

A multispecies statistical age-structured model to assess predator–prey balance: application to an intensively managed Lake Michigan pelagic fish community

Iyob Tsehaye, Michael L. Jones, James R. Bence, Travis O. Brenden, Charles P. Madenjian, and David M. Warner

Abstract: Using a Bayesian modeling approach, we developed a multispecies statistical age-structured model to assess trade-offs between predatory demands and prey productivities, with the aim to inform management of top predators. Focusing on the Lake Michigan fish community, we assessed these trade-offs in terms of predation mortalities and productivities of alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) and functional responses of salmonines. Our predation mortality estimates suggested that salmonine consumption has been a major driver of prey dynamics, with sharp declines in alewife abundance in the 1960s–1980s and the 2000s coinciding with increased predation rates. Our functional response analysis indicated that feedback mechanisms are unlikely to help maintain a predator–prey balance, with Chinook salmon (*Oncorhynchus tshawytscha*) and lake trout (*Salvelinus namaycush*) consumption declining only at the lowest prey densities, while the other salmonines consumed prey at a maximum rate across all observed prey densities. This study demonstrates that a multispecies modeling approach combining stock assessment methods with explicit consideration of predator–prey interactions can provide a basis for tactical decision-making from a broader ecosystem perspective.

Résumé : Nous avons employé une approche de modélisation bayésienne pour élaborer un modèle statistique multi-espèces structuré par âge pour évaluer les compromis entre les demandes de prédation et la productivité des proies, afin d'éclairer la gestion des prédateurs de niveau trophique supérieur. Dans le cadre de l'étude, axée sur la communauté de poissons du lac Michigan, nous avons évalué ces compromis en termes de mortalité par prédation et de productivité du gaspateau (*Alosa pseudoharengus*) et de l'éperlan (*Osmerus mordax*), ainsi que des réactions fonctionnelles de salmoninés. Nos estimations de la mortalité par prédation donnent à penser que la consommation des salmoninés a joué un rôle important dans la dynamique des proies, de fortes baisses de l'abondance du gaspateau dans les années 1960–1980, puis dans les années 2000 coïncidant avec des taux de prédation accrus. Notre analyse des réactions fonctionnelles indique qu'il est peu probable que des mécanismes de rétroaction contribuent au maintien d'un équilibre prédateurs–proies, la consommation des saumons quinnats (*Oncorhynchus tshawytscha*) et des touladis (*Salvelinus namaycush*) ne diminuant que quand les densités de proies sont à leur plus faible, alors que la consommation des autres salmoninés était maximum pour toutes les densités de proies observées. L'étude démontre qu'une approche de modélisation multi-espèces qui combine des méthodes d'évaluation des stocks à la prise en considération explicite des interactions prédateurs–proies peut fournir la base d'une prise de décisions tactique dans une perspective écosystémique large. [Traduit par la Rédaction]

Introduction

Fisheries management has relied heavily on single-species stock assessment methods, wherein feedback interactions between target species and the rest of the ecosystem have been effectively ignored (Link and Garrison 2002; Van Kirk et al. 2010). Based on historical reconstruction of abundances-at-age of fish stocks using observational data, these methods provide estimates of key population and fishery parameters and associated uncertainties, allowing tactical decision-making in fisheries management (e.g., setting annual total allowable catches (TAC) and target reference points) (Quinn and Deriso 1999; Plagányi et al. 2012). However, owing to greater recognition of indirect effects of fishing on nontarget species and effects of ecological interactions on target species, there has been a growing interest in the application of ecosystem modeling (e.g., Ecopath with Ecosim and Atlan-

tis) to inform fisheries management (Christensen et al. 1996; Jennings and Kaiser 1998; NRC 1999). Because they place fisheries in a broader ecological context, ecosystem-based approaches can be used for a large-scale assessment of changes in response to anthropogenic or environmental perturbations and thus have been acknowledged as valuable tools for strategic evaluation of management policies. However, ecosystem-based approaches are not typically developed to fit models to data to assess stock-specific population dynamics or to apply standard statistical methods, such as Markov chain Monte Carlo sampling (MCMC), to quantify parameter uncertainty (Jurado-Molina et al. 2005; Plagányi et al. 2012), explicit consideration of which is considered essential for effective fisheries management (Walters and Martell 2004; Jones and Bence 2009). In light of these limitations, ecosystem-based approaches cannot be used in lieu of stock assessments to inform tactical decision-making and may only be used to provide

Received 11 June 2013. Accepted 20 December 2013.

Paper handled by Associate Editor Cliff Kraft.

I. Tsehaye, M.L. Jones, J.R. Bence, and T.O. Brenden. Quantitative Fisheries Center, Department of Fisheries and Wildlife, Michigan State University, 293 Farm Lane, Room 153, East Lansing, MI 48824, USA.

C.P. Madenjian and D.M. Warner. US Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105, USA.

Corresponding author: Iyob Tsehaye (e-mail: tsehaye@msu.edu).

a context for assessments and criteria for selecting appropriate management actions (Christensen and Pauly 2004).

One way to overcome the aforementioned limitations of ecosystem models is to employ multispecies models of intermediate complexity that incorporate the best features of single-species models while accounting for broader ecosystem considerations in view of a few well-defined objectives (Danielsson et al. 1997; Plagányi and Butterworth 2012; Plagányi et al. 2012). Instead of addressing the full range of biological, habitat, environmental, and fishery interactions that constitute fully implemented ecosystem approaches, such models would focus on major ecological processes and components that are needed to address the management objectives in question (ICES 2000; Christensen and Pauly 2004; Pikitch et al. 2004). Predator-prey interactions are a major ecological process regulating the trophic structure of many aquatic ecosystems (Carpenter et al. 1985; Christensen 1996; Bax 1998), and manipulation of the abundance of top predators, whether through exploitation or supplementation, can significantly alter the rest of the food web, especially their primary prey species. Therefore, employing modeling approaches that combine stock assessment methods with explicit consideration of predator-prey interactions would potentially allow for effective fisheries management from a broader ecosystem perspective (Link and Garrison 2002).

