were then summed across all areas and the fishing mortality rates ($F_{a,1998}$) needed to produce the predicted total catch at age were estimated using the Baranov catch equation with the lakewide estimates of natural and sea lamprey mortality rates from above. The estimated $F_{a,1998}$ were then divided by the maximum $F_{a,1998}$ to give the vulnerability pattern.

To estimate year-specific fishing mortality on a fully vulnerable age (f_y), an age structured model was built to tune these fishing mortality rates against observed harvest. Using the number of yearling equivalents stocked the number at age in a given year could be calculated by:

$$N_{a+1,y+1} = N_{a,y} \, exp(-Z_{a,y}) \tag{8}$$

where $Z_{a,y}$ is the instantaneous mortality rate consisting of the lakewide age-specific natural mortality, lakewide age- and year-specific sea lamprey mortality and fishing mortality ($F_{a,y}$), which is the product of the year-specific fishing mortality (f_y) and the lakewide fishery vulnerability function (S_a).

Year-specific fishing mortality rates (f_y) could then be estimated by tuning the predicted total catch to the observed catch. Total lakewide harvest including commercial,

recreational, incidental and assessment catches for 1985-1998 was used as complied by the Lake Michigan Technical Committee for the Lake Michigan Committee meeting March, 2000. Since no harvest information was available prior to 1985, some assumptions were needed to describe how fishing mortality behaved prior to 1985. Sport fishing effort in Wisconsin's waters of Lake Michigan increased more or less gradually from the mid-1960s until the 1980s (Hansen et al. 1990). Hence, we assumed the sport fishing mortality rates increased linearly from zero from 1965 to 1985. Based on patterns in total mortality estimates and anecdotal descriptions in areas subject to tribal commercial fishing (IAAWG 1979; Technical Fisheries Review Committee 1992) we assumed that commercial fishing mortality was negligible prior to 1977 and increased linearly from 1978 to 1984. We note in passing that there may have been significant unreported commercial harvest in the state licensed whitefish fishery in earlier years.

From the total harvest data, we determined that in 1985 approximately 66% of the fishing mortality was recreational. Therefore, from 1985 to 1965, we allowed the recreational portion of the fishing mortality to decline linearly to zero from the 1985 value. The 1985 commercial harvest was higher than in 1986 or 1987 and we felt this high value reflected a unique event associated with the 1985 consent decree. To adjust for the above average commercial harvest in 1985, we assumed that 27% rather than 35% of the mortality in 1985 declined linearly to zero from 1985 to 1977 and then was zero for the remaining years. We based the 27% figure on the ratio of the average commercial harvest from 1985-1987 to the total harvest in 1985.

Since we required effort and catchability rather than year-specific fishing mortality rates (f_y), catchability was estimated by dividing the fishing mortality rate in 1996 by the targeted effort for salmonines in 1996 from Benjamin and Bence (in press b).

Relative effort was then generated for all other years by dividing the fishing mortality rate (f_y) by the estimated catchability.

Steelhead, Brown trout and Coho salmon

Natural mortality rates and maturation mortality for each species were taken from the CONNECT model (Rutherford 1997). To estimate vulnerability for each species, the age-specific instantaneous fishing mortality rate in CONNECT was divided by the maximum instantaneous rate for that year and the average was taken over all years. Catchability was estimated for each species by dividing the instantaneous fishing mortality in 1996 for a fully vulnerable age in CONNECT by the targeted salmonine effort in 1996 from Benjamin and Bence (in press b). Relative effort for each species from 1985-1995 was then calculated by dividing the instantaneous fishing mortality of a fully vulnerable age by the estimated catchability. Effort prior to 1985 was assumed to decline linearly to zero in 1965. To obtain relative effort for 1997-1998, relative effort estimates were tuned to produce harvest at the level of the observed lakewide total harvest, excluding the weir fishery, for 1997 -1998 (as complied by the Lake Michigan Technical Committee for the Lake Michigan Committee meeting March, 2000). Maturity schedules and mortality were implemented as in Koonce and Jones (1994) with coho salmon, brown and steelhead suffering a pulse of spawning mortality at the end of the year after all other sources of mortality had occurred. Sea lamprey mortality was assumed to be zero.

Chinook salmon

Chinook salmon population dynamics was modeled using a modified version of the age-structured model described by Benjamin and Bence (in press a) and mortality rates were either assumed known or were estimated by fitting the model to fishery data.

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Mortality components include baseline instantaneous natural morality, time-varying

natural mortality (stress related modeled from 1985-1996 to coincide with observed BKD

mortality), fishing, and maturation (spawning) mortality (eqs. 3 and 4).

Age- and year-specific natural mortality rates were assumed to occur throughout

the year at constant rates and consisted of age-specific constant baseline mortality and

age- and year-specific stress-related mortality (Benjamin and Bence in press a). Age-

specific baseline mortality rates were model inputs and were set to 0.7, 0.3, and 0.1 for

ages 0, 1, and 2-5, respectively. Stress-related mortality was modeled as the product of

an age and year parameters. Independent parameters for stress-related age-effects were

estimated for ages 0, 1, 2, and 3-5. Ages 3-5 were assumed to experience the same

natural mortality rate. Independent year-effect parameters were estimated for 1985-1996.

Fishing mortality in the stock assessment model was estimated using similar

methods to those described in Benjamin and Bence (in press a), and was modeled as an

instantaneous event occurring at the end of July in each year. Fishing mortality (F) was

defined by the assumption that the proportion surviving the pulse fishery was e^{-F} and that

F was a function of age-specific vulnerability (S_a) and year-specific fishing intensity (f_y):

$$F_{a,y} = S_{a,y} f_y. \tag{9}$$

The model estimated vulnerability for ages 0-2, while ages 3-5 were assumed to be fully

selected to the fishery. Fishing intensity was calculated by the model:

$$f_y = qE_y \cdot dev_y, \tag{10}$$

where q is a constant catchability coefficient parameter, E_y is observed fishing effort, and

$\ln(dev_y)$ is a normally-distributed process error parameter such that the sum of the log-

scale dev_y parameters equals zero. The $\ln(dev_y)$ parameters were estimated for 1985-1999. For 1967 to 1984, fishing intensity was assumed to increase linearly from zero to the 1985 level estimated by the model (IAAWG 1979). Fishery harvest is the proportion of the population abundance remaining at the end of July that dies from fishing, as described in Benjamin and Bence (in press a). Fishing mortality in the simulation model presented in Chapter 3 was assumed to occur throughout the year and the instantaneous fishing rate, F, for each age in each year was calculated by eq. 9.

Mature chinook salmon will enter streams to spawn, and will inevitably die during or after the spawning run. Observed data from the recreational fishery and the spawning weirs allowed us to separately estimate maturation (spawning) mortality. Similar to Benjamin and Bence (in press a), maturation mortality in the stock assessment was modeled as an instantaneous event occurring immediately after fishing mortality and before additional natural mortality. Age-specific maturation was estimated independently for ages 1-4. Age-0 fish were assumed to have no mortality due to spawning, while all age 5 fish surviving to the time of spawning run were assumed to die at that time. 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. From 1985 through 1999, maturity was assumed to be a logistic function of weight at age during the summer- fall:

$$P_{m,a,y} = \frac{1}{1 + e^{-(\beta_{0,a} + \beta_{1,a} W_{HAR,a,y})}} \tag{11}$$

Note that the parameters of this function ($\beta_{0,a}$ and $\beta_{1,a}$) were age-specific, so the logistic function varied among ages. The source of summer-/fall weight at age data ($W_{HAR,a,y}$) is described below ("Weight at age and Growth"). For years prior to 1981, a constant maturity schedule was used based on results reported by Stewart (1980): ($P_{m,a} = 0$, 0.12, 0.33, 1.0, 1.0, 1.0 for ages 0 through 5 respectively). From 1981 through 1984 the maturity at each age was linearly interpolated between the value assumed for 1980 and the value estimated for 1985. Th same maturation model (eq. 11) was used in the simulation model presented in Chapter 3 but the timing of the maturation mortality pulse was moved to the end of the year.

The stock assessment model was fit to estimates from observed fishery data and included: (1) annual total harvest from 1985-1999, (2) annual fishing effort directed at chinook salmon from 1985-1999, (3) age-frequency compositions of the annual total harvest from 1985-1997, (4) age-frequency compositions of the annual total harvest of mature fish from 1985-1997, and (5) age-frequency compositions of the annual weir harvest of fish captured during the spawning run from 1985-1996. Parameters were adjusted while fitting the model in order to best match model estimates to observed fishery data, using a maximum likelihood approach (see Benjamin and Bence in press a).

Recruitment

Recruitment was quantified as the number of individuals (or smolt-equivalents) entering the lake fishery, and equaled the sum of hatchery and naturally-reproduced production. Recruitment was defined as age 0 for chinook salmon and as age 1 for other species. Records of hatchery plants by all agencies were summarized by Holey (1995) and Benjamin (1998). We used this information and unpublished updated summaries (USFWS, Green Bay, WI). Natural reproduction of chinook and coho salmon was

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estimated from regression analysis (Smith, K.D., Michigan Department of Natural

Resources, unpublished manuscript), stream surveys (Carl 1980), weir harvest records

(e.g., Pecor 1992; Hay 1992), and by the ratio of wild to hatchery adults sampled in the

lake (Patriarche 1980; Hesse 1994) or in tributary streams (MDNR unpublished data),

assuming equal survival between hatchery and wild fish from smolt-to-adult. Numbers

of steelhead smolt-equivalents were estimated by Rand et al. (1993) for 1975 to 1990,

and then updated. Brown trout (Rutherford 1997) and lake trout (Holey et al. 1995) were

assumed to have no natural reproduction.

To estimate numbers of hatchery smolt-equivalents for all species, actual numbers

of fall fingerlings or yearlings stocked were adjusted for survival from stream to the lake,

or for survival immediately post-stocking. These adjustments and survival rates varied

by species and size of fish.   For lake trout, stocked numbers of yearling equivalents were

calculated from stocking information provided by the USFWS Great Lakes by R. Elliott

(GBFRO) by adding the number of yearling stocked in a given year and the adjusted

numbers of fingerlings stocked in the previous year. Fingerlings were adjusted by

multiplying by 0.4. Yearling lake trout were assumed to have 100% survival during

stocking. Stocking numbers (in yearling equivalents)for steelhead, coho salmon and

brown trout for 1965-1996 (except brown trout, see below) were taken from CONNECT.

Stocking numbers for 1997 were obtained from Jory Jonas (Michigan Department of

Natural Resources, Charlevoix, Michigan) as compiled for the State of the Lake and for

1998 from the summary of stocking in Lake Michigan distributed at the Lake Michigan

Lake Committee Meeting (March 2000).   For steelhead, the numbers stocked were

multiplied by 0.5 and wild recruits were added to correspond with the treatment of stocking for the 1990's in the CONNECT steelhead model. For coho salmon, the number stocked were multiplied by 0.5 to estimate yearling equivalents stocked and wild production, 5% of the yearling equivalents stocked, was added to correspond with the treatment of stocking in the 1990's in the CONNECT coho model. For brown trout, stocking numbers of fingerlings and yearlings from Benjamin and Bence (in press b) from 1965-1996 were used to estimate stocked numbers of yearling equivalents. Stocked numbers of yearling equivalents for a given year was estimated by the sum of the number of fingerlings stocked in the year before with 25% survival and the number of yearlings stocked for that year. Stocking in 1997 and 1998 was assumed to have the same proportions of yearlings and fingerlings as in 1996 (46% fingerlings, 54% yearlings), and the number of yearling equivalents stocked was estimated as above. Yearling brown trout were assumed to have 100% survival during stocking. Recruitment of chinook salmon to age 0 was a model input calculated as the sum of estimated wild smolts and stocked fingerlings multiplied by an assumed post-stocking survival of 0.75. Stocked fingerling data were obtained from Benjamin and Bence (in press b) and updated for 1997-1999 using the same source as for other species. Estimated wild smolts were obtained from CONNECT.

Weight at age and growth

For coho salmon, mean weight at age was determined from samples of harvest and at weirs. There were distinct modes separating fish in their first (age 1) and second (age 2) lake year. Weight at age for the harvest (used in tuning models against observed

harvest biomass) was estimated as the average weight of a harvested fish (averaged over reporting agencies and weighted by the number of fish harvested). Differences in weights of harvested fish in different jurisdictions reflect the seasonal progression of the fishery as coho salmon migrate around the lake, and weight at age for the start and end of the year for age 2 fish was extrapolated from these patterns.

For chinook salmon, weight-at-age (ages 1 and above) in the 1960s and most of the 1970s is based on observed mean weight at age reported for spawning run fish by Rybicki (1973). Weight at age starting in 1985 is based on mean weight at age from biological samples of sport harvested fish in Michigan (unpublished Michigan DNR data). Standard harvest/spawning weights in the modeling calculations were taken as harvest weights for ages 1-2 and spawning run weights for ages 3 and above. Conversion was based on ratios calculated from unpublished Michigan DNR weights of both types in the same years. Estimation of weight-at-annulus formation from harvest/spawning weights was based on the proportion of annual growth through harvest, estimated from backcalculated weights reported by Wesley (1996). Age 0 fall weight was assumed constant and was based on the assumption that the same proportion of annual growth occurs by fall for age 0 as was observed for age 1 by Wesley (1996), and average age 1 growth. Weight at age for the period between 1978 and 1985 was interpolated between values used in 1978 and 1985.

Lake trout weight at age was based on observed weight at age in Michigan DNR spring surveys. These surveys provided no evidence for large changes in growth over time, and weight at age was assumed constant over time. Fish in the southern part of the

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lake grew somewhat faster and weight at age schedules for the north and south were combined, weighted by estimates of abundance in different areas of the lake. To obtain weight at age for the age 10+ age group, all fish older than age 10 were grouped together and the average weight was calculated using a weighted average with weighting factors used in the average being an increasing power of 0.5 for increasing ages (i.e., the weight at age 11, 12, 13 ... had the corresponding weighting factors of 1, 0.5, 0.25, ...). This procedure assumes that each subsequent age in the 10+ group was half as abundant as the previous age.

Steelhead length-at-age were obtained from back-calculated growth curves (Seelbach 1993), and weight at age was obtained from a length-weight relationship. For steelhead, all fish older than age 5 were grouped together and the average weight for the 5+ group was calculated using the same weighted average procedure used for lake trout. Data on weight at age for brown trout were available from samples from Wisconsin and Michigan DNR creel surveys (Michigan and Wisconsin DNR unpublished data). Weight at age was assumed constant over time.

Gross conversion efficiency

For lake trout, chinook salmon and coho salmon, bioenergetics models based on Stewart and Ibarra (1991) were used to estimate individual gross conversion efficiency at age for each species. Temperature, energy density, and diet information (1978-1981) from Stewart and Ibarra (1991) were used to estimate gross production and consumption by age for each species using weight at age schedules described above. Weight at

annulus formation for age 0 chinook was assumed to be 4.54 g as in Stewart and Ibarra (1991). Mean weights at harvest were used as ending weights for the last age of chinook and coho while a weighted average of the mean weight at annulus formation of age 11+ lake trout was used as the end weight for age 10+. Weighting factors for this 11+ average were assigned as increasing powers of 0.5 as previously described for the 10+ group, such that age 11 was weighted 1, age 12 weighted 0.5 etc.

The lake trout model was extended to include age 10 lake trout by assuming the diet of age 10 lake trout was the same as age 9 lake trout. Spawning losses for lake trout were incorporated as in Stewart et al. (1983). The chinook model was extended in a similar manner to include age 4 by extending the Stewart and Ibarra (1991) age 3 chinook model to a full 365 day year by assuming that the diet remained unchanged after day 214 and by assuming age 4 chinook had the same diet as age 3 chinook, and spawned and died on day 214. To account for the declining growth of chinook salmon during the mid 1980s, two sets of GCEs were estimated using the same diet information as above (1978-1981) but using two weight schedules, one that applied prior to 1979 and one that was the average weight at age observed during 1985-1999. Because of the earlier maturity observed in the 1970s GCE was not estimated or used for ages 4 or 5 prior to 1979. During 1979 through 1984 the same GCE was used for these ages as was estimated for the 1985-1999 period. For ages 1-3 GCE was interpolated linearly from the value assumed for 1978 and the one assumed for 1985. Because we assumed that fall weight at age zero was constant, the same GCE was used throughout the assessment period for that age.

For steelhead and brown trout, no species specific bioenergetics models for Lake Michigan were available. Therefore, the average gross conversion efficiencies were calculated from GCEs of similar sized lake trout and chinook. Using the weight at age at annulus formation schedule in CONNECT for each species, the GCE for a similar sized lake trout and chinook salmon were averaged together to produce a GCE by age for each species. For age 5+ steelhead, a weighted average, as described above for lake trout, was taken using the weight at annulus formation for all steelhead age 5 and above.

Diet Composition

We estimated consumption of small alewife, large alewife (size categories as defined by Stewart et al. 1981) and other fish using diet composition information summarized by Rand et al. (1993), Stewart et al. (1981) and Stewart and Ibarra (1991), and Elliott (unpublished data; U. S. Fish and Wildlife Service, Green Bay, WI) for chinook, coho and lake trout and steelhead. We assumed brown trout to have similar diets as steelhead.

For coho salmon, lake trout, and steelhead we calculated a weighted (by number of days in each seasonal period) average percent (by weight) contribution to diet based on information reported by Stewart and Ibarra (1991), Stewart et al. (1981), and Rand et al. (1993). For chinook salmon, we calculated a weighted average percent for each year (or time period since diet information for 1981-1983 and 1994-1995 was available in pooled form) because of the more comprehensive sampling for this species and because it is the dominant consumer of alewife. Before 1981, the first year with diet information, the 1981-1983 diet composition was used. In 1993 and after 1995 the 1994-1995 diet

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composition was used. Diet composition from 1989-1992, when no data were available
were interpolated between 1988 and the assumed diet for 1993.

Consumption Estimates

   Lake trout, Brown trout, Steelhead, and Coho salmon

   Biomass at age was calculated using the weight at age at annulus formation.
Consumption can be calculated from estimates of gross production per year and GCE.
Gross production each year is estimated as the sum of yield, production lost to death, and
change in standing stock biomass. Since constant instantaneous fishing mortality rates
were assumed, production at age lost to death and yield in each year can be calculated
simultaneously by

$$D_{a,y} = Z_{a,y} * N_{a,y} * W_a * (1/(G_a - Z_{a,y}) * [\exp(G_a - Z_{a,y}) - 1] \qquad (12)$$

where G_a is the instantaneous growth rate, estimated by

$$G_a = \ln(W_{a+1}/W_a) \qquad (13)$$

Instantaneous growth rate can not be estimated for the last age so species specific
assumptions were made for G_a of the last age group. For brown trout, steelhead and lake
trout, G_a was assumed to be zero for the last age group. For coho salmon, which grow
considerably during their last year, G_a was estimated using the weight at harvest
averaged over all years for age 2 coho as W_{a+1}. For coho salmon, brown and steelhead,
the production lost to spawning mortality was then estimated by

$$R_{a,y} = N_{a,y} * \exp(-Z_{a,y}) * W_{a+1} * P_m \qquad (14)$$

Weight at the next age was used to estimate biomass lost because spawning was assumed
to have occurred after all growth during the year was completed. For lake trout, no

biomass was lost due to spawning. For the last age of coho and brown trout, production

lost to spawning was not added because all fish were assumed to die spawning.

Total gross production is then the sum of $D_{a,y}$, $R_{a,y}$ and the change in standing

stock which can be estimated by $B_{a+1,y+1}-B_{a,y}$. For the last age group, $B_{a+1,y+1}$ was

estimated as

$$B_{a+1,y+1} = B_{a,y}*\exp(G_a-Z_{a,y}) \tag{15}$$

This age-specific production was then divided by the age-specific GCE and summed over

all ages to obtain total consumption. Year-specific consumption of each prey type was

estimated by multiplying the year-specific proportion of each prey type in the diet by the

total consumption for each year.

Chinook Salmon

Production was estimated using an approach similar to the methods described

above for the other salmonines, with the added complication that harvest and maturation

were modeled as a pulse 7/12ths of the way through the year. Production was estimated

as a function of fishery yield, production lost to natural in-lake mortality, production lost

to spawning mortality, and change in biomass of the standing stock:

$$X_{a,y} = Y_{a,y} + D_{a,y} + R_{a,y} + B_{a+1,y+1} - B_{a,y} \tag{16}$$

Yield was estimated as the product of harvest mean weight at age at harvest

($W_{HAR,a,y}$)and harvest-at-age ($C_{a,y}$):

$$Y_{a,y} = W_{HAR,a,y}C_{a,y}. \tag{17}$$

Because fishery harvest and spawning mortality were modeled as instantaneous events

occurring 7/12ths of the way through the year, production lost to natural in-lake mortality

was first estimated for the first 7 months prior to fishing and spawning, and then for the last 5 months beginning immediately after fishing and spawning:

$$D_{a,y} = M_{a,y} N_{a,y} W_{ANN,a,y} \left(1/\left(G_{a,y} - M_{a,y} \right) \right) \left(e^{\left(G_{a,y} - M_{a,y} \right)} - 1 \right) , \qquad (18)$$

where $N_{a,y}$ was used for the first 7 months, and adjusted for the last 5 months to account for natural mortality, fishing, and spawning mortality from earlier in the year. For the first 7 month period, the instantaneous growth rate ($G_{a,y}$) was calculated as:

$$G_{a,y} = Ln \left(W_{HAR,a,y} / W_{ANN,a,y} \right) / \left(7/12 \right) , \qquad (19)$$

where $W_{HAR,a,y}$ is the mean weight at age at harvest, and $W_{ANN,a,y}$ is the mean weight at age at annulus formation, defined as the start of the year for age a fish. For the last 5 month period, $G_{a,y}$ was calculated as:

$$G_{a,y} = Ln \left(W_{ANN,a+1,y+1} / W_{HAR,a,y} \right) / \left(1 - 7/12 \right) . \qquad (20)$$

The estimate of production lost to spawning mortality ($R_{a,,y}$) was modified from equation 14 to account for the difference in the way fishing mortality was estimated, such that:

$$R_{a,y} = N_{a,y} e^{\left(-M_{a,y} \right)} \left(1 - P_{F,a,y} \right) W_{HAR,a,y} P_{m,a,y} \qquad (21)$$

As for other salmonines, age-specific production ($X_{a,y}$) was divided by age-specific gross

conversion efficiency (GCE) to obtain estimates of age-specific consumption. Consumption was summed over ages to obtain annual totals. Year-specific consumption of each prey type was estimated by multiplying the year-specific proportion of each prey type in the diet by the total consumption for each year.

Below are the five .dat files used in fitting the parameter estimation model

presented in Chapter 2. They contain all the data used in the likelihood equations along

with all the other information assumed known.

Awbl.dat

```
# DATA FOR LAKE MICHIGAN ALEWIFE AND BLOATER CAA
# BY EMILY B. SZALAI  LAST MODIFIED 7/13/01
# First year of trawl survey
1962
# Last year of trawl survey
1999
# First year of predator abundance data
1965
# First year of hydroacoustic survey data
1993
# Last year of Hydroacoustic survey data
1996
# First alewife age
0
# Last alewife age
6
# First bloater age
0
# Last bloater age
7
# first bloater age in trawl survey
0
# last bloater age in trawl survey
7
# number of rainbow smelt ages 0-5
6
# number of slimy sculpin ages 0-5
6
# number of deep water sculpin ages 0-5
6
# first lake trout age
1
# last lake trout age
10
# first coho age
1
# last coho age
```

2
first chinook age
0
last chinook age
5
first rainbow trout age
1
last rainbow trout age
5
first brown trout age
1
last brown trout age
5
#
#Habitat volume of Lake Michigan
4800

Altprey.dat

#Data for alewife-bloater CAA Model by Emily B. Szalai
#Alternative prey biomass from swept-area estimates provided by Guy F. 12/99
#Updated 7/16/2001 For 1998 used average of 94-99
#
Biomass(kg) of small (< 90 mm)rainbow smelt by year
For years 1965-1972 used avgerage biomass estimate from 1973-1977
477200 477200 477200 477200 477200 477200 477200
477200 224000 282000 788000 991000 101000 970000
659000 3603000 2100000 1948000 885000 920000 1620000
1281000 1211000 4168000 2518000 180000 1190000 944000
1101000 360000 375000 629000 133000 456600 786000
Biomass (kg) of large (> 90 mm) rainbow smelt by year
For years 1965-1972 used avgerage biomass estimate from 1973-1977
10666400 10666400 10666400 10666400 10666400 10666400 10666400
10666400 10894000 9560000 13437000 9609000 9742000 12585000
13884000 15717000 24397000 29246000 18970000 9983000 15168000
16731000 14975000 24265000 9323000 11596000 19850000 17741000
16879000 7802000 4058000 6104000 3726000 5205200 4336000
Biomass(kg) of slimy sculpin by year
For years 1965-1972 used avgerage biomass estimate from 1973-1977
3073400 3073400 3073400 3073400 3073400 3073400 3073400
3073400 962000 3007000 4537000 5487000 1374000 866000
1568000 1366000 1720000 397000 564000 214000 295000
259000 698000 850000 513000 315000 1314000 1220000 914000
1566000 1537000 2867000 2253000 2559600 4575000
Biomass(kg) of deepwater sculpin by year
For years 1965-1972 used avgerage biomass estimate from 1973-1974

144

8473000 8473000 8473000 8473000 8473000 8473000 8473000 8473000
5612000 11334000 30767000 33901000 26970000 30928000
50432000 85352000 66965000 49663000 98550000 72210000 85173000 58132000
91194000 63147000 35108000 72281000 31438000 40638000 34188000
21505000 27686000 43991000 49513000 38011200 47361000

Awblerror.dat

#Data for alewife-bloater CAA Model by Emily B. Szalai
#Estimated errors in trawl and hysroacoustic survey data
#Updated 7/13/01
#Estimated standard error of alewife year effects for trawl data 1962-1999
1.736417   1.195118
1.629004   1.122164
1.535537   1.058777
1.535537   1.058777
1.620708   1.116983
0.999023   0.688154
0.972835   0.670262
0.97768   0.673572
0.967961   0.666915
0.96323   0.663672
0.946262   0.65205
0.824182   0.567752
0.816109   0.562196
0.818989   0.564292
0.840549   0.579152
0.840708   0.57914
0.820051   0.565098
0.821836   0.566327
0.825017   0.568315
0.823426   0.567177
0.865093   0.595715
0.836531   0.575982
0.83822   0.577129
0.834897   0.574867
0.838558   0.57737
0.834724   0.574751
0.834782   0.574812
0.847297   0.583298
0.870009   0.598967
0.86267   0.59398
0.872408   0.600609
0.888822   0.611767
0.894472   0.615579
0.923623   0.635743
0.907138   0.624221

```
0.891516        0.61361
9999            9999
9999            9999
#
#Estimated standard errors of bloater year effects for trawl data 1962-1999
1.278789 1.451733 1.328923 1.382948 1.360281 1.404705 1.463497 1.497112
1.198713 1.358631 1.362316 1.417823 1.394716 1.438675 1.498968 1.533402
1.134043 1.279884 1.257983 1.309913 1.289666 1.336069 1.390992 1.420699
1.134043 1.279884 1.257983 1.309913 1.289666 1.336069 1.390992 1.420699
1.198713 1.358631 1.362316 1.417823 1.394716 1.438675 1.498968 1.533402
0.723792 0.820982 0.782276 0.813903 0.800374 0.825571 0.860283 0.880398
0.71193 0.806663 0.767489 0.798738 0.785763 0.81163 0.845507 0.864717
0.71193 0.806663 0.767489 0.798738 0.785763 0.81163 0.845507 0.864717
0.708183 0.802138 0.761322 0.792382 0.779578 0.805553 0.839108 0.858031
0.704555 0.797762 0.755399 0.78627 0.773627 0.799699 0.832947 0.851598
0.691602 0.782101 0.734453 0.764594 0.752506 0.778979 0.811158 0.828891
0.598259 0.678163 0.594073 0.617971 0.607721 0.627899 0.654114 0.66914
0.593316 0.672268 0.588036 0.611843 0.601843 0.622374 0.64823 0.662835
0.594566 0.673843 0.586751 0.61033 0.60029 0.620582 0.646399 0.661057
0.609389 0.690262 0.605899 0.630327 0.620043 0.641288 0.667912 0.682923
0.600446 0.680573 0.579361 0.602528 0.592524 0.612529 0.638049 0.65264
0.595643 0.674872 0.579114 0.602288 0.592386 0.612649 0.638109 0.65254
0.598099 0.677799 0.580879 0.604065 0.594112 0.614359 0.639909 0.654422
0.600317 0.680448 0.58585 0.609404 0.599385 0.619764 0.64554 0.660168
0.597934 0.677592 0.580958 0.604342 0.594402 0.614686 0.640238 0.654731
0.623957 0.70753 0.601987 0.626274 0.615939 0.636798 0.663299 0.678377
0.606486 0.687786 0.587166 0.610986 0.600919 0.621351 0.647211 0.661916
0.606486 0.687786 0.587166 0.610986 0.600919 0.621351 0.647211 0.661916
0.606486 0.687786 0.587166 0.610986 0.600919 0.621351 0.647211 0.661916
0.606486 0.687786 0.587166 0.610986 0.600919 0.621351 0.647211 0.661916
0.606486 0.687786 0.587166 0.610986 0.600919 0.621351 0.647211 0.661916
0.606367 0.687625 0.58705 0.610842 0.600779 0.621198 0.647049 0.661745
0.616007 0.699201 0.594001 0.617952 0.607523 0.627375 0.653703 0.669033
0.629085 0.713666 0.611825 0.636657 0.626174 0.64737 0.674329 0.689667
0.625535 0.709347 0.605609 0.630181 0.6198 0.640892 0.667565 0.68273
0.627303 0.711469 0.607271 0.631896 0.621466 0.642546 0.669306 0.68455
0.625535 0.709347 0.605609 0.630181 0.6198 0.640892 0.667565 0.68273
0.625535 0.709347 0.605609 0.630181 0.6198 0.640892 0.667565 0.68273
0.672716 0.764304 0.6417 0.667514 0.656165 0.677527 0.705974 0.722608
0.642627 0.729917 0.613349 0.638041 0.627229 0.647761 0.67493 0.690767
0.642627 0.729917 0.613349 0.638041 0.627229 0.647761 0.67493 0.690767
#
#CV  for adult alewife hydroacoustic estimates
 0.40 0.25 0.25 0.32
#CV for young of the year alewife hydroacoustic estimates
 0.36 0.45 0.15 0.54
# CV for bloater hydroacoustic estimates
```

0.16 0.29 0.27 0.20

Awblinit.dat

#Initial parameter values for alewife-bloater CAA model
Updated 2/23/2003
#log_q for adult alewife hydro survey
0
#log_q for yoy alewife hydro survey
0
#log_q for bloater hydro survey
0
#log_init_pop_aw
#21.47 20.03 21.79 21.33 16.65 16.65
#log_init_pop_bl
11.04 11.16 17.03 16.92 19.21 19.21 19.21
#log_init_recruit_aw
25 25 25 25 25 25 25 25 25 25 25 25 25 25 25 25 25 25 25 25 25 25 25 25 25 25 25 25 25
25 25 25 25 25 25 25 25
#log_init_recruit_bl
20 20 20 20 20 20 20 20 20 20 20 20 20 20 20 20 20 20 20 20 20 20 20 20 20 20 20 20 20
20 20 20 20 20 20 20 20

Funcresp.dat

Data for alewife-CAA Model by Emily B. Smith
Parameters for functional response.
All from SIMPLE And SCOL II (GCE)
Updated 12/13/02
#
search constant per predator body length
1.98E-6
#
HABITAT OVERLAPS FROM   SIMPLE
#
ALEWIFE-OVERLAP FOR AGE 6+ SET EQUAL TO AGE 5 FROM SIMPLE
Habitat overlaps for alewife by age with   lake   trout
1 1 1 1 1 1 1
Habitat overlaps for alewife by   age   with   coho
1 1 1 1 1 1 1
Habitat overlaps for   alewife by   age   with   chinook
1 1 1 1 1 1 1
Habitat overlaps for   alewife by   age   with   rainbow trout
1 1 1 1 1 1 1
Habitat overlaps for   alewife by   age   with   brown   trout
0.7 1 0.8 0.8 0.8 0.8 0.8
#

BLOATER - OVERLAPS FOR AGE 6+ SET EQUAL TO AGE 5
Habitat overlaps for bloater by age with lake trout
1 1 1 1 1 1 1 1
Habitat overlaps for bloater by age with coho
0.1 0.1 0 0 0 0 0 0
Habitat overlaps for bloater by age with chinook
0.1 0.1 0 0 0 0 0 0
Habitat overlaps for bloater by age with rainbow trout
0.1 0.1 0 0 0 0 0 0
Habitat overlaps for bloater by age with brown trout
0.1 0.1 0.1 0.1 0.1 0.1 0.1 0.1
#
RAINBOW SMELT
Habitat overlaps for rainbow smelt by age with lake trout
0 0.5 1 1 1 1
Habitat overlaps for rainbow smelt by age with coho
1 0.6 0.6 0.6 0.6 0.6
Habitat overlaps for rainbow smelt by age with chinook
1 1 1 1 1 1
Habitat overlaps for rainbow smelt by age with rainbow trout
1 0.75 0.75 0.75 0.75 0.75
Habitat overlaps for rainbow smelt by age with brown trout
1 0.75 0.75 0.75 0.75 0.75

#
SLIMY SCULPIN
Habitat overlaps for slimy sculpin by age with lake trout
1 1 1 1 1 1
Habitat overlaps for slimy sculpin by age with coho
0.1 0.1 0.1 0.1 0.1 0.1
Habitat overlaps for slimy sculpin by age with chinook
#0.1 0.1 0.1 0.1 0.1 0.1
Habitat overlaps for slimy sculpin by age with rainbow trout
0.1 0.1 0.1 0.1 0.1 0.1
Habitat overlaps for slimy sculpin by age with brown trout
0.2 0.2 0.2 0.2 0.2 0.2
#
DEEPWATER SCULPIN
Habitat overlaps for deepwater sculpin by age with lake trout
0.3 0.3 0.3 0.3 0.3 0.3
Habitat overlaps for deepwater sculpin by age with coho
0 0 0 0 0 0
Habitat overlaps for deepwater sculpin by age with chinook
0 0 0 0 0 0
Habitat overlaps for deepwater sculpin by age with rainbow trout
0 0 0 0 0 0

Habitat overlaps for deepwater sculpin by age with brown trout
0 0 0 0 0 0
#
#
MAXIMUM GCE's FROM SCOL II
lake trout
0.205037 0.19238 0.161662 0.143462 0.144346 0.128036 0.115909 0.104652 0.095365
0.084538
coho
0.302 0.234
chinook (Max. GCE's from Jim's CAA model)
0.2707 0.2786 0.1877 0.1037 0.0369 0.0369
rainbow trout
0.237766 0.221432 0.212774 0.154487 0.144215
brown trout
0.2314372 0.221432 0.212774 0.154487 0.154487
Gmax(kg) for CHS
0.5815 2.5896 5.0175 5.717 4.01 0.01
consumption by predators from SCOL II
599.6469
3332.011
9027.261
15248.91
23718.82
34322.44
39205.89
47507.23
59576.74
68551.65
75099.37
83745.64
89890.04
89565.63
85412.86
91588.05
91794.15
94391.64
90299.26
92598.92
92568.5
86332.33
99031.48
82531.94
81188.48
84149.73
91114.74
91238.23

149

81015.6
79512.46
101370.2
120014.2
95729.01
120295.5
120295.5
Proportion of small alewife, large alewife, and other fish in consumption from SCOL II

0.30609877   0.039344   0.654557
0.27163269   0.175473   0.552894
0.2844447   0.239608   0.475947
0.31737736   0.251924   0.430699
0.26314987   0.333768   0.403082
0.24291606   0.396242   0.360842
0.27500902   0.367528   0.357463
0.26159143   0.401525   0.336883
0.23648702   0.450722   0.312791
0.26193975   0.42448   0.313581
0.26961594   0.431732   0.298652
0.25632055   0.454864   0.288816
0.23758517   0.48366   0.278755
0.23963457   0.483218   0.277148
0.28125929   0.419997   0.298744
0.27335491   0.437747   0.288898
0.27440399   0.458109   0.267487
0.27320033   0.448743   0.278057
0.35443351   0.326868   0.318698
0.29684841   0.396998   0.306154
0.36227697   0.330637   0.307086
0.3752112   0.352151   0.272638
0.43588714   0.349209   0.214904
0.42589115   0.340368   0.233741
0.39572388   0.367143   0.237133
0.36483412   0.396304   0.238862
0.32590392   0.443795   0.230301
0.28962396   0.477718   0.232658
0.26797463   0.48078   0.251246
0.26865688   0.476627   0.254716
0.24985764   0.520116   0.230026
0.23041592   0.556449   0.213135
0.25087924   0.509482   0.239639
0.2171374   0.57993   0.202933
0.2171374   0.57993   0.202933
Proportion of consumption from chinook and other predators
0.144736842 0.526315789 0.328947368
0.034980535 0.637747446 0.327272019

0.48990813   0.292420216   0.217671654
0.578734499   0.219821306   0.201444195
0.435767733   0.330701123   0.233531144
0.507276683   0.278331922   0.214391395
0.59686009   0.208172247   0.194967663
0.554063588   0.240784695   0.205151717
0.54022633   0.251899335   0.207874335
0.572158747   0.228239685   0.199601568
0.623988955   0.188499222   0.187511824
0.617688883   0.191410492   0.190900625
0.513785974   0.271930907   0.214283119
0.536917821   0.254231038   0.208851141
0.564917283   0.25470048   0.180382236
0.534548034   0.252260345   0.213191622
0.32791402   0.393398253   0.278687728
0.457490147   0.287065202   0.255444651
0.344643068   0.38991063   0.265446302
0.387662449   0.408983869   0.203353682
0.376866305   0.502845828   0.120287867
0.374889423   0.511555509   0.113555067
0.415864292   0.45072031   0.133415397
0.46756353   0.388710063   0.143726407
0.542749741   0.322447331   0.134802928
0.612762391   0.259282833   0.127954776
0.656281678   0.209206369   0.134511952
0.655369883   0.209782983   0.134847134
0.677835275   0.194374602   0.127790124
0.705107526   0.174175813   0.120716661
0.68015993   0.190343093   0.129496977
0.72615712   0.158494851   0.11534803
0.667644449   0.143208865   0.189146685
Lake trout other fish diet proportions 1981-1993
0.40 0.56 0.51 0.51 0.42 0.42 0.42 0.42 0.42 0.42
consumption per predator from SCOL II based on bioenergetics
lake trout
0.917385252   2.065542461   3.587326355   4.924855488   5.366366166   6.195763697
       6.686746743   6.994411536   12.78158861   0
coho
3.280284111   5.136837009
brown trout
2.668738727   6.519267979   6.734972567   0.027245395   0
steelhead
2.842515897   8.193812042   6.182241894   10.57000433   0
proportion of diet from fish from SCOl II
lake trout
0.54 0.96 1 1 1 1 1 1 1 1
coho

0.75 1
#chinook
1 1 1 1 1 1
brown trout
0.54 0.78 0.74 0.74 0.74
rainbow trout
0.54 0.78 0.74 0.74 0.74
Consumption per predator for chinook ages 0-4, 1967-1999

1.978891146	0	0	0	0
1.978890315	8.693059654	0	0	0
1.978892909	8.688400387	22.26011038	0	0
1.978895634	8.683723737	22.24631347	55.12805633	0
1.978894065	8.679020673	22.2326376	55.12789775	0
1.978890594	8.674353504	22.21894389	55.12795265	0
1.978885376	8.669697182	22.2053333	55.12794289	0
1.97889229	8.665000457	22.19169119	55.12804715	0
1.978887695	8.66036226	22.1780674	55.12785279	0
1.978895703	8.655693399	22.1645938	55.12783641	0
1.9788909	8.651079156	22.1511118	55.12806458	0
1.978890657	8.31551978	21.06108817	55.12784326	0
1.978892365	7.955871908	19.40729125	46.91116294	0
1.978893536	7.603370335	17.82167571	41.59774426	0
1.978895282	7.248262532	16.28707367	35.35974072	0
1.978891016	6.899129571	14.74489523	29.9409621	4.285760879
1.978891721	6.540079132	13.19606062	25.18750632	9.771665738
1.978891552	6.163903391	11.61843138	21.04892144	14.67298063
1.978891938	5.201034512	9.744509684	16.81998295	19.59144921
1.978819294	4.930392218	9.163040409	14.60133572	17.06347176
1.978813463	5.200035642	11.67446825	22.72630248	51.55550823
1.978768248	4.870060899	10.98378161	21.4179121	36.96693704
1.978734062	5.411685914	11.20630935	24.9592657	53.166273
1.97875516	5.027166207	12.72350936	28.77450344	55.00858998
1.978697167	6.433954302	13.22799412	27.15270433	50.04514546
1.978678934	6.727827425	14.37061702	34.7419529	61.08497558
1.978678507	4.331012451	16.25097974	30.92707125	108.7906829
1.978775141	4.279067342	13.98907699	26.4449114	103.1448733
1.978865009	6.027428883	15.20387846	31.21191059	54.82412876
1.978888575	4.419542096	15.30541331	40.67952634	56.44471421
1.97889256	3.209207024	11.29596384	15.5466301	14.14092567
1.978893137	3.253922745	12.80065959	26.81120879	26.77203207
1.978888865	3.256717708	12.82649997	26.77096576	26.80437077

Predabund.dat

#Data for alewife-bloater CAA Model by Emily B. Szalai
#Predator abundance from 1965-1999 from SCOL II
#Updated 09/17/2002

#

#Average Number of lake trout ages 1 to 10

986580.4544 0 0 0 0 0 0 0 0 0

1367845.133 678954.7688 0 0 0 0 0 0 0 0

1436468.531 941171.5881 535384.9901 0 0 0 0 0 0 0

1629225.688 988215.2193 741346.4387 416894.0047 0 0 0 0 0 0

1548715.598 1120624.759 777554.7601 575097.8771 316680.0278 0 0 0 0 0

1517871.24 1065060.259 880778.5086 600914.4449 433747.54 236115.5303 0 0 0 0

1653797.862 1043664.672 836195.3047 678124.5525 449995.4676 320593.8804 174862.4842 0 0 0

2016025.829 1136925.532 818505.4515 641374.3461 504202.7385 329716.4897 235413.7529 129192.5621 0 0

1836334.138 1385700.037 890675.8203 625441.273 473486.4463 366228.4278 240061.0947 172554.9574 95621.34843 0

1747869.541 1261968.13 1084386.046 678025.0254 458440.2485 340932.7555 264385.5284 174571.0143 126802.7358 0

1988747.721 1200961.919 986484.1876 822377.2391 493448.873 327233.8642 244038.7926 190740.438 127367.0671 0

2019089.41 1366228.876 937773.6521 745312.475 594248.0362 349166.0319 232248.4862 174670.1554 138169.3195 0

1835309.862 1386828.823 1065661.557 705841.825 534730.9225 416842.4172 245714.7065 164917.7776 125623.642 0

1930765.461 1260376.362 1080552.189 799079.0826 502810.7259 371838.0033 290854.3618 173101.3582 117761.6758 0

1860407.255 1325441.558 979897.6565 804509.5091 562354.4938 344817.6515 256029.7332 202369.1385 122245.7864 0

1990526.632 1276654.158 1028052.521 723621.8249 557479.2711 378429.1961 233083.3384 175100.3139 140708.1522 0

1694929.843 1365423.615 987860.0602 752774.2422 493363.2659 368177.7708 251004.9054 156705.1563 119904.8173 0

1752166.693 1162211.909 1054066.797 717648.9656 505662.184 319341.9614 239974.0408 165820.9364 105585.1881 0

1929842.097 1201000.513 895101.0927 759728.791 474997.2742 321628.3286 204196.2124 155859.0863 110079.4341 0

876221.6735 1322280.902 922800.1806 640430.5383 495444.3131 296627.219 202023.0258 130359.4308 101640.4772 0

2169118.942 599927.6608 1011713.728 652816.9816 410292.6275 302632.3922 182254.8618 126295.6883 83523.39997 0

2274344.812 1484592.209 457880.1218 709447.8447 411558.753 245631.4896 181940.0138 111430.2946 79133.5561 0

1782350.946 1555394.257 1127865.141 316338.4349 436196.3397 239864.9769 143910.6699 108429.7375 68163.0089 0

1496064.366 1218437.489 1178424.34 770322.8519 190047.7757 246381.1513 136351.6065 83430.34101 64686.58419 0

1745686.602 1022981.845 923978.3752 803790.3057 460146.5368 104680.2268 136604.3683 77092.00914 48569.17854 0

2063640.917 1194946.812 780354.5621 639200.4141 485492.1824 259606.0991

58495.91206 77540.95453 44684.57074 0
2151839.237 1412739.158 913108.2371 547594.0204 397777.6536 280523.5393
147627.0432 34357.93411 46168.91328 0
2137937.332 1475195.161 1087816.38 653124.0119 352370.1677 241667.0337
168347.9245 88233.03659 21339.9412 0
2296657.976 1465510.839 1136407.428 784611.3992 429279.0025 219140.8923
150282.3813 105154.8408 55552.06403 0
1932577.502 1574615.789 1130244.871 824626.5962 523523.7974 272682.4317
138141.4073 96025.9752 67973.84458 0
2173798.841 1324392.101 1211193.856 810711.7083 539321.9428 326332.6691
167946.7402 84648.52001 59985.3123 0
1526493.449 1491271.976 1024577.677 885161.7299 543341.286 341269.9079
204138.0874 104378.7992 52434.89826 0
1775198.038 1047257.744 1154917.625 754848.1894 605657.0076 351581.5254
215689.2174 129295.1315 66221.27067 0
1782426.116 1216762.504 806656.3898 834132.0333 502067.5634 383036.5379
215785.7928 129651.2915 78955.29229 0
1782426.116 1216762.504 806656.3898 834132.0333 502067.5634 383036.5379
215785.7928 129651.2915 78955.29229 0
#
Avg Abundance of coho   by   age   (1-2)   and   year
0   0
250418.6575 0
656952.8067 177004.5856
456538.7009 459363.4697
1265325.552 315794.3351
1377858.68   865831.8466
1114898.291 932696.6919
1069484.649 746578.4583
933236.2934 708466.4046
1475452.418 611562.3764
985547.5348 956486.4346
1222020.423 632027.0915
1253628.589 775248.654
1093568.468 786748.4885
1662703.762 678918.2885
1222990.33   1021153.365
1023209.035 743025.0958
905326.0063 614963.4619
959165.1203 538262.8763
1228181.672 564140.4644
1078133.409 714596.6537
926441.0084 573124.4442
932399.4919 503605.7561
1300029.983 520061.5769
945222.8541 725652.3382
943554.9741 568697.7412

980669.806   589226.4106
1087055.939   577339.8956
677014.1562   638832.1363
579745.333   333988.1667
947909.3758   314443.6153
1224305.452   629826.7434
1043621.031   867681.6928
818194.2303   672672.3452
818194.2303   672672.3452
#
Avg Abundance of   chinook   by   age   (0-5)   and   year
0 0 0 0 0 0
0 0 0 0 0 0
429751.2784 0   0   0   0
368408.4936 245370.4902 0   0   0   0
385032.4576 210151.4279 158441.2588 0   0   0
1026395.716 219431.194   135145.9868 64962.92883 0   0
1269320.094 584405.8234 140539.3101 55117.10267 0   0
1122457.203 722055.066   372775.621   57011.18668 0   0
1697667.809 637921.8798 458714.1651 150412.2876 0   0
2026007.186 963946.9309 403629.4763 184096.8531 0   0
2445217.084 1149323.688 607455.9218 161120.3693 0   0
1982570.377 1385862.172 721371.1395 241179.427   0   0
1853775.769 1122624.255 866349.2855 284862.1681 0   0
3188190.301 1048737.985 698990.4299 340265.4429 0   0
3010689.265 1802014.712 650384.4095 273045.885   0   0
3703347.284 1700140.805 1113099.532 252679.5668 0   0
3189112.662 2096998.9   1057151.4   446948.9731 0   0
4082059.06   1810706.402 1321474.061 448943.501   22559.63468 0
4311190.91   2323916.558 1156079.879 591499.6074 43108.20827 150.8621403
4965603.086 2460891.95   1502853.341 543714.3663 81217.30867 419.9902272
4051969.612 2841915.173 1611050.744 740517.9896 95084.33988 1024.840617
3963833.395 2331802.189 1497003.186 860037.9361 154778.0017 1438.365872
4048552.403 2276407.418 1200003.33   592252.0005 247414.8814 5077.163587
3869179.732 2336007.435 1012565.746 436943.1432 139399.7018 5097.924755
5231981.496 2238304.32   938640.7398 298409.3898 96409.61742 3343.523047
5880060.47   3045870.626 989506.9017 234587.9071 57228.33483 993.0458786
4710639.987 3402790.668 1113207.35   268705.4534 37896.18332 455.2515258
4253186.233 2740112.238 1137334.687 214482.4773 36881.2459   237.0208604
4134976.941 2490364.68   901090.2665 176872.2278 18666.58013 131.1703553
4004861.308 2417279.143 1185067.358 124243.94   12977.47485 4.469931963
4885886.584 2343437.377 1585523.297 358456.0879 9519.093357 3.393849274
4653799.166 2845656.426 1501632.1   703073.5479 44753.17194 19.82004419
4413337.125 2727144.554 2081548.841 649433.4228 42292.91725 153.4405784
3547260.774 2584004.29   2034785.613 1234036.032 132458.0066 340.9226585
3591298.191 2079345.439 1931751.036 1229832.353 295442.4884 3133.717274
#

Avg Abundance of rainbow trout by age(1-5) and year

94166.91032	0	0	0	0
185868.2759	81221.81787	0	0	0
114746.098	159981.1513	62585.84628	0	0
278985.5744	98557.72663	122782.3389	33806.33936	0
286521.7531	239124.2727	75339.23738	70080.62852	0
232366.1034	245069.185	182061.4268	48657.00855	0
414724.5259	198332.1103	185843.1013	103880.3926	0
508811.6815	353239.4097	149800.8863	111243.5715	0
829018.2778	432469.6849	265738.251	93031.1912	0
554189.8962	703156.3484	324044.1443	152054.1836	0
719818.8688	469067.7587	524763.9536	188033.2794	0
951388.0674	607980.1265	348667.3493	296465.0596	0
646032.9257	801886.7243	450120.3246	215273.6583	0
524178.6624	543374.3455	591310.8767	260163.0283	0
952481.414	439959.8284	399085.1543	335234.61	0
893116.514	797773.1051	321842.2035	242966.3827	0
742419.0601	746483.4252	581263.416	194076.1315	0
491231.8344	619227.6646	541723.1255	318625.1547	0
820713.6704	408862.1258	447580.5085	309180.5545	0
1385347.136	681665.3751	294348.0813	260755.5942	0
908124.2999	1148226.117	488786.4455	177684.799	0
1113754.867	752235.6691	822099.9306	265571.2931	0
1122129.113	922567.6808	538581.2007	439067.6247	0
673649.5967	929504.3341	660534.5241	316313.7021	0
860671.0797	558010.8841	665500.8473	367489.1416	0
871836.5085	712928.2716	399521.251	373802.4923	0
1012226.53	715714.1252	502838.6981	237984.2585	0
1001480.075	823035.6953	495308.1036	269277.1912	0
993618.4467	812349.0986	566176.4631	264234.4251	0
1129578.27	805972.1939	558824.9714	297453.719	0
1019053.143	916255.7451	554438.2212	297134.3839	0
987606.5751	826603.4226	630303.7815	295405.8325	0
1028813.851	817633.4953	588353.1602	307017.6886	0
925526.184	853857.7758	588363.7438	293718.5432	0
925526.184	853857.7758	588363.7438	293718.5432	0

#

#Avg Abundance of brown trout by age (1-5) and year

0	0	0	0	0
18199.75833	0	0	0	0
33547.69574	10202.7496	0	0	0
69010.33578	18743.05071	3787.654729	0	0
106832.2788	38425.33857	6906.009985	1076.980662	0
120748.8959	59283.25385	14052.00809	1946.510791	0
168316.4402	66778.81162	21517.23621	3926.088603	0
281719.7117	92770.10176	24056.19346	5959.369094	0

652704.6166	154747.8802	33168.81997	6604.391294	0
579034.0646	357314.0845	54913.6692	9026.679053	0
454083.8052	315910.123	125846.0697	14813.93842	0
563704.5343	246900.1873	110429.9386	33652.8477	0
744754.8149	305466.024	85660.07965	29272.58566	0
623532.934	402207.9785	105184.9811	22508.41016	0
636756.7089	335600.6062	137459.6611	27397.57796	0
602151.897	341556.7296	113836.3837	35491.61803	0
651255.9599	321900.2794	114988.6479	29135.58297	0
657704.0353	346970.8446	107559.1202	29173.57692	0
876689.936	349218.9134	115067.4893	27050.42207	0
875142.2432	463915.8909	114945.2892	28686.10169	0
799330.7871	461527.7869	151553.6625	28405.48215	0
831697.7368	421438.3017	150301.3085	37288.37607	0
592463.1391	441193.8779	138424.095	37297.74512	0
805742.6232	316162.9615	146917.3036	34910.29964	0
791292.7181	432687.6514	106724.5261	37641.42857	0
860887.331	428699.9397	148640.0016	27891.57458	0
817925.5082	465402.5572	147918.8599	39146.85581	0
843948.2445	443367.105	160782.9181	38961.53363	0
903507.6991	458086.5145	153854.7413	42588.56201	0
957875.8261	491282.1165	159510.9928	40911.90394	0
981302.9246	521955.5927	171835.1193	42634.07424	0
1023791.124	534808.6593	182927.9392	46056.16894	0
986079.4709	557936.2876	187419.185	49025.8408	0
966696.4304	547608.4695	200733.6613	51566.80855	0
966696.4304	547608.4695	200733.6613	51566.80855	0

Survey.dat

Data for alewife-bloater CAA Model by Emily B. Szalai
Observed year effects from trawl survey data for alewife and bloater
Observed biomass from hydroacoustic surveys of alewife and bloater
Updated 2/13/2003
#
#
TRAWL SURVEY DATA
#
Alewife year effect for year 1962-1997 for age 0 and age 3+ (9999 missing value)
0.734297	2.620397
1.793844	3.33543
3.087469	3.043394
2.017563	4.358424
1.185049	4.78334
3.80697	1.69733
2.836418	2.106245
4.150209	2.279781

4.17984	1.966759
1.893811	2.225125
3.889474	0.616442
2.683019	1.825276
5.315345	0.541599
3.267781	1.41973
4.537853	0.916014
3.24033	-0.19451
2.775378	0.2579
3.701179	0.194624
4.886939	-0.51194
5.080376	0.094754
2.126993	-0.60361
3.242949	-1.50225
3.310497	-1.61399
3.243975	-1.55501
2.159304	-0.55087
3.534968	-0.70734
1.428037	-1.3384
4.254836	-1.56671
4.052675	-1.23399
1.099938	-1.11332
0.983756	-0.68027
1.128417	-0.60926
0.303298	-0.94897
0.549285	-0.22869
-0.92334	0.767569
-0.86026	0.975965

Day Between mid-date for trawls in each year and mid-date in 1999 (1962-1997)
36
36
32
37
43
35
27
28
22
32
30
27
21
14
21
14
17
18

20
20
15
16
16
13
12
15
10
18
15
-7
-6
2
3
4
-8
-2
0
0
#
#
#
Bloater year effects of year 1962- 1997 by age and year ages 0-7
-2.58311 4.24064 3.469584 3.009534 0.854588 -1.58769 -3.31083 -3.81203
-3.03938 3.227216 2.630348 2.347304 0.360088 -1.887 -3.26671 -3.75564
-2.5365 2.019093 1.576195 1.579327 0.403835 -0.98703 -2.43163 -2.7093
-2.5365 2.755128 2.008125 1.951677 0.878591 -0.63643 -1.55506 -5.43293
-3.03938 1.706991 1.178604 1.313358 0.144438 -0.98054 -1.81262 -2.27832
-2.64066 -3.57842 -0.46735 0.740767 0.302877 -0.09573 -0.93588 -1.82394
-2.38749 -0.60047 -0.59139 0.132853 0.010813 -0.43781 -0.77233 -1.7534
-2.01807 0.969002 -1.04662 -0.244 -0.18132 -0.29976 -0.68829 -1.19583
0.240135 1.294968 -0.21516 -0.13782 -0.2495 -0.17792 -0.59767 -1.2922
-1.03324 0.955049 -0.52378 -0.50136 -1.0398 -0.97053 -1.09923 -1.71363
-1.76614 -0.85467 -1.15602 -1.07557 -1.74695 -2.06985 -2.29477 -3.83795
-0.22343 -1.30849 -2.61213 -1.70017 -2.37509 -2.84302 -4.26828 -5.06295
0.1536 -0.10841 -3.18717 -3.21642 -3.52722 -3.51038 -4.69167 -4.92461
-0.78971 0.143055 -1.86713 -2.72443 -3.57652 -3.67201 -4.58903 -5.46906
-1.45128 -1.28576 -2.11152 -2.38404 -3.65023 -4.14623 -4.84672 -5.47183
-0.29556 -1.92146 -2.81144 -2.76236 -3.42681 -4.40254 -4.96206 -5.16076
1.663658 1.425841 -2.95504 -2.80625 -3.10534 -3.41625 -4.83329 -5.35987
1.606874 2.407765 -0.07598 -2.12433 -3.1413 -3.73225 -4.28322 -5.19096
3.069752 2.52047 0.410453 -0.49271 -2.69961 -3.32243 -4.65733 -5.59793
3.109964 4.714235 1.048391 0.612625 -1.23605 -3.3097 -4.82132 -5.5911
4.561486 4.066298 1.205095 0.14762 -1.1136 -2.60003 -4.49858 -5.30809
5.561741 5.919077 1.592817 1.428036 0.307418 -2.26196 -4.21643 -4.32975
3.603663 6.572836 2.81723 1.614216 0.200633 -1.15029 -2.96047 -4.48751

3.98628 6.791133 3.79989 2.110115 0.676546 -0.79984 -2.33447 -3.92441
4.265112 7.422017 4.150544 2.960131 1.531155 0.044426 -2.01652 -4.17933
4.113977 8.81286 4.452841 2.967903 1.419252 -0.05986 -1.28691 -4.70743
2.792367 8.474901 5.265237 3.856757 2.536243 0.812665 -0.3493 -2.71183
3.840411 7.923474 5.123194 4.068321 2.155665 1.04406 -0.73206 -2.29548
2.007523 7.393716 4.118784 3.797856 2.646337 1.320423 0.8314 -0.75446
-0.00445 6.774735 4.352125 4.40746 2.56765 1.711743 0.912068 -0.38826
-0.3453 5.660682 4.637553 3.826487 2.742895 1.923687 1.129808 0.330104
-0.17635 4.742612 3.958893 4.28284 3.262435 2.269607 1.790752 1.179496
-1.0692 -0.57718 0.851064 2.963586 2.639851 2.108901 2.215243 1.845146
-1.99965 -1.74369 -0.45629 2.238882 2.159272 1.706011 1.167072 1.335689
-1.06292 -1.3266 1.650619 2.396154 2.377201 2.292263 1.866024 1.663835
-0.31017 0.407103 -0.07066 1.326799 1.25166 1.442647 1.471476 0.920408
#
#
HYDROACOUSTIC SURVEY DATA- From 1998 An Integrated Acoustic and Trawl
Based #Prey Fish Assessment Strategy for Lake Michigan pg. 77
#
Adult Alewife biomass (metric tons) by year(1993-1996)
13384 21695 45049 91333
Young of year Alewife biomass (metric tons) by year 1993-1996
31027 13984 148394 8407
Bloater biomass(metric ton) by year 1993-1996
476927 251196 239735 275387

Weight.dat

Data for alewife-bloater CAA Model by Emily B. Szalai
Updated 1/11/2000
WEIGHT AT AGE FOR PREY- based on trawl survey data
#Weight at age for predators based on SCOL II
alewife
0.0002 0.01 0.02 0.032 0.04 0.047 0.054 0.07
LENGTH AT AGE 1-9 FOR BLOATER FROM growth modeling 1965-1999
183.154 207.393 227.792 244.96 259.409 271.569 281.803 290.416 297.664
181.863 209.142 229.276 246.221 260.482 272.484 282.585 291.086 298.24
180.549 208.31 230.95 247.66 261.724 273.56 283.521 291.905 298.96
178.875 209.309 232.016 250.535 264.203 275.707 285.388 293.536 300.393
174.003 207.159 232.245 250.962 266.226 277.493 286.975 294.955 301.671
173.002 206.143 232.935 253.206 268.33 280.664 289.768 297.429 303.878
172.715 207.486 233.912 255.275 271.439 283.499 293.334 300.593 306.703
172.412 209.029 236.471 257.328 274.189 286.946 296.464 304.226 309.956
172.463 211.742 240.101 261.355 277.508 290.566 300.446 307.817 313.829
171.034 208.495 239.716 262.258 279.151 291.99 302.37 310.223 316.082
171.245 208.422 238.025 262.699 280.512 293.862 304.008 312.211 318.417
171.758 216.258 244.095 266.261 284.735 298.073 308.069 315.666 321.808
167.25 217.362 250.499 271.228 287.734 301.491 311.424 318.868 324.525

162.381 207.06 246.19 272.066 288.252 301.141 311.883 319.639 325.452
159.889 202.348 237.341 267.988 288.254 300.932 311.026 319.44 325.514
157.051 201.522 234.365 261.434 285.14 300.817 310.623 318.432 324.94
153.963 195.734 230.786 256.674 278.01 296.696 309.052 316.781 322.936
149.623 190.085 223.537 251.607 272.339 289.425 304.389 314.284 320.474
143.816 182.755 215.836 243.186 266.136 283.086 297.056 309.29 317.381
139.267 173.675 206.291 234.001 256.909 276.133 290.331 302.032 312.28
136.998 171.833 200.198 227.087 249.93 268.816 284.664 296.368 306.015
134.988 171.934 200.187 223.193 245 263.528 278.845 291.699 301.191
134.357 169.674 199.647 222.568 241.232 258.924 273.955 286.382 296.81
136.181 165.951 195.108 219.855 238.778 254.187 268.794 281.203 291.463
138.103 169.535 193.67 217.309 237.371 252.713 265.206 277.048 287.109
137.331 164.114 190.766 211.231 231.275 248.287 261.295 271.888 281.93
137.605 165.025 187.419 209.703 226.815 243.574 257.798 268.675 277.532
141.012 163.345 186.511 205.431 224.258 238.715 252.875 264.892 274.082
141.637 165.178 184.136 203.802 219.864 235.847 248.119 260.139 270.341
140.379 156.531 177.842 195.005 212.808 227.348 241.817 252.927 263.808
140.595 167.846 181.177 198.767 212.933 227.627 239.628 251.57 260.74
144.081 166.212 188.992 200.136 214.841 226.682 238.965 248.997 258.98
146.142 168.091 186.725 205.906 215.289 227.669 237.639 247.982 256.428
147.157 171.864 190.038 205.467 221.349 229.118 239.369 247.624 256.188
148.192 172.63 193.095 208.149 220.928 234.083 240.518 249.009 255.847
#
WEIGHT BY YEAR (1965-1996) FOR ALTERNATIVE PREY
small (<90 mm)rainbow smelt (avgweight of lifestage(ls) 0 rs from trawl data
1966-1997)
0.00527 0.00527 0.00527 0.00527 0.00527 0.00527 0.00527 0.00527 0.00527 0.00527
0.00527 0.00527 0.00527 0.00527 0.00527 0.00527 0.00527 0.00527 0.00527 0.00527
0.00527 0.00527 0.00527 0.00527 0.00527 0.00527 0.00527 0.00527 0.00527 0.00527
0.00527 0.00527 0.00527 0.00527 0.00527
large (>90 mm) rainbow smelt (avgweight of ls7 rs from trawl data 1966-1997)
0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709
0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709
0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709 0.0709
slimy sculpin (avg wt for all ls from trawl data 1965-1997)
0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009
0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009
0.009 0.009 0.009 0.009 0.009 0.009 0.009
deep water sculpin (avg wt for all ls from trawl data 1965-1997)
0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009
0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009 0.009
0.009 0.009 0.009 0.009 0.009 0.009 0.009
#
WEIGHT AT AGE FOR PREDATORS- FROM SCOL II
lake trout (1-11)
0.030437 0.218535 0.615904 1.19584 1.902372 2.676988   3.470269 4.245325 4.977302
6.196222   6.196222

```
# coho (1-3)
0.030 1.021    2.222603
# chinook (0-5)
0.0045 0.586   3.1756 8.1931 10.3675 13.119  13.119
0.0045 0.586   3.1756 8.1931 10.3675 13.119  13.119
0.0045 0.586   3.1756 8.1931 10.3675 13.119  13.119
0.0045 0.586   3.1756 7.4845 10.3675 13.119  13.119
0.0045 0.586   3.1756 7.4845 10.3675 14.361  14.361
0.0045 0.586   3.1756 7.4845 10.3675 14.361  14.361
0.0045 0.586   3.1756 7.4845 10.3675 14.361  14.361
0.0045 0.586   3.1756 7.4845 10.3675 14.361  14.361
0.0045 0.586   3.1756 7.4845 10.3675 14.361  14.361
0.0045 0.586   3.1756 7.4845 10.3675 14.361 14.361
0.0045 0.586   3.1756 7.4845 10.3675 14.361  14.361
0.0045 0.586   3.1756 7.4845 10.3675 14.361  14.361
0.0045 0.586   3.1756 7.4845 10.3675 14.361  14.361
0.0045 0.586   3.0626 7.2001 10.1687 13.8155  13.8155
0.0045 0.586   2.9361 6.7659 9.5928 12.7807  12.7807
0.0045 0.586   2.8096 6.3317 9.017    12.0171  12.071
0.0045 0.586   2.6831 5.8975 8.4412 11.2534 11.2534
0.0045 0.586   2.5566 5.4633 7.8653 10.4898 10.4898
0.0045 0.586   2.4301 5.0291 7.2895 9.7261 9.7261
0.0045 0.586   2.3036 4.5949 6.7137 8.9625 8.9625
0.0045 0.586   1.9891 4.0832 5.9739 7.7668 7.7668
0.0045 0.586   2.0017 3.9099 5.7042 7.9687 7.9687
0.0045 0.586   2.0384 4.2497 5.969   9.1125 9.1125
0.0045 0.586   1.9483 4.2866 6.4195 9.6971 9.6971
0.0045 0.586   2.1218 4.3643 6.7269 10.5566 10.5566
0.0045 0.586   2.0189 4.6794 7.0007 11.2297 11.2297
0.0045 0.586   2.4066 4.8601 7.3379 11.5067 11.5067
0.0045 0.586   2.5202 5.2934 8.7143 15.625  15.625
0.0045 0.586   1.8563 5.5349 8.8163 14.6839 14.6839
0.0045 0.586   1.8129 4.7052 8.0439 11.6902 11.6902
0.0045 0.586   2.3591 4.9034 7.5731 12.1888 12.1888
0.0045 0.586   1.8079 5.0352 7.6961 12.0795 12.0795
0.0045 0.586   1.5112 4.0172 6.4552 8.2757  8.2757
0.0045 0.586   1.5112 4.0172 6.4552 8.2757   8.2757
# rainbow trout (1-6)
0.005 0.680    2.495   3.8102 5.443 5.443
# brown trout (1-6)
0.2 0.8 2.3 3.7 3.7 3.7
#
# LENGTH-WEIGHT COEFFICIENTS (a b) FROM SIMPLE
# alewife
498 0.33
# weight-length params (ln(alpha) beta) for bloater by year from growth modeling
```

```
-14.092        3.44337
-14.0801       3.44566
-14.0683       3.44794
-14.0521       3.45109
-14.045        3.45241
-14.0424       3.45279
-14.0438       3.45233
-14.0441       3.45204
-14.0481       3.45099
-14.0458       3.4512
-14.042        3.4517
-14.0386       3.45212
-14.0341       3.45279
-14.0317       3.45303
-14.0331       3.45242
-14.0387       3.45091
-14.0532       3.44762
-14.0689       3.44408
-14.0849       3.44048
-14.0995       3.43708
-14.0989       3.43658
-14.0953       3.43669
-14.086        3.43793
-14.0725       3.44009
-14.0657       3.44105
-14.0629       3.44133
-14.0682       3.4401
-14.0748       3.43876
-14.0841       3.43691
-14.0982       3.43421
-14.1144       3.43109
-14.1218       3.42968
-14.1253       3.42901
-14.1247       3.42914
-14.124        3.42926
# rainbow smelt
520.7 0.396
# slimy sculpin
300 0.33
# deep water sculpin
300 0.33
# lake trout
467.2969 0.3195
# coho
481.04 0.31
# chinook
481.7 0.31
```

rainbow trout
459.68 0.366
brown trout
395.65 0.389

Appendix C

Methods used to Estimate the Parameters of the Lake Michigan Stock Assessment Model

for Chinook Salmon.

This appendix was written by Jim Bence (Michigan State University) to document

the analysis that he completed to describe the relationship between chinook salmon

growth and mortality events. These models were included in the decision model

described in Chapter 3 and I have included this appendix to provide further details on the

chinook salmon mortality models.

Here we first describe the approach to estimating the parameters of an age

structured stock assessment for chinook salmon in Lake Michigan. This was an updated

version of the model developed by Benjamin and Bence (in press a), which we used to

produce the estimates of abundance and consumption for Madenjian et al. (2002). We

then describe how we used results from that assessment model to explore the relationship

between time-varying natural mortality and individual chinook salmon size.

Estimation of stock assessment parameters

The equations defining the age structured stock assessment model are in Table 19,

and the symbols used in those equations are defined in Table 20. This is the same model

described in Appendix A. Here we have added details and repeated information needed

to understand the process of fitting the model to observed data. We do not repeat the

rationale underlying the model or all sources and values for assumed constants.

The system model

The model recognizes two time periods, with natural mortality operating only

during those periods, and numbers at the beginning of the year (and period 1) are given

by eq. T19.1. Between those two periods fishing mortality and mortality associated with maturation occur as pulses in that order. Predictions of the number present at the end of the first period before pulses of mortality (eq. T19.2), after the fishing pulse (eq. T19.3) but before the maturation pulse, and after the maturation pulse at the start of the second period (eq. T19.4) are used to either predict observed quantities or in calculations of consumption (Appendix A).

Natural mortality was modeled as a background rate plus a time varying component (eq. T19.5), and the time-varying component was modeled as the product of an age and year specific effect (eq. T19.6). The background rates were assumed known. Prior to 1985 and after 1997, the time varying component was assumed to be zero. For 1985 through 1996, the year specific effects were estimated. Separate age specific effects were estimated for ages 0, 1, 2. Ages 3, 4 and 5 were assumed to have the same age effect and this was fixed as a reference baseline ($\gamma = 1.0$) and not estimated.

The proportion of fish surviving the fishing pulse is $\exp(-F_{a,y})$ (eq. T19.7), where $F_{a,y}$ is the product of age-specific vulnerability and year specific fishing intensity (eq. T19.8). Vulnerability was estimated for ages 0, 1 and 2. Vulnerability for ages 3 through 5 was assumed equal and fixed to a reference baseline of 1.0.

For 1985 through 1999, fishing intensity was assumed to be proportional to observed fishing effort up to an estimated multiplicative error (eq. T19.8). For 1967 to 1984, fishing intensity was assumed to increase linearly from zero to the 1985 level estimated by the model.

From 1985 through 1999, proportion of mature chinook salmon at age was assumed to be follow a logistic function of weight-at-age during the summer- fall (eq.

T19.9) for ages 1 through 4. Proportion mature at age 0 was assumed to be zero and maturity at age 5 was assumed to be 1.0. For years prior to 1981, a constant maturity schedule was used based on results reported by Stewart (1980): ($P_{m,a}$ = 0, 0.12, 0.33, 1.0, 1.0, 1.0 for ages 0 through 5 respectively). From 1981 through 1984, the maturity at each age was linearly interpolated between the value assumed for 1980 and the value estimated for 1985.

The initial numbers at age in 1967 and the numbers of fish that recruited each year at age-0 were assumed known based on stocking records and estimates of the numbers of wild fish in the system.

The observation model

The model used observed fishery information to estimate the dynamics of the population. This information included: (1) annual total harvest from 1985-1999, (2) age-frequency compositions (proportions at age) of the annual total harvest from 1985-1997, (3) age-frequency compositions of the annual total harvest of mature fish from 1985-1997, (4) age-frequency compositions of the annual weir harvest of fish captured during the spawning run from 1985-1996, and (5) annual fishing effort directed at chinook salmon from 1985-1999. Sources of these data are described by Benjamin and Bence (in press a) and in Appendix A. A Bayesian approach was used in estimating parameters, taking the parameters associated with the highest posterior density as point estimates (Schnute 1994). AD Model Builder Software (version 6.02) was used to estimate parameters using a quasi-Newton method based on derivatives obtained by automatic differentiation (see "The objective function" below).

Fishery catch-at-age was predicted by eq. T19.11, and total annual harvest and proportions at age were calculated from these, for comparison with observed quantities. The catch-at-age of mature fish in the fishery harvest is given by eq. T19.12, and associated proportions were calculated from these for comparison with observations. The numbers at age in the spawning run were predicted by eq. T19.13, and proportions at age calculated from these were compared with observed age-frequency compositions of the annual weir harvest for 1985 through 1996.

Strictly speaking, the observed effort was not treated as data to which predictions were compared. Instead fishing intensity was assumed proportional to observed effort up to multiplicative error and these errors were estimated. These errors derive both from measurement error associated with observations of effort and process error because catchability will actually vary over time. Deviations of fishing intensity from direct proportionality were penalized during the model fitting process. Thus, in effect, qE_y is a prior estimate for f_y (see "The objective function" below).

The objective function

Above we defined a system and observation model and we adjust the estimated parameters of these models to obtain the best fit to the data. This best fit is defined by the the minimum value of the negative log posterior density, which is our objective function. The adjustable parameters are the fishery catchability (q), fishery vulnerabilities (S_0, S_1, S_2), fishery effort deviations (ξ_y for years 1985 through 1999), parameters associated with time-varying natural mortality including age-effects (λ_a for ages 0 through 3) and

year effects (γ_y for years 1985 through 1996), and parameters associated with maturity at age ($\beta_{0,a}$ and $\beta_{0,a}$ for ages 1 through 4).

The posterior density function is proportional to the product of the likelihood given the data and the prior density of the parameters. We minimized the negative log of this density, (which we sometimes call the negative log-likelihood), which can be expressed as sum of components (eq. T19.14). In our application all the priors were bounded uniforms on a log-scale, except for those associated with the effort deviations (which were lognormal priors). As a result we drop the priors for those parameters with uniform prior from the likelihood equations, since these priors are constant within the bounds. The priors are still implicit, and were implemented by using bounded estimation for these parameters in the Ad Model Builder software. All parameters were estimated on a log-scale. Bounds were set widely enough apart so they had little influence on the solution when parameters converged to a solution within the bounds. Bounds were used to ensure a proper posterior density function and to avoid the model becoming stuck at implausible solutions that did not maximize the posterior density during the fitting process.

Total annual harvest was assumed to follow a lognormal distribution with an assumed known dispersion parameter (eq. T19.15). The proportions-at-age were assumed to behave as though calculated from multinomial samples (eq. T19.16) with effective sample sizes equal to either the actual number of age determinations or data type specific maximum number intended to avoid over-weighting observed age compositions based on large samples (Fournier and Archibald 1982). The deviations

about the assumed direct proportionality between fishing intensity and effort were assumed to be lognormal with a known dispersion parameter (eq. T19.17).

The effective sample sizes (the n's in equation T19.16) and the dispersion parameters (σ_C^2 and σ_ξ^2) act to weight how important the various data and priors are considered during the fitting process. These were set at 0.08 and 0.04 for σ_C^2 and σ_ξ^2 and 100, 50 and 50 for the effective sample sizes for the harvest, mature harvest and weir harvest. The dispersion parameter for the harvest was set based on the average of coefficient of variation estimates for the Michigan creel surveys. The other values were chosen after a sequence of repeated fits of the model in an attempt to avoid strong patterns in the residuals, and achieve a match between the specified dispersion values for the effort deviations and for annual recreational catch, and ones calculated based on the estimated effort deviations or log-scale differences between observed and predicted harvest, after the model had converged to a solution.

The mortality versus individual size models

The assessment model produced estimates of "age effects" and "year effects" for time varying natural mortality. The age-effects were quite small for ages 0 and 1 (about 0.007), and quite high for age-2 (12.9) relative to the reference value for age-3 and older (1.0). The year effect was estimated to be quite small in 1985 and for this analysis we assume that year effects on a log-scale were at the lower bound used during estimation for 1983 and 1984.

The implied trends in estimated natural mortality together with weight of age-3 fish at annulus formation are given in Figure 30. While the relationship between natural mortality and size is not clear cut in this figure or in other exploratory ones using

different measures of fish size, it is clear that mortality increased after a period of low growth and recovered after a period when growth had increased above that during the slowest growth period. Another way of looking at these data is to consider how changes in mortality are related to size achieved by the start of age-3 (Figure 31). This suggests there is some inertia to mortality (it tends to be similar to that observed in the previous year), and that it tends to decrease when larger sizes are in the process of being achieved. The subsequent analysis of the relationship between natural mortality and growth conditions is based on the year effects, and takes into account the above observations.

We developed two closely related models that attempt to describe the growth effect and "inertia". In the first of these models the year effect is assumed to be a deterministic function of the year effect observed at the previous time step and size attained at annulus formation by age-3:

$$\ln(\gamma_y) = \mu + \rho \ln(\gamma_{y-1}) - \beta \ln(W_{ANN,3,y+1}) \tag{1}$$

The second of these models differs only in allowing for process error:

$$\ln(\gamma_y) = \mu + \rho \ln(\gamma_{y-1}) - \beta \ln(W_{ANN,3,y+1}) + \varepsilon_y \tag{2}$$

These two models were fit to the "observed" year effects (estimated previously in the stock assessment model). In the first of these models, all variations between predicted and observed were treated as measurement errors. In the second, all deviations between observed and predicted were treated as process errors. Errors on the log-scale of eqs. 1 and 2 were assumed normally distributed and point estimates were obtained by minimizing the negative concentrated likelihood by altering μ, $\ln\rho$, and $\ln\beta$:

$$-\log(conc) = \frac{k}{2} \log \left(\sum_y \left(\ln \tilde{\gamma}_y - \ln \gamma_y \right)^2 \right) \tag{3}$$

where *k* is the number of years involved in the comparison of observed and predicted values. Both ρ and β were assumed to only take positive values and were estimated on the log-scale. All three parameters were restricted within bounds: μ (-50, 50), lnρ (-2.3,0), and lnβ (-10,10). By specifying bounds we are assuming a prior uniform distribution for these parameters on their respective scales, so that all values within the bounds are assumed a priori equally likely and all values outside the bounds are assumed impossible. Using such bounds ensures that when a Bayesian posterior distribution is determined it will be a proper one. The bounds for μ and lnβ were arbitrary chosen as large and small values below or above which parameter values would be quite unlikely. The bounds for lnρ correspond to values of 0.1 and 1.0 for ρ. Initially a much smaller value for the lower bound for lnρ was used, but in the case of the process error model, the resulting MCMC chains were quite sticky. When low values for ρ were visited the chain remained in the vicinity of these low values for long sequences even though these combinations of parameters had low likelihood values. The point estimate for σ² (which is concentrated out of the likelihood) was obtained as:

$$\sigma^2 = \frac{\sum\limits_{y}\left(\ln \tilde{\gamma}_y - \ln \gamma_y\right)^2}{k} \tag{4}$$

Here σ² represents either the measurement error variance or the process error variance depending on whether the model of eq. 1 or eq. 2 is used. Point estimates for all the parameter estimates are in Table 21.

Note that the measurement error model essentially assumes that next year's time-varying mortality will be the same as this year's with an adjustment for growth. The process error model led to very uncertain estimates of effects due to history and growth and random year to year variation plays a substantial role. We decided that the measurement error model was implausible, since it seemed unlikely to us that most of the variation between observed and predicted mortality came about because of poor estimates of mortality. The process error model was therefore pursued further.

Posterior distributions for the parameters of the process error model were estimated by Markov Chain Monte Carlo (MCMC) methods. A chain of 20 million was run, with output saved every 2000 steps, leading to 10,000 saved samples. Because of the use of concentrated likelihood the output of the chain for the process error variance had to be post-processed. This was done following the same two-stage procedure used in Chapter 2 for variance about a stock-recruitment model. The estimate of variance originally calculated for each set of parameters is the most likely variance estimate given those parameters. This was replaced in each sample in the chain by a single draw from a scaled inverse chi-square distribution, with degrees of freedom equal to v-3, where v is the number of observations used in fitting the mortality model. Calling the result of eq. 4 for the ith sample MSE_i:

$$\hat{\sigma}_i^2 = \frac{v \cdot MSE_i}{X_i} \qquad (5)$$

where X_i was generated from a Chi-square distribution with v degrees of freedom.

In general the resulting chains were well behaved and appeared to provide reasonable estimates of the posterior distributions. Autocorrelations fell to near zero after less than 50 steps for all four parameters, and all effective sample sizes exceeded 500.

The trace plots did not reveal long-term correlations. See Chapter 2 for further explanation of these diagnostics.

The marginal posterior distributions for ρ, β, and σ are shown in Figures 32 through 34. These distributions indicate that there is a substantial probability that growth in fact has relatively little impact on mortality and that the observed patterns could reflect chance events associated with process errors, combined with inertia in the system.

Our above analysis does not fully take into account observed patterns in growth and mortality. In particular there is at least anecdotal information suggesting that natural mortality did not become high, as it was during the late 1980s, from 1967 through 1982, and during those years chinook size at age was generally larger (e.g., Stewart et al. 1981). We developed two alternative mortality models based on this information and making stronger assumptions regarding the relationship between mortality and individual size and for inertia with respect to mortality. The premise of these models is that the system consists of two states for each age, a high natural mortality state and a low natural mortality state. In the first of these alternative models it is assumed that after the high mortality state is first entered the system must stay in that state for five years before further transitions are possible. When such transitions are possible, the transition probability from a high mortality state to a low mortality state increases with increases in weight at annulus formation at the next age in the next year following a logistic function:

$$P_{a,y,H \to L} = \frac{1}{1 + \exp(-b_{1,a}(W_{ann,a+1,y} - b_{2,a})} \tag{6}$$

The transition probability from a low mortality state to a high mortality state is the complement of that given by equation 6. The parameter values were chosen by trial and error so that in Monte Carlo simulations using the observed/assumed weight-at-age data from 1980 through 1999, an average of about seven high mortality years occurred. These parameters produce a substantial increase in the probability of making the transition from high to low over the range of observed weight-at-age, as is illustrated for age 3 (Figure 35).

The second alternative model resembles the first, in that the transition from low to high mortality is given by equation 6. However, to mimic patterns like the observed mortality sequence, the probability of transitions from the low to high mortality state can no longer be the complement of the probability of a transition from the high to low mortality states. In this model transition from high to low mortality occurs deterministically when "growth is good enough". Thus the transition probability is 1.0 when weight at annulus formation for the next age in the next year exceeded a threshold $W_{a,c}$. The same values of b_1 and b_2 were used as in the first alternative model and $W_{a,c}$ was again chosen by trial and error to produce on average of about 7 years of high mortality in Monte Carlo simulations using the observed sequence of weight-at-age. For these parameters there is a non-negligible probability of transition to high mortality even when above the threshold, but not a certain transition to bad even when growth is substantially below the threshold. This allows the mortality to stay low even following the occasional poor growth year as we have seen. The model even can allow no mortality event to occur given the observed growth sequence, although this is relatively rare given the current parameter values.

We note that these two alternative models are not statistically derived models, and we do not provide uncertainty estimates for b_1's and b_2's (or for the second alternative $W_{a,c}$'s). These models cannot attempt to mimic year-to-year quantitative variation in mortality rates, but do reproduce periods of high mortality following periods of slow chinook salmon growth. In applying these models to produce actual mortality rates, it would be reasonable to assume a zero or near zero year effect for low mortality state years and a value equal to the average for 1986-1992 for high mortality years. Calculating this average on a log-scale yields $\gamma = 0.0986$, which corresponds to a $M_{TVM,2,y} = 1.27$.

It is possible given these models for salmon to achieve unreasonably low sizes even when mortality has not become very high. This is rare for the two alternative models but is not infrequent for the model described by eq. 2. To ameliorate this, all three models are augmented by the rule that when $\ln(\gamma)$, as determined by any of the above models is less than 5.0, $\ln(\gamma)$ is set to 5.0 with probability:

$$P_{a,y,\gamma \to 5} = \frac{1}{1 + \exp(-b_1(b_2 - W_{HAR,3}))} \tag{7}$$

The constants b_1 and b_2 were set to 6 and 4.15 respectively as follows. As mean weight in fall for age-3 falls below 4.9, if there is no ongoing mortality event, we assumed that the probability of a mortality event increases. We assumed that the probability of having this mortality event (when otherwise the model did not have one) was near zero for weights just below 4.9, but increased to near 1.0 as the mean length approached a value

for which 95% of the age-3 fish in the fall were larger than in every year. We looked at distributions of Michigan creel caught chinook salmon of age-3 for months starting in August, by year. The lowest 5th percentile was 3.4kg (in 1986).

Table 19. Equations defining the Lake Michigan stock assessment model.

System Dynamics Model

$$N_{a+1,y+1} = N_{a,y}e^{-M_{a,y}}(1-P_{F,a,y})(1-P_{m,a,y})$$ (T19.1)

$$N_{a,y,1}^{+} = N_{a,y}e^{-7/12M_{a,y}}$$ (T19.2)

$$N_{a,y,2}^{-} = N_{a,y,1}^{+}(1-P_{F,a,y})$$ (T19.3)

$$N_{a,y,2} = N_{a,y,2}^{-}(1-P_{m,a,y})$$ (T19.4)

$$M_{a,y} = M_a + M_{TVM,a,y}$$ (T19.5)

$$M_{TVM,a,y} = \lambda_a \gamma_y$$ (T19.6)

$$P_{F,a,y} = 1 - \exp(-F_{a,y})$$ (T19.7)

$$F_{a,y} = S_a f_y$$ (T19.8)

$$f_y = qE_y\xi_y \qquad \xi \sim LN(0,\sigma_\xi^2)$$ (T19.9)

$$P_{m,a,y} = \frac{1}{1 + e^{-(\beta_{0,a} + \beta_{1,a}W_{HAR,a,y})}}$$ (T19.10)

Observation Model

$$C_{a,y} = N_{a,y,1}^{+}(1 - \exp(-F_{a,y}))$$ (T19.11)

$$C_{m,a,y} = N_{1,a,y}^{+}(1 - \exp(-F_{a,y}))P_{m,a,y}$$ (T19.12)

$$N_{sp,a,y} = N_{2,a,y}^{-}P_{m,a,y}$$ (T19.13)

Table 19. cont.

Objective Function

$$-LogL = \sum_{i=1}^{5} -L_i + \text{Ignored Constant} \tag{T19.14}$$

$$L_1 = \frac{1}{2\sigma_C^2} \Sigma \left(\ln \tilde{C}_y - \ln C_y \right)^2 \tag{T19.15}$$

For $i = 2$, 3 and 4 (age compositions for harvest, mature harvested fish, weir return fish),

with subscripts to distinguish the three data types dropped on the right hand side:

$$L_i = \Sigma_y n_y \Sigma_a \tilde{p}_{a,y} \ln(p_{a,y}) \tag{T19.16}$$

$$L_5 = \frac{1}{2\sigma_\xi^2} \Sigma \ln(\xi)^2 \tag{T19.17}$$

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Table 20. Definition of symbols used in equations for chinook salmon stock assessment model.

Symbol	Description
$N_{a,y}$	Abundance-at-age at start of year
$N^+_{a,y,1}$	Abundance-at-age at end of first period
$N^-_{a,y,2}$	Abundance-at-age after fishing pulse
$N_{a,y,2}$	Abundance-at-age after spawning pulse (start of 2nd period)
$M_{a,y}$	Instantaneous natural mortality rate
M_a	Constant age-specific portion of natural mortality
$M_{TVM,a,y}$	Time varying component of natural mortality
λ_a	Age effect for time varying natural mortality component
γ_y	Year effect for time varying natural mortality component
$P_{F,a,y}$	Proportion of fish that die during fishing pulse
$F_{a,y}$	Fishing "rate" determining the proportion dieing during fishing pulse
S_a	Fishery vulnerability
f_y	Fishing intensity
q	Fishery catchability
E_y	Observed fishing effort
ξ_y	Fishery effort deviation
$P_{m,a,y}$	Proportion of fish that mature
$\beta_{0,a}$	Intercept parameter for age-specific logistic maturation function
$\beta_{1,a}$	Slope parameter for age-specific logistic maturation function
$W_{HAR,a,y}$	Observed weight in late summer/fall (time of harvest and maturation)
$C_{a,y}$	Predicted catch by age and year
$C_{m,a,y}$	Predicted catch of mature fish by age and year

Table 20, cont.

Symbol	Description
$N_{sp,a,y}$	Predicted number of mature fish in spawning runs by age and year
C_y	Predicted annual recreational harvest
$\tilde{C}_y$	Observed annual recreational harvest
$p_{a,y}$	Predicted proportion (for the year) of catch. These quantities are defined for recreational harvest, mature recreational harvest, and weir catch
$\tilde{p}_{a,y}$	Observed proportion (for the year) of catch. These quantities are defined for recreational harvest, mature recreational harvest, and weir catch
L	Total posterior density
L_i	Log of likelihood or prior component
σ_C^2	Dispersion parameter for recreational harvest
σ_ξ^2	Dispersion parameter for effort deviations
n_y	Effective sample size (one defined for each year for recreational, mature recreational and weir caught fish).

Table 21. Parameter estimates and their asymptotic standard errors for the models described by equations 1 (measurement error model) and 2 (process error model).

Parameter estimates for the measurement error model						
			Asymptotic correlation matrix			
parameter	estimate	asymptotic SE	$\ln\rho$	$\ln\beta$	μ	σ^2
$\ln\rho$	-9.07E-08	1.37E-04	1			
$\ln\beta$	2.56E+00	1.73E-01	0.0019	1		
μ	2.00E+01	3.37E+00	0.0021	0.9998	1	
σ^2	4.10E+00	3.38E-04	-1	-0.0019	-0.0021	1

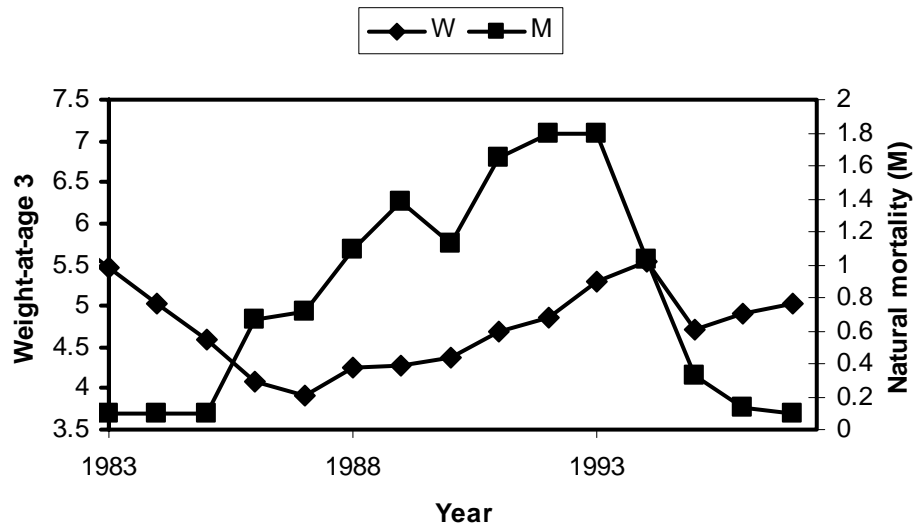| Parameter estimates for the process error model						
			Asymptotic correlation matrix			
parameter	estimate	asymptotic SE	$\ln\rho$	$\ln\beta$	μ	σ^2
$\ln\rho$	-2.62E-01	2.76E-01	1			
$\ln\beta$	6.38E-01	3.40E+00	0.6001	1		
μ	1.85E+00	1.04E+01	0.656	0.9961	1	
σ^2	3.78E+00	4.48E-07	-0.7995	-0.123	-0.1685	1

Figure 30. Temporal patterns in weight at annulus formation for age 3 (*W*, diamonds) and model estimated natural mortality rate at age-2 (*M*, squares).
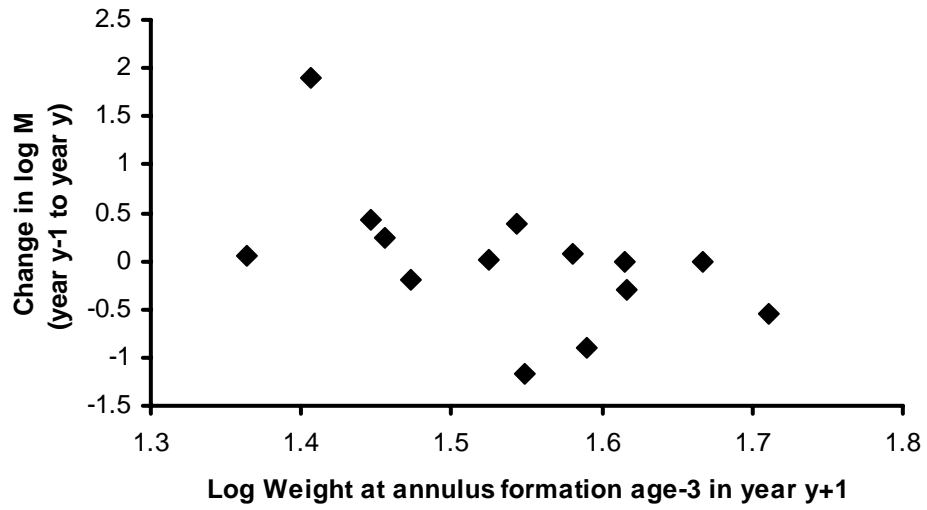
Figure 31. Relationship between changes in mortality at age-2 from year *y*-1 to year *y*
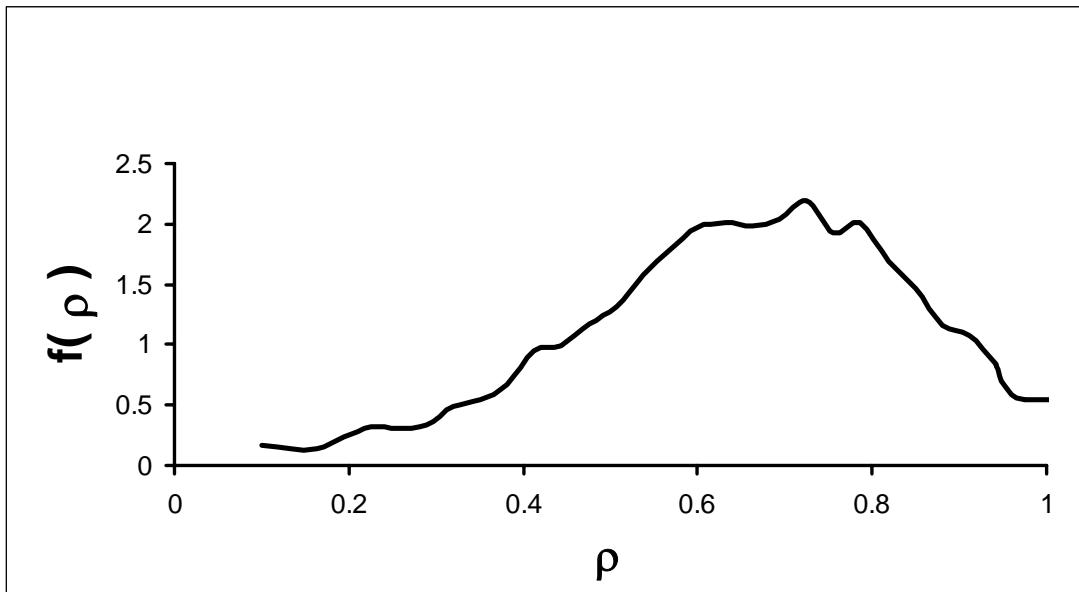
and weight at annulus formation in year y+1.

Figure 32. Estimated posterior density for ρ, which is the effect of last year's natural mortality year effect on this year's year effect (eq. 2).
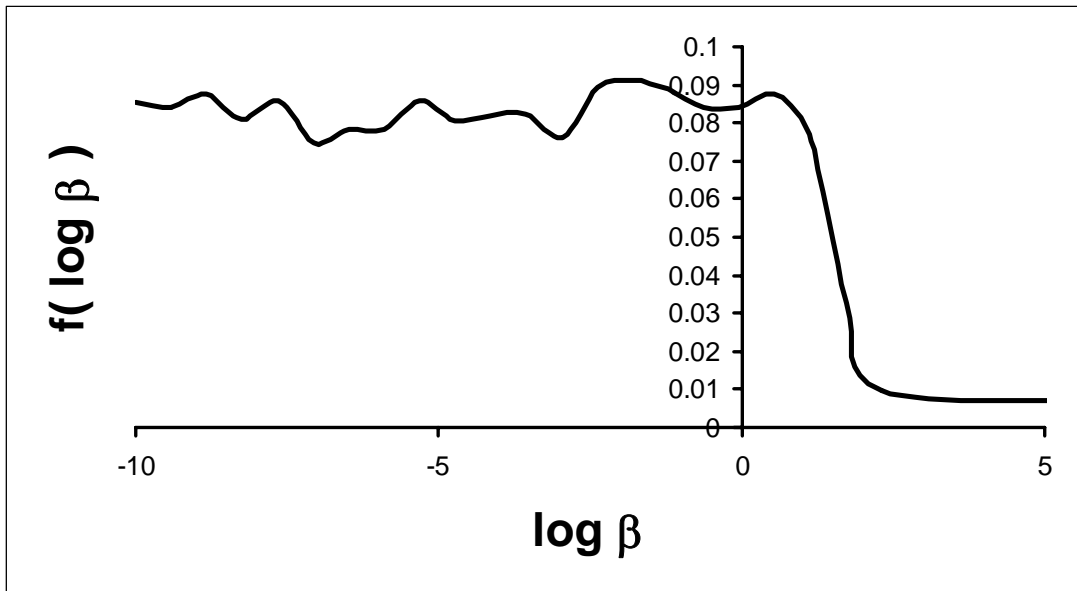
Figure 33. Estimated posterior density for β, the effect of age-3 weight at time of annulus

formation in year *y*+1 on the year effect for natural mortality in year *y* (eq. 2).
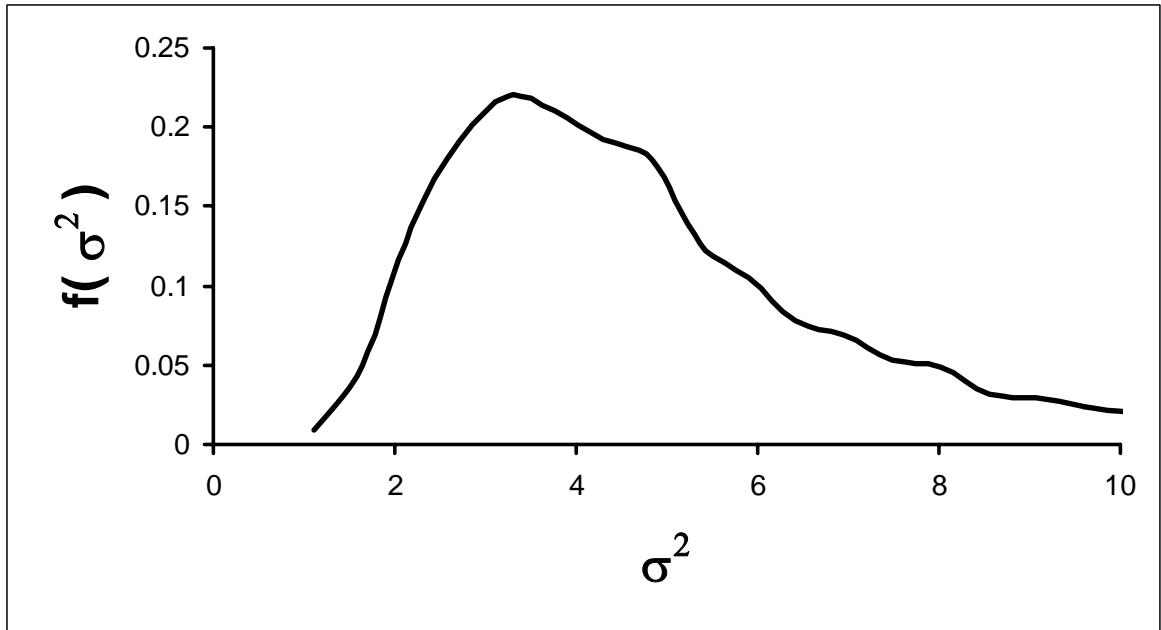
Figure 34. The estimated posterior density for σ^2, the variance for the process errors (ε) in equation 2.
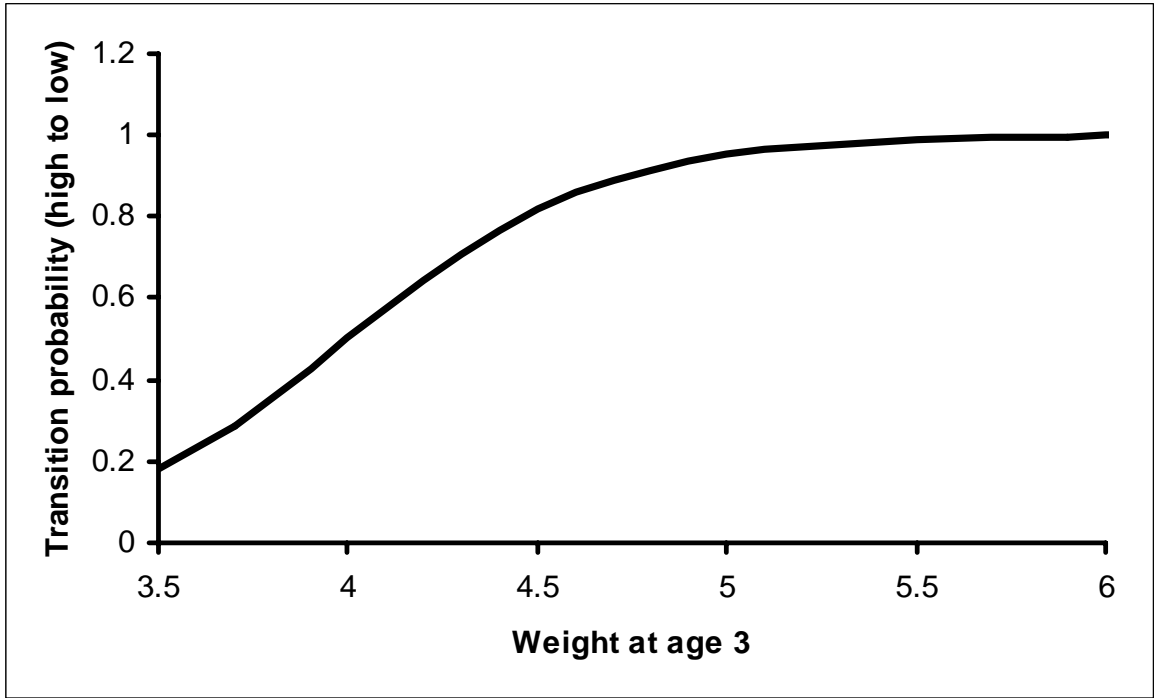
Figure 35. Probability of transition from high to low mortality regime for age-2 predicted

for a given weight at age 3 (annulus formation) by equation 6, with $b_1 = 3.0$ and $b_2 = 4.0$