Quantifying the effects of salmonine predation on alewife (*Alosa pseudoharengus*) and bloater (*Coregonus hoyi*) population dynamics in Lake Michigan, 1962-1999.

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Abstract

We reconstructed the population dynamics of alewife (*Alosa pseudoharengus*) and bloater (*Coregonus hoyi*) in Lake Michigan by fitting dynamic population models to historic prey fish survey data (bottom trawl and hydroacoustic indices) from 1962 to 1999. These models extend traditional statistical catch-at-age models to account for mortality due to the salmonine predators and allowed recruitment variability. Chinook salmon predation was assumed to follow a Type II functional response while all 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. We estimated recruitment, stock size, stock-recruitment model parameters, and the effective search rate of chinook salmon at low prey abundances, and developed Bayesian posterior distributions for key quantities. The amount of uncertainty in the parameters of the stock-recruitment relationship for alewife and bloater was large, with a variety of potential shapes of the stock-recruitment function. Also, recruitment variability unexplained by stock size was high. Our uncertainty in the parameters of the functional response for chinook salmon was moderate. Estimates of chinook salmon consumption rates suggest that chinook salmon were food-limited in the late 1980s and were experiencing similar levels of food-limitation by the end of the 1990s. Additionally, estimates of instantaneous predation mortality rates on adult alewife are currently approaching the levels estimated for the mid 1980s.

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. In the Lake Michigan ecosystem, the importance of maintaining adequate prey fish abundance to support the economically important salmonine fishery has become a primary management concern (Madenjian et al. 2002). 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.

Because the abundance of all five salmonine species in Lake Michigan had been maintained primarily through stocking, the natural feedback of poor survival of young predators (before the age of stocking) during times of low prey abundance did 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 Chinook salmon (*Oncorhynchus 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, Hansen and Holey 2002, Benjamin and Bence 2003 a and b). To protect against future collapses of the Chinook salmon fishery, a tool to quantify the effects of stocking on prey fish abundances and predict the effects of future stocking policies was needed (Stewart and Ibarra 1991).

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 quantitatively estimate predation mortality rates and the ability of prey to reproduce at low population abundances (i.e. a stock-recruitment function). Additionally, they emphasized the effect that incorporating uncertainty in these dynamic models may have on the outcomes of different stocking scenarios.

The technique of incorporating predation mortality into fisheries stock assessments has been explored in several other ecosystems (e.g. Livingston and Methot 1998, Tsou and Collie 2001, Cox et al. 2002). 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 (Christensen and Walters 2004) for fish communities.

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

Here we extend the Livingston and Methot (1998) approach to the Lake Michigan where two prey species (alewife (*Alosa pseudoharengus*) and bloater (*Coregonus hoyi*)) share a common suite of predators. We have attempted to quantitatively reconstruct alewife and bloater populations in Lake Michigan from 1962 to 1999 while estimating key parameters governing their dynamics (e.g. stock-recruitment parameters) for use in population models projecting their future abundance using available survey data. To accomplish this, we have modified the statistical catch-at-age framework to incorporate a multispecies functional response model to capture the dynamic link, in the form of a time-varying predation mortality rate, 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 techniques to quantify the uncertainty in all of our estimated parameters for use in future investigations of stocking policies in Lake Michigan.

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 unexploited fish populations where a measure of the absolute abundance of a source of time-varying mortality exists (e.g. predator abundance). Therefore, the fisheries statistical catch-at-age approach may be applicable to solving some of the “inverse” problems, that is estimating the parameters governing population dynamics from a time-series of population abundances, encountered in basic population dynamics studies (Wood 1997).

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. Since no large scale fishery currently operates on either alewife or bloater, predation mortality provides the only source of the time-varying mortality necessary for the SCAA estimation method. As in SCAA, 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 estimated key parameters governing alewife and bloater dynamics, including those describing the stock-recruitment relationships and the functional response by searching for the set of parameter values that provide the best match to observed survey indices for both prey populations and assessment estimates of salmonine consumption. Uncertainty in these parameters was assessed using Bayesian statistical techniques to describe the posterior probability distributions of all estimated parameters.

Prey fish surveys

Fall bottom trawl survey

Fall bottom trawl surveys have been conducted annually since 1962 at fixed locations throughout Lake Michigan by the United States Geological Survey-Great Lake Science Center (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*)). Both alewife and bloater populations were sampled for age determination using the fall bottom trawl survey (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.

Age-specific general linear models incorporating effects for year, location and depth allowing for correlated errors among samples from the same location within a year were fit to natural log of the CPUE data (Krause 1999) to estimate lakewide abundance indices by age class for alewife and bloater. 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 indices are expressed on the natural logarithmic scale and are relative to the mean abundance estimated in the last year of the trawl survey data, 1999, differing 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 and older 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 and older age class rather than individual age classes. Additionally, age-1 and age-2 alewife are incompletely sampled by the bottom trawl survey since these ages are not closely associated with the bottom during the time of trawling, so the CPUE data for these age class may not reflect trends in true abundance. Therefore, we only utilized age-0 and age-3 and older 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, 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. 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 and older) while bloater abundance estimates were combined across all age classes . Variance estimates were then calculated for the lakewide estimates of abundance. 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. Additional details on the hydroacoustic survey methods are reported by 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 rainbow trout (steelhead lifehistory, *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 (Madenjian et al. 2002, Szalai 2003). In our calculations of the mortality rates on alewife and bloater due to predators, we used geometric mean predator abundances derived from these assessments(Szalai 2003). 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, as suggested by available size at age data. Predator length and weight at age were obtained from the same stock assessments. (Szalai 2003).

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 salmonine 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, was 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

We constructed age-specific dynamic population models of both alewife and bloater where total instantaneous mortality rates were the sum of background natural mortality rate and predation mortality rates. Symbols used in model development are defined in Table 1. Here we provide an overview of the general model structure. Details regarding model development and parameterization can be found in the accompanying appendix.

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+ where estimated independently as model parameters. For alewife, the abundance at ages 1 to 6+ in the first year was assumed to follow a stable age distribution predicted by background natural mortality rates and the abundance of age-1 was estimated as a model parameter.

Abundances of each species at age in all subsequent years was predicted by

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

with the exception of the last age group for each species where all surviving fish were accumulated (see appendix for details).

Natural mortality rates were not estimated during model fitting as the data provided little information to estimate these parameters. Therefore, these parameters were fixed at constant values for each species and age (Table 2). See the appendix for details on how these values were derived. Background natural mortality were assumed constant over time with one exception, a second source of background mortality was applied to the adult alewife population in 1967 to simulate the large dieoff event that occurred in that year. The strength of this dieoff was estimated as a model parameter.

Instantaneous predation rates were assumed to change with changes in the abundance of both the predators and the prey and were calculated separately for each age class of the five salmonine species. The predation rates inflected by each salmonine species was not calculated identically for all predator species. In Lake Michigan, despite large apparent changes in the abundance of prey, there have not be measurable changes in the growth rates of lake trout, coho salmon, brown trout and rainbow trout (Madenjian et al. 2002). This suggests that all historical levels of prey abundance have been sufficient to maintain observed predator growth rates. When this data is interpreted in terms of a predator’s functional response (i.e. Type II or Type III), this suggests that the predator is not prey-limited and is consuming at a rate close to its maximum consumption rate over the range of historically observed prey abundances. Therefore, consumption per predator (kg) for lake trout, coho salmon, brown trout and rainbow trout were all assumed to be constant from 1965-1999, and fixed at the average consumption per predator from Madenjian et al. (2002), and this consumption was distributed across the prey types as a function of the predators preference for each prey type and the relative abundance of each prey type (see appendix for details).

For Chinook salmon, declines in growth rate, and presumably, consumption rates have occurred over the historical period as prey abundance declined (Madenjian et al. 2002). Therefore we chose to use a Type II functional response to predict the predation rates of chinook salmon predators (see appendix for details in parameterization).

$$A_{i,j,y} = \frac{\alpha_{i,j,y}\tilde{N}_{i,y}}{1+\sum_{i}\left(\alpha_{i,j,y}\tilde{N}_{i,y}w_{i,y}\Big/C_{\max,i}\right)} \tag{2}$$

The attack rates for each predator-prey combination, $\alpha_{i,j,y}$, was parameterized as in Jones et al. (1993) as a function of a predator’s effective searching efficiency, proportional to its length, and its preference for each prey type based on its relative size and degree of availability due to shared habitats. For management purposes, an important parameter is the degree to which Chinook salmon predation rates decline with declines in prey abundance, which is influenced by the attack rates from the functional response. We initially attempted to estimated parameters governing all three aspects of the attack rate, however there was insufficient information in the data. Therefore, we chose to estimate only the proportionality constant between predator length and effective searching efficiency, γ, since this parameter influences how quickly consumption rates increase at low prey abundances. The instantaneous consumption rates predicted by eq. 2

were then converted to instantaneous predation rates which were used in eq.1 (see appendix for details).

From our reconstruction of population abundances over time, we were able to calculate predictions of the expected values for both the prey fish survey and the predator consumption estimates (see appendix for details). For the hydroacoustic surveys, predicted indices were calculated from the estimates of population biomass and a catchability coefficient was estimated for each prey type (age-0 alewife, age-1+ alewife, and bloater), to adjust for the proportion of the population not measured in the survey. For the fall bottom trawl survey, the year-specific indices used as a data source are calculated as relative indices (see above), so no correction for sampling only part of the population is needed. However, the timing of the fall bottom trawl survey shifted from an October mid-date in the 1960s through 1980s to a mid-date of late September in the 1990s. This shift of approximately 2 weeks 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 2). 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.

The model predictions of predator consumption and prey survey indices were then compared to the observed data in each year and the degree of agreement between the predictions and the observed quantities were assessed using a likelihood function. The parameters of the model were then adjusted numerically, using AD Model Builder software (Otter Research 2000) to provide the greatest degree of agreement between the predicted and observed quantities (see appendix for details). AD Model Builder software also provides samples for the joint posterior distributions for all estimate parameters using a Metropolis-Hastings algorithm.

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 , β , and σ_r^2 were estimated for both species (Quinn and Deriso 1999).

$$Ln(R_{s,y} / S_s, y) = \ln(\alpha_s) - \beta_s S_{s,y} + e_{s,y} \qquad (3)$$

where $e_{s,y}$ is a normally distributed error term with mean zero and variance $\sigma_{s,r}^2$. For alewife, stock size was indexed by the abundance of age-2 and older 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.

Results

Predictions of the recruitment of alewife that maximize the posterior likelihood show that recruitment has generally increased since the 1960s with the exception of one strong year class in 1967 and adult (age 2+) abundance has declined since the introduction of salmonine predators (Figure 1a). For bloater, recruitment peaked in the late 1980s, followed by a subsequent peak in the adult (age 2+) population in the early 1990s (Figure 1b). The stock-recruitment function fit to the predictions of stock and recruitment that maximize the joint posterior density show a strongly domes function for alewife, suggesting a high degree of compensation (Figure 1c). For bloater, little compensation in recruitment has occurred over the range of historical stock sizes (Figure 1d).

Predictions of fall bottom trawl survey abundance indices based on the parameters that maximize the posterior likelihood generally matched the observed values well (Figure 2). For adult alewife (age-3 and older), 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 2a). The predicted trawl indices for age-2 and older bloater generally matched the trends in the observed indices well although there were some discrepancies between observed and predict values for ages 0 and 1 (Figures 2b-d). However, the predicted indices for age-7 and older bloater did not decline as rapidly as the observed indices in the 1970s (Figure 2d).

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

Predictions of total consumption by all salmonine predators matched well with the time series of predator assessment-based values (Figure 4a). However, the model slightly overestimates consumption during the final three years (1997-1999, Figure 4a). The model had more difficulty matching the proportion of total consumption by prey type (Figure 4b). The predicted proportion of large alewife was larger than the predator assessment-based 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 4b). The predicted proportion of small alewife generally remained more constant than the predator assessment-based proportion of small alewife (Figure 4b). 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 4c). 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 4c). Additionally, the predicted consumption per predator for age-1 Chinook salmon was consistently higher than the predator assessment-based values from mid 1980s on. The predicted consumption per predator for age-3 Chinook salmon was consistently lower than the predator assessment-based values from the 1960s through 1980 and the predicted consumption per predator for age-3 did not reach the high level observed in the predator assessment some years in the mid 1990s (Figure 4c). 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 4d). 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 $C_{\max,chs}$.

Estimates of the instantaneous predation rates by age on alewife and bloater, at the parameter values that maximize the posterior likelihood, summarize the differing effects predation has had on the dynamics of these two populations. In general, alewife have sustained much larger predation rates than bloater throughout the time series (Figure 5). Predation rates on adults (age-1 and older) of both species peaked in the mid 1980s concurrent with the peak in predator abundance in Lake Michigan (Figure 5). Additionally predation rates on adults (age-1 and older) in the late 1990s are similar to or larger than those observed during the peak predator abundance in the mid 1980s (Figure 5). Peak predation rates on age-0 alewife and bloater occurred during the late 1970s (Figures 5a,c). For alewife, instantaneous predation rates have been greater than two times background natural mortality rates since the 1980s (Figures5a,b). Instantaneous predation rates on bloater, even in the mid 1980s, have never been larger then one half the background natural mortality rates (Figures 5c,d).

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 3). 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 3). The trace plots for each parameter generally showed no long range (> 120,000 iterations) 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 values of the means and distributional shapes 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 4). In general, the correlations were 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 and older 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 and older alewife (Figure 6). The uncertainty in these parameters is relatively low with the coefficients of variation (CV) ranging from 18.3 to 39.1%. The uncertainty in the catchability of age-1 and older alewife, with a 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 too 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 6d). 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 that 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 6e). The estimated posterior of the survival of age-1 and older alewife from the 1967 dieoff confirms that the alewife population most likely suffered a large dieoff (Figure 6f). 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 6f).

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 7). For alewife, the CV of $\ln(\alpha_{aw})$ is relatively low at 23.9% while the CVs 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 7a,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 7c).

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 7). 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%.

Discussion

We were able to achieve our goal of reconstructing alewife and bloater dynamics in Lake Michigan from 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. The lack of a substantial fishery on either of the key prey species suggests that the statistical catch-at-age methodology is applicable to species that suffer significant time-varying mortality from sources other than fishing. This suggests that the statistical catch-at-age approach may be applicable to demographic analysis of non-harvested species and may provide insights into the “inverse” problem of estimating demographic parameters from a series of observed population abundances in ecological studies (Wood 1997). Clearly, reconstructing the population dynamics of a 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 affect the predation rates on 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 lacking large piscivores. With the introduction of five salmonine species through stocking, predation pressure rose rapidly, causing declines in the overall abundance of alewife in the system (Figures 1, 2, 5). These declines in alewife abundance led to consequent declines in the consumption rates of Chinook salmon (Figures 4c,d). This apparent food limitation of Chinook salmon coincided with collapse of the Chinook salmon population in the late 1980s (Holey et al. 1998). Our estimates of predation pressure suggest that levels in the late 1990s were rapidly approaching the levels seen during the period preceding the Chinook salmon collapse (Figure 5). 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 have been approaching conditions where such a collapse was a serious risk.

The decline of alewife in Lake Michigan can be explained by the increasing predation pressure from stocked salmonines as suggested by Madenjian et al. (2002). Here we quantitatively demonstrated that the levels of consumption predicted based on estimates of salmonine abundance and growth rates are sufficient to account for the large declines in adult alewife abundance. Levels of recruitment in alewife were estimated to have increased with increasing predation pressure as the stock size of alewife declined. This suggests that salmonine predators exert top-down control over alewife abundance in Lake Michigan. Top-down control of fish populations in large aquatic systems, such as Atlantic cod in the North-West Atlantic, has been documented for several large aquatic ecosystems (Bundy 2001, Daskalov 2002, Schindler et al. 2002, Harvey et al. 2003). However, in most cases, decreases in abundances of top predators have led to changes in the food web (Pauly et al. 1998, Schindler et al. 2002). In Lake Michigan, we have the interesting opportunity to document the changes in an fish community with the non-experimental introduction of a suite of top predators. The introduction of salmonine predators for societal and economic benefits have provided the opportunity to learn about the large-scale impacts of a pelagic predator on a previously unexploited prey population.

Due to the concern that stocked salmonines, in particular Chinook salmon, may be consuming more alewife then the population is capable of sustaining, there is particular interest in the steepness of the functional response curve at low prey densities. For most of the salmonine predators in Lake Michigan, the steepness of the functional response at low prey densities can not be estimated, since these predators had shown no measurable decrease in growth through the late 1990s, and presumably consumption, over the wide range of densities of prey that had been observed historically in Lake Michigan. For Chinook salmon, decreases in growth rates, and hence consumption, over the 1962-1999 range of alewife abundances have allowed us to estimate the steepness of the functional response, γ , at low prey densities. The maximum joint posterior estimate of this parameter leads to a minimum historical ration for an age 3 Chinook salmon in Lake Michigan in 1986 at 34% of maximum ration and a maximum historical ration in 1970 at 95% of maximum ration. Estimates of prey abundances from the late 1990s suggest that an age 3 Chinook salmon is consuming close to 50% of its maximum ration. The rations estimated in the late 1990s mirror those rations estimated for the early 1980s, prior to the Chinook salmon fishery collapse and BKD outbreak.

While the results presented here suggest some implications of our uncertainty about prey fish dynamics in Lake Michigan on the consequences of different stocking policies for salmonine predators, a full analysis is beyond the scope of this report. 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 will play an important but unpredictable role in the future dynamics of alewife population (Figure 7). 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, using techniques employed in decision analysis (Raiffa 1968), based in part on the results reported here, supports these speculations (Jones and Bence, in press).

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 occur in the Lake Michigan ecosystem. The only source of predation risk for large salmonines in Lake Michigan is attacks by the parasitic sea lamprey (*Petromyzon marinus*) and the potential influence of these attacks on foraging behavior of Lake Michigan salmonines is unknown. 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, 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 (unpublished data). 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. Clearly, for lake trout, brown trout, rainbow trout, 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 during 1962-1999, lower growth rates for these predators were not been linked to lower prey abundances (Eby et al. 1995, Szalai 2003).

Some lack of fit we 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 slight recovery of the population in the 1990s (Figure 4b). 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 2a). If changes in the energy density of the prey species, in particular alewife, or changes in the energy density of the predators, in particular Chinook salmon, occurred over time as the abundance of prey changed, this phenomenon could have led to similar patterns as those found in our estimates of alewife abundance. 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, unpublished data) and therefore, historical changes in the energy density of Chinook salmon may be plausible. Lipid levels in alewife had not increased or decreased in Lake Michigan between 1969 and 1995 (Madenjian et al. 2000) and while changes in energy density of alewife has been observed in Lake Ontario (Rand and Stewart 1998), and after 1995 in Lake Michigan (Madenjian et al. 2006), it appears unlikely that large changes in energy density of alewife occurred during the critical periods for our estimation of the functional response, the 1970s and the early 1990s.

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 this type 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.

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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*
$R_{s,y}$	Recruitment in numbers of prey species *s*
$S_{s,y}$	Stock size at the beginning of the year for 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})
M_{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*
$w_{i,y}$	Mid-year weight (kg) of prey type *i*
$p_{oth,j,y}$	Proportion in weight of alternative prey in diet of predator type *j*
$\alpha_{i,j,y}$	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})
$\ell_{i,j,y}$	Length ratio between prey type *i* and predator type *j*
$l_{j,y}$	Mid-year length of predator type *j* (cm)
$F_{i,j,y}$	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 $\hat{C}_y$

$\hat{C}_{a,y}^{chs}$	Predicted consumption per predator (kg) of chinook salmon
$\hat{T}_{s,k,y}$	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. Values for parameters assumed known during model fitting (LT: lake trout, CHS: chinook salmon, CO: coho salmon, ST: rainbow trout (steelhead lifehistory), and BT: brown trout, AW: alewife (all ages), JBL: juvenile bloater, ABL: adult bloater, RS: rainbow smelt (all sizes), SS: slimy sculpin, DW: deepwater sculpin).

Species	Natural mortality rates per year									
			age-0					age-1 and older		
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
	Habitat overlap values by predator species and prey type									
			AW	JBL	ABL	RS	SS	DW		
LT			1	1	1	0.1	0.1	0.1		
CHS			1	0.1	0	0	0	0		
CO			1	0.1	0	0	0	0		
ST			1	0.1	0	0	0	0		
BT			1	0.1	0.1	0	0	0		

Table 3. 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	(1.27, 3.55)	878
β_{aw}	0.306	0.04	(0.02, 0.74)	620
$\sigma^2_{aw,r}$	4.07	2.91	(1.75, 8.40)	1201
$\ln(\alpha_{bl})$	0.315	0.25	(-0.65, 1.28)	8602
β_{bl}	0.186	0.04	(-0.21, 0.64)	5087
$\sigma^2_{bl,r}$	5.39	2.24	(3.16, 8.97)	6560
γ	1.54E-06	7.0E-14	(1.24E-06, 1.85E-06)	2178
q_{ad}	0.140	0.003	(0.07, 0.27)	3005
q_{yoy}	0.771	0.02	(0.47, 0.99)	6111
q_{bl}	0.665	0.03	(0.35, 0.98)	1980
q_{tr}	0.023	0.0006	(0.007, 0.083)	1668
M_{67}	-1.65	1.35	(-4.40, -0.077)	1723

Table 4. Correlations between MCMC samples drawn from the posterior distributions of all estimated parameters.

	$\ln(\alpha_{aw})$	β_{aw}	$\sigma^2_{r,aw}$	$\ln(\alpha_{bl})$	β_{bl}	$\sigma^2_{r,bl}$	γ	M_{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					
M_{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

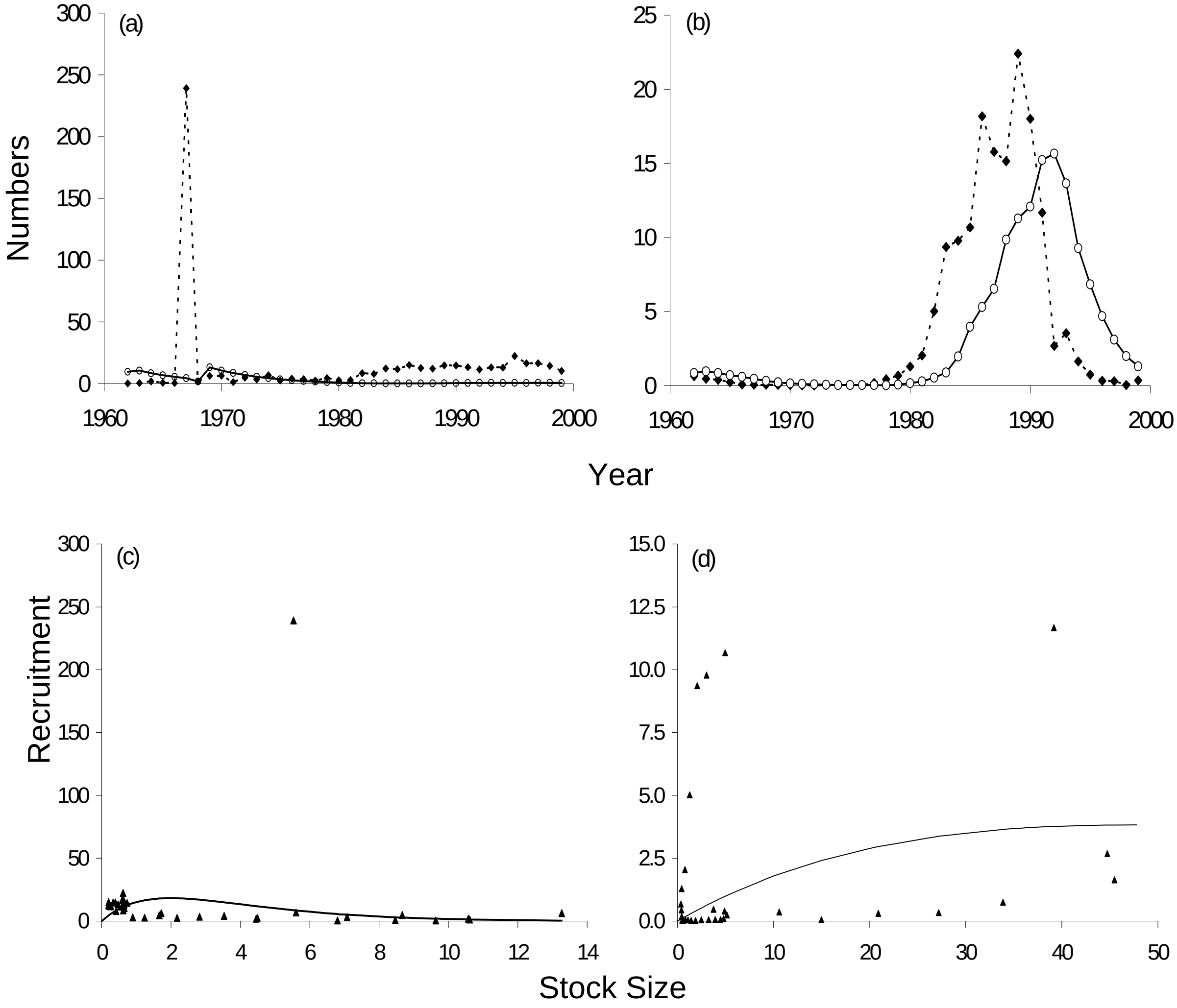

Figure 1. Maximum posterior estimates of (a) numbers (x10^9) of age 0 (diamonds and dashed line) and numbers (x 10^{10}) of age 2+ (circles and solid line) alewife at the beginning of the year, (b) numbers (x10^9) of age 0 (diamonds and dashed line) and age 2+ (circles and solid line) bloater at the beginning of the year, (c) predicted stock-recruitment curve for alewife. Stock size is numbers (x10^{10}) of age 2+ fish at the beginning of the previous year and recruitment is numbers (x10^9) of age 0 fish at the beginning of the year., (d) predicted stock-recruitment curve for bloater. Stock size is numbers (x10^{13}) of eggs produced (see text for details) by mature bloater at the beginning of the previous year and recruitment is numbers (x10^9) of age 0 fish at the beginning of the year.

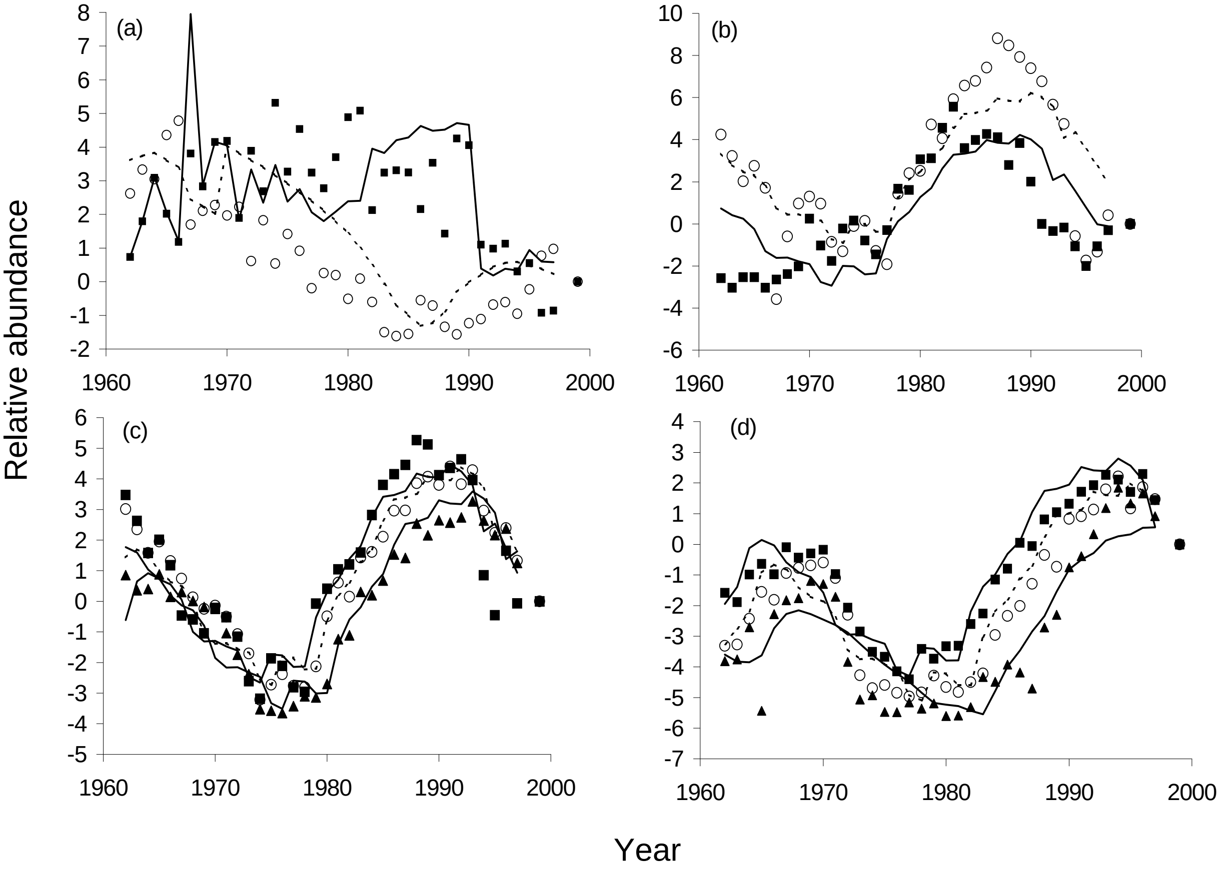

Figure 2. Observed (symbols) and predicted (lines) fall bottom trawl survey indices for (a) age-0 (squares and solid line) and age-3 and older (circles and dashed line) alewife, (b) age-0 (squares, solid), age-1 (circles, dashed), (c) age-2 (squares, solid), age-3 (circles, dashed), age-4 (triangles, solid), and (d) age-5 (squares, solid), age-6 (circles, dashed), and age-7 and older (triangles, solid) bloater in Lake Michigan, 1962-1999.

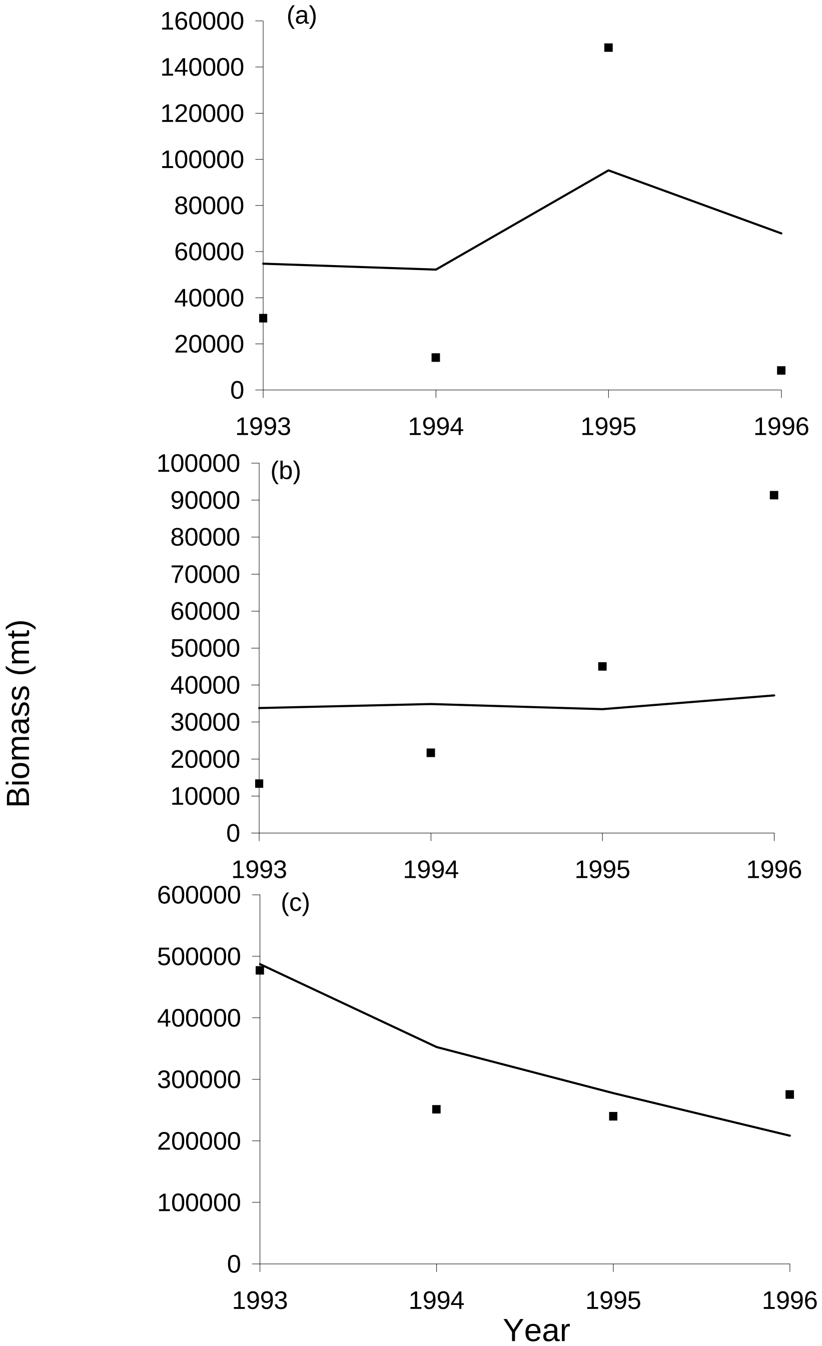

Figure 3. Observed (symbols) and predicted (lines) fall hydroacoustic biomass estimates of (a) age-0 and (b) age-1 and older alewife, and (c) bloater in Lake Michigan, 1993-1996.

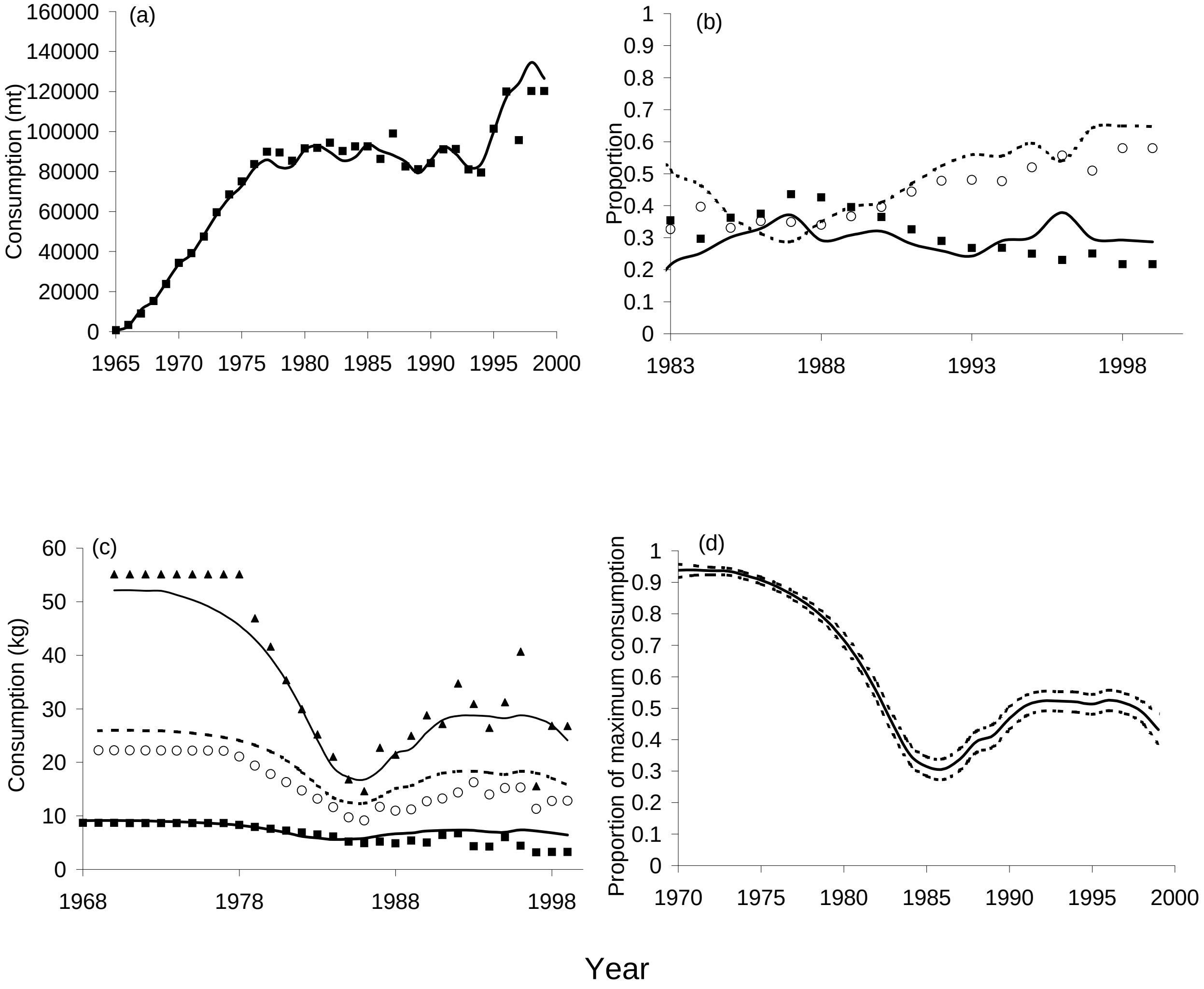

Figure 4. Predator assessment-based (symbols) and predicted (line) (a) consumption of all prey types, (b) proportion of small alewife (squares, solid line) and large alewife (circles, dashed line) in the total consumption by all five salmonine species in Lake Michigan, 1965-1999,(c) consumption per predator for age-1 (squares, solid line), age-2 (circles, dashed line), and age-3 (triangles, solid line) chinook salmon, (c) predicted proportion of maximum consumption achieved (solid line) and 95% credibility intervals for age-3 chinook salmon in Lake Michigan, 1968-1999.

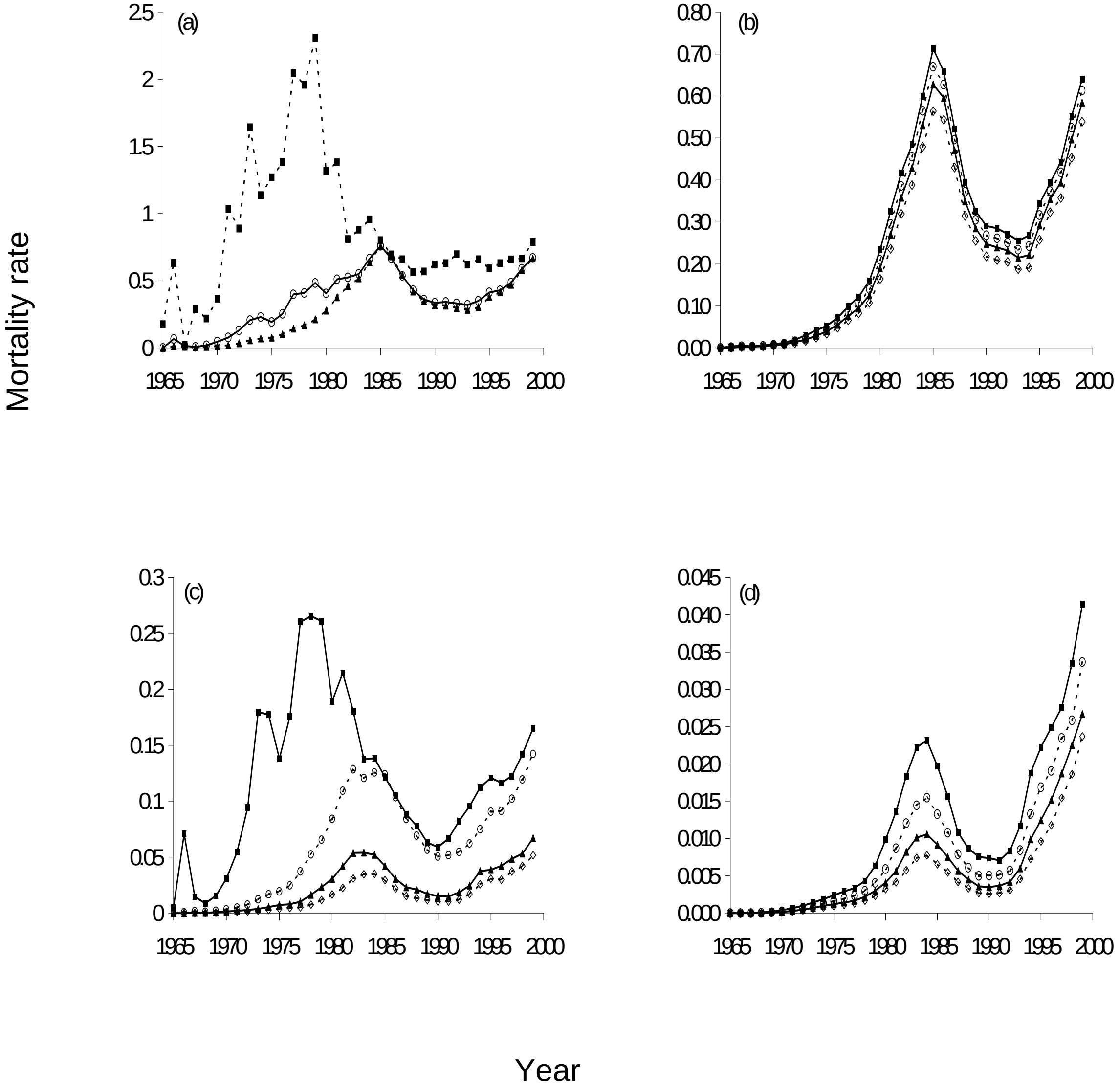

Figure 5. Predicted instantaneous predation rates (P) on (a) age-0 (squares, dashed line), age-1 (circles, solid line), and age-2 (triangles, dashed line), (b) age-3 (squares, solid line), age-4 (circles, dashed line), age-5 (triangles, solid line), and age-6 and older (diamonds, dashed line) alewife,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

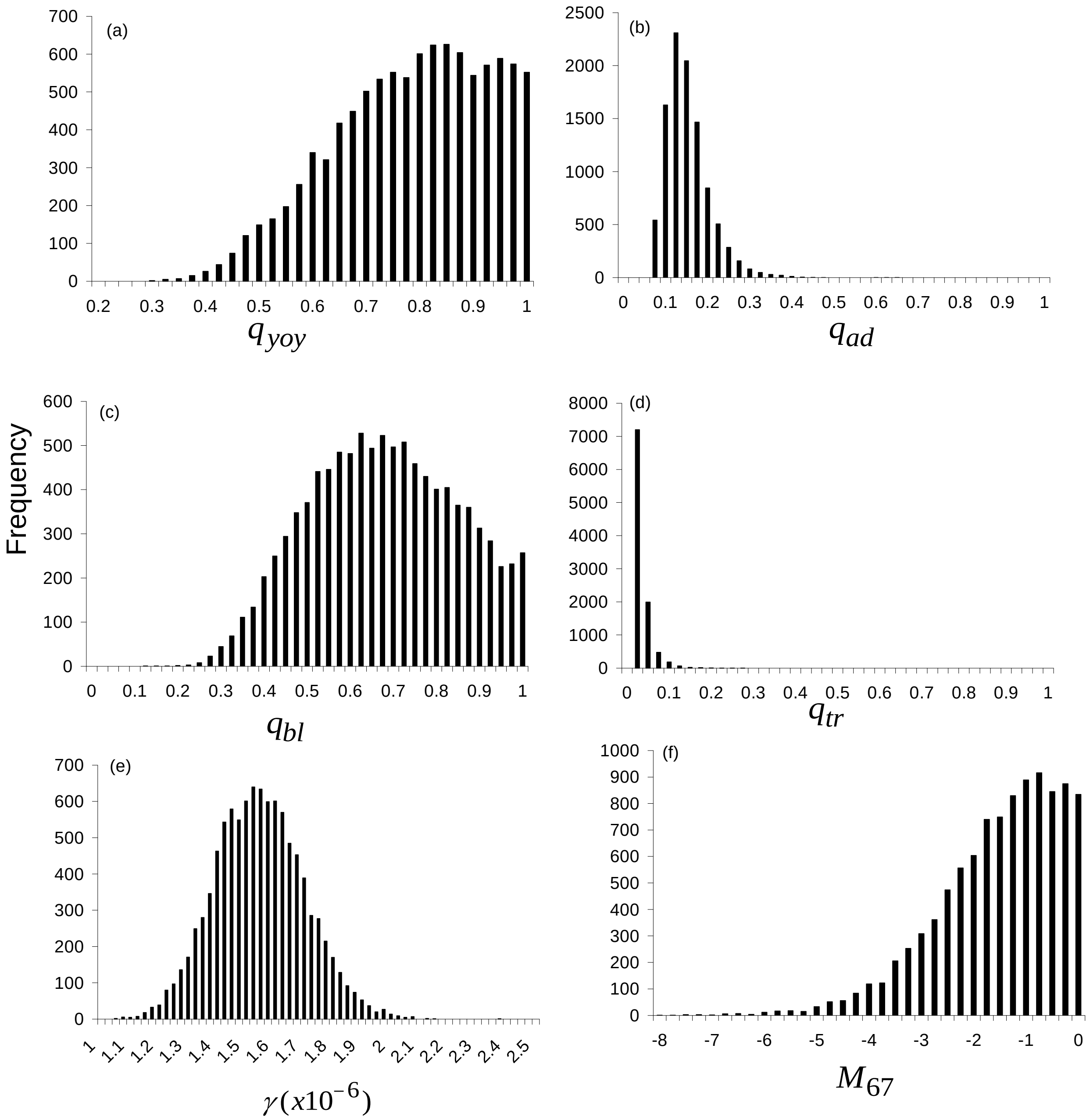

Figure 6. Posterior density functions (unnormalized) of the catchability coefficients of (a) age-0 and (b) age-1 and older alewife hydroacoustic survey, (c)bloater hydroacoustic survey,(d) age-0 alewife fall trawl survey for 1991-1999, and (e) the length-base scalar of the effective searching efficiency on an optimal sized prey for salmonine predators, and (f) instantaneous mortality rate (M_{67}) on age-1 and older alewife during the dieoff in 1967 in Lake Michigan.

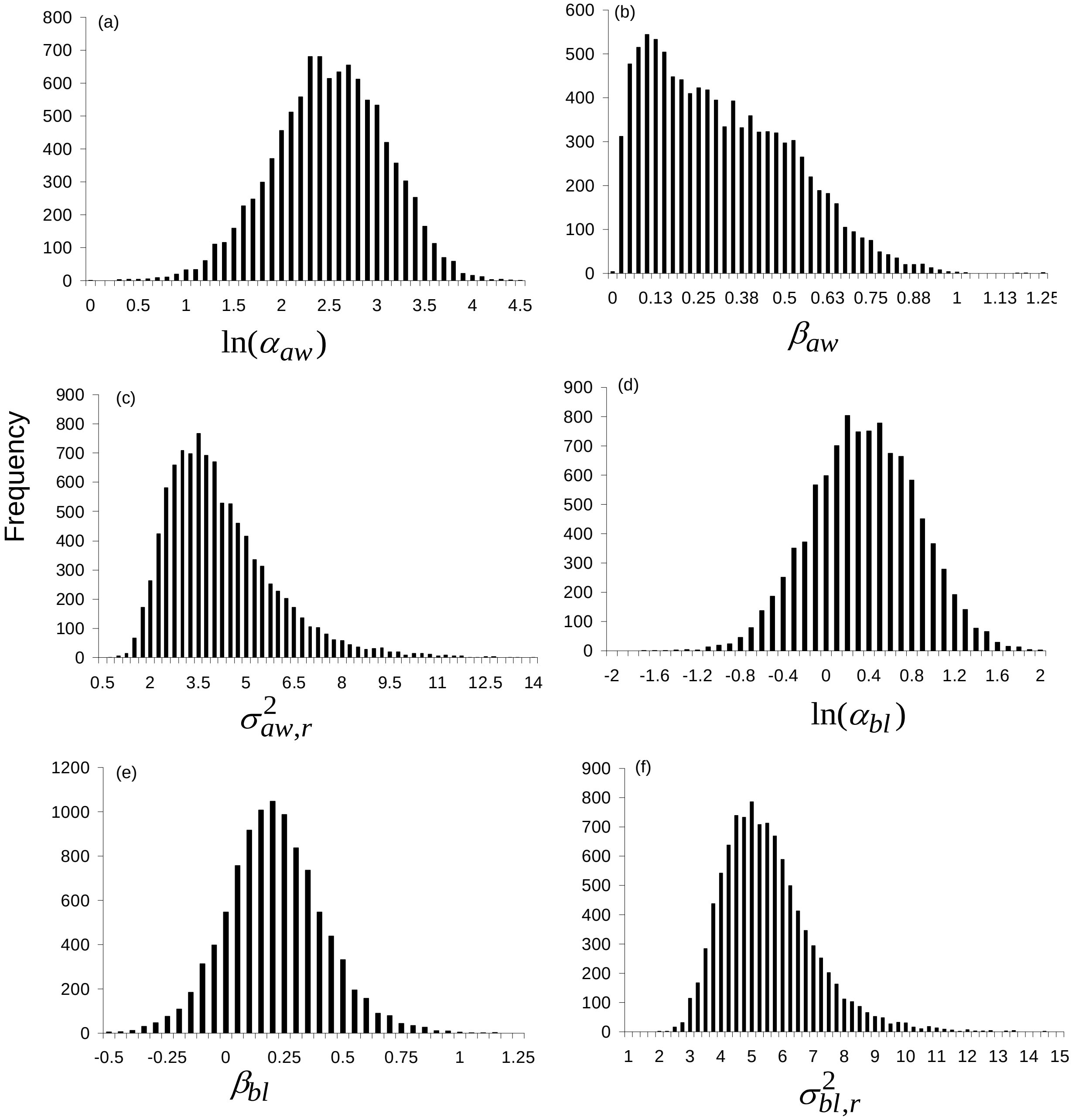

Figure 7. Posterior density function (unnormalized) of the (a) $\ln(\alpha_{aw})$, (b) β_{aw}, and (c) $\sigma^2_{aw,r}$ parameter of the Ricker stock-recruitment function for alewife and, (d) $\ln(\alpha_{bl})$, (e) β_{bl}, and (f) $\sigma^2_{bl,r}$ parameter of the Ricker stock-recruitment function for bloater in Lake Michigan.

Appendix

Symbols used in model development are defined in the text. Equations governing alewife and bloater population dynamics and for the prediction of survey indices and assessment estimates of consumption are in Tables A1 and A2. These equations are referenced in the text by *Tx.y*, where *x* is the table number and *y* is the equation number within Table *x*.

Numbers at age of alewife and bloater for later years and ages greater then zero were calculated by eq. TA1.1. Older alewife and bloater were accumulated in the last age group (*l*) by eq. TA1.2.

Mortality rates

Instantaneous total mortality rates for alewife and bloater consisted of two additive sources, background natural mortality rates and predation mortality rates (eq. TA1.3). Background natural mortality rates were not estimated during model fitting but supplied as known quantities (Table 4). While it was not possible to estimate natural mortality rates during model fitting, there was enough information to distinguish between widely separated values of natural mortality rates. Initial values for these natural mortality rates were obtained by applying Pauly's equation for each species (Pauly 1980). We initially assumed that the background natural mortality rates for age-0 fish would be higher than those for older fish. We then iteratively refit the complete model with differing higher values (e.g. 25% , 50%, 100% higher) of natural mortality rates for age-0 fish than older fish and found the Akiake's Information Criteria (AIC) was lowest for the model with higher age-0 mortality for alewife but not for age-0 bloater. We repeated this procedure for the value of natural mortality for older fish, investigating values both above and below the initial value and found the model with the lowest AIC had the values of natural mortality shown in Table 4 of the text (See Szalai 2003 for more details). These 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 and older alewife in 1967 by eq. TA1.4

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 rainbow trout (steelhead lifehistory) 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 (Szalai 2003). 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) (Table 4). 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. TA1.6a.

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. TA1.6b. The maximum consumption rates per predator of Chinook salmon were estimated from the maximum observed consumption per predator by Madenjian et al. (2002) (Table 4).

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. TA1.7). 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. TA1.8. 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 a predator to approximate its mid-year length.

Habitat overlap values were set on the perception of the degree of spatial and temporal overlap between predator and prey species (Koonce and Jones 1994). The habitat overlap values were assumed to be known and ranged from zero, indicating that a predator was unable to eat a given prey type, to one, indicating that the predator consumed a given prey type at the rate predicted by a Type II functional response (Table 4).

Instantaneous predation rates on alewife and bloater by age were calculated by eq. TA1.5 using the "average" abundance of each prey type. The consumption of age-0 to age-6+ alewife and age-0 to age-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, as described by Szalai (2003), to find an "average" abundance of alewife and bloater that produced the appropriate amount of consumption.

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. TA1.6 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. TA2.2. Total consumption by all predator types ($\hat{C}_y$) is then predicted by eq. TA2.3 for comparison with observed quantities. Additionally, we also predicted the consumption (in weight) per predator ($\hat{C}^{chs}_{a,y}$) for ages 1-3 Chinook salmon for comparison with observed quantities (eq. TA2.4). We also predicted the proportion of total consumption (by weight) on small (ages 0 and 1) and large (age-2 and older) 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 occurred in the fall of each year. 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 age-3 and older alewife for 1962-1997 were predicted by eq. TA2.5a. 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. TA2.5b.

Fall hydroacoustic survey indices were predicted by the biomass of bloater (all ages), age-0 alewife, and age-1 and older alewife present at the time of the survey (again after 10/12th's 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 and older 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 sampling (MCMC) using a Metropolis-Hastings algorithm to sample from the posterior distributions 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 A3).

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

The first six components ($\ell_1 - \ell_6$) were all assumed to follow normal or lognormal 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 A3). 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 trawl 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 Dirichlet distribution (Table A3; Williams and Quinn 1998). The effective sample size of a Dirichlet 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 straying into unlikely 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.

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 , β and σ_r^2 were obtained from each MCMC sample by linear regression as described above. Then, we drew samples of α and β 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 σ_r^2 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 σ_r^2 (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 shape of the distribution and mean of each third was examined. Substantial differences in the means or the shape of the 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).

Table A1. Model equations describing the alewife and bloater population dynamics. Note: In some cases for brevity we refer to combinations of species (*s*) and age (*a*) by a single subscript for prey (*i*) or predator (*j*) type.

Population dynamics model

$$N_{s,a+1,y+1} = N_{s,a,y} e^{-Z_{s,a,y}} \tag{TA1.1}$$

$$N_{s,l,y+1} = N_{s,l-1,y} e^{-Z_{s,l-1,y}} + N_{s,l,y} e^{-Z_{s,l,y}} \tag{TA1.2}$$

$$Z_{s,a,y} = M_{s,a} + P_{s,a,y} \quad y \neq 1967 \cap s \neq aw \tag{TA1.3}$$

$$Z_{aw,a,1967} = M_{aw,a} + P_{aw,a,1967} + M_{67} \tag{TA1.4}$$

$$P_{s,a,y} = \sum_{j} \frac{A_{i,j,y} * \tilde{N}_{j,y}}{N_{i,y}} \tag{TA1.5}$$

Predator other than chinook salmon: $$A_{i,j,y} = \frac{C_{\max,j}}{w_{i,y}} \frac{\alpha_{i,j,y} \tilde{N}_{i,y}}{\sum_{i} \alpha_{i,j,y} \tilde{N}_{i,y}} \tag{TA1.6a}$$

Chinook salmon: $$A_{i,j,y} = \frac{\alpha_{i,j,y} \tilde{N}_{i,y}}{1 + \sum_{i} \left(\alpha_{i,j,y} \tilde{N}_{i,y} w_{i,y} \middle/ C_{\max,i} \right)} \tag{TA1.6b}$$

$$\alpha_{i,j,y} = \gamma * l_{j,y} * F_{i,j,y} * HO_{i,j} \tag{TA1.7}$$

$$F_{i,j,y} = \exp\left((\ell_{i,j,y} - \ell_{opt})^{2} \middle/ spw \right) \tag{TA1.8}$$

Table A2. Model equations used in the observation sub-model. Note: In some cases for brevity we refer to combinations of species (*s*) and age (*a*) by a single subscript for prey (*i*) or predator (*j*) type.

$$C_{i,j,y} = \frac{A_{i,j,y}}{Z_{i,y}} N_{i,y}(1 - e^{-Z_{i,y}}) * w_{i,y} \qquad \text{(TA2.1)}$$

$$C_{tot,j} = \frac{\sum_i C_{i,j,y}}{1 - p_{oth,j,y}} \qquad \text{(TA2.2)}$$

$$\hat{C}_y = \sum_j C_{tot,j} \qquad \text{(TA2.3)}$$

$$\hat{C}^{chs}_{a,y} = C_{tot,chs} \Big/ \tilde{N}_{chs,a,y} \qquad \text{(TA2.4)}$$

$$\hat{T}_{s,k,y} = Log\left(\frac{\sum_a N_{s,a,y} e^{-\frac{10}{12} Z_{s,a,y}}}{\sum_a N_{s,a,1999} e^{-\frac{10}{12} Z_{s,a,1999}}} \right) \qquad \text{(TA2.5a)}$$

Excluding age-0 alewife, 1962-1990

For age-0 alewife, 1962-1990:

$$\hat{T}_{aw,0,y} = Log\left(\frac{N_{aw,0,y} e^{-\frac{10}{12} Z_{aw,0,y}}}{q_{tr} N_{aw,0,1999} e^{-\frac{10}{12} Z_{aw,0,1999}}} \right) \qquad \text{(TA2.5b)}$$

$$H_{s,k,y} = q_k Bs,_{k,y} \qquad \text{(TA2.6)}$$

Table A3. 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	$\ell_1 = \sum_{y} \sum_{k=1}^{2} \lambda_{k,y}^{aw} (\hat{T}_{k,y}^{aw} - T_{k,y}^{aw})^2$ $\lambda_{k,y}^{aw} = \frac{1}{\tau_{k,y}^{aw}}$	Normal (CL)
Bloater trawl survey	$\ell_2 = \sum_{a,y} \lambda_{a,y}^{bl} (\hat{T}_{a,y}^{bl} - T_{a,y}^{bl})^2$ $\lambda_{a,y}^{bl} = \frac{1}{\tau_{a,y}^{bl}}$	Normal (CL)
Alewife hydroacoustic survey	$\ell_3 = \sum_{y} \sum_{k=1}^{2} \lambda_{k,y}^{aw} (\ln(\hat{H}_{k,y}^{aw}) - \ln(H_{k,y}^{aw}))^2$ $\lambda_{k,y}^{aw} = \frac{1}{\upsilon_{k,y}^{aw}}$	Lognormal (CL)
Bloater hydroacoustic survey	$\ell_4 = \sum_{y} \lambda_{y}^{bl} (\ln(\hat{H}_{y}^{bl}) - \ln(H_{y}^{bl}))^2$ $\lambda_{y}^{bl} = \frac{1}{\upsilon_{y}^{bl}}$	Lognormal (CL)
Total Consumption	$\ell_5 = \sum_{y} \lambda^{C} (\ln(\hat{C}_y) - \ln(C_y))^2$	Lognormal (CL)
Chinook consumption per predator	$\ell_6 = \sum_{a,y} \lambda^{cp} (\hat{C}_{a,y}^{chs} - C_{a,y}^{chs})^2$	Normal (CL)
Consumption prey type composition	$\ell_7 = -\sum_{y} \left[\ln\Gamma(\gamma) - \sum_{j=1}^{3} \left[\ln\Gamma(\gamma_{j,y}) + (\gamma_{j,y} - 1)\ln\theta_{j,yy} \right] \right]$ $\gamma_{j,y} = \gamma\hat{\theta}_{j,y}$	Dirichlet
Recruitment penalty function	$\ell_8 = \sum_{y} \frac{1}{\varsigma} ((\hat{R}_{y}^{aw} - \overline{R}^{aw})^2 + (\hat{R}_{y}^{bl} - \overline{R}^{bl})^2)$	Normal