Several attempts have been made to incorporate predator-prey interactions into multispecies stock assessment models. Among these attempts, multispecies virtual population analysis (MSVPA), which is an extension of the single-species virtual population analysis (VPA), has been cited as one of the most successful methods to account for predation mortality in fishery models (Tsou and Collie 2001; Jurado-Molina et al. 2005). MSVPA was first developed for the North Sea fish community, but has since been applied elsewhere, including the Bering Sea (Livingston and Jurado-Molina 2000; Jurado-Molina et al. 2005) and the Georges Bank (Tsou and Collie 2001). A major weakness of MSVPA is its lack of statistical assumptions, which impedes the inclusion of observation and process errors into parameter estimation. Building upon MSVPA and its variants, recent studies have begun incorporating predation interactions into statistical catch-at-age (SCA) models, which allow the application of statistical estimation procedures in a multispecies context. There is a growing number of examples of such applications of multispecies SCA models to assess the effect of predation on exploited populations, including models to assess Pacific cod (*Gadus macrocephalus*) and northern fur seal (*Callorhinus ursinus*), predation on walleye pollock (*Gadus chalcogrammus*) in the Bering sea (Livingston and Methot 1998), Stellar sea lion (*Eumetopias jubatus*) predation on pollock in the Gulf of Alaska (Hollowed et al. 2000), Pacific cod predation on walleye pollock in the eastern Bering Sea (Jurado-Molina et al. 2005), and Pacific cod predation on arrowtooth flounder (*Atheresthes stomias*) and walleye pollock in the Gulf of Alaska (Van Kirk et al. 2010). Although these models quantified the magnitude of predation on target species, they did not account for feedback interactions between the consumptive demands of predators and productivities of prey fishes, which are important drivers of the dynamics of fish communities.

Using a Bayesian modeling approach, this study aimed to develop a multispecies SCA model to assess trade-offs between predator consumptive demands and forage fish productivities and to quantify associated uncertainties, focusing on a Lake Michigan fishery, where predator abundance is manipulated through supplemental stocking. In view of a presumed coupling between the lake's salmonine predators and major prey species, alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) (Madenjian et al. 2002; Tsehaye et al. 2014), quantifying these trade-offs should be a prerequisite for successful management of the Lake Michigan salmonine fisheries from a broader ecosystem perspective. We assessed these trade-offs for the Lake Michigan system by estimating parameters that govern the changes in abundance and productivity of alewife and rainbow smelt and the corresponding

functional feeding responses of the hatchery-supported salmonines. Ultimately, a quantitative understanding of such trade-offs would allow fishery managers to explore how management of predator populations might affect system dynamics.

Background on Lake Michigan

Owing to the combined effects of habitat degradation, overfishing, eutrophication, and invasive species, the fish community of Lake Michigan has changed considerably over the past century, with many important native species greatly reduced or extirpated and invasive species becoming more dominant (Mills et al. 1993; Eshenroder and Burnham-Curtis 1999). Most importantly, abundances of the once-dominant top predator, lake trout (*Salvelinus namaycush*), were greatly reduced in the middle of the 20th century owing to predation by sea lamprey (*Petromyzon marinus*) and overfishing, leading to expansion of invasive alewife and rainbow smelt populations to undesirable levels (Madenjian et al. 2002). To control these invasive planktivores species and rehabilitate native species, Lake Michigan has been intensively managed for several decades, with millions of native (lake trout) and nonnative (Pacific) salmonines, including Chinook salmon (*Oncorhynchus tshawytscha*), lake trout, steelhead trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), and coho salmon (*Oncorhynchus kisutch*), stocked annually since 1965 (Claramunt et al. 2012). There is good evidence that these stocking efforts have led to reduced alewife densities, allowing recovery of several native species, including deepwater sculpin (*Myoxocephalus thompsoni*), yellow perch (*Perca flavescens*), and burbot (*Lota lota*) (Madenjian et al. 2002). Additionally, the introduction of salmonines into the lake has offered the opportunity for the creation of new recreational fisheries, bringing considerable economic benefits to the region (Kotchen et al. 2006; Fenichel et al. 2010; Dettmers et al. 2012).

While the stocking of salmonines is believed to have led to the reestablishment of several native species, predator and prey abundances in Lake Michigan have fluctuated considerably since the initiation of the stocking program. Therefore, a pivotal question that Lake Michigan managers must address annually is how many salmonines can be stocked to achieve a delicate balance between rehabilitating native fishes (mainly lake trout) by maintaining invasive prey species (mainly alewife) at relatively low levels and sustaining economically important recreational fisheries by maintaining adequate prey fish for the nonnative predators (i.e., Pacific salmonines) (Madenjian et al. 2002; Bunnell et al. 2006; Dettmers et al. 2012). Early in the stocking program, salmonine abundance increased as stocking rates increased, suggesting that the lake's prey population could support even greater stocking levels (Stewart et al. 1981). By contrast, declining alewife abundance and Chinook salmon mass mortality events in the 1980s suggested that salmonine abundance levels may have exceeded prey fish productivity, which resulted in fishery managers reducing stocking rates in 1991 (Stewart and Ibarra 1991; Hansen and Holey 2002; Benjamin and Bence 2003). Although both the salmonine community and alewife population rebounded following these reductions in stocking rates, predator and prey abundances continued to fluctuate (Madenjian et al. 2002; Claramunt et al. 2012). Even with additional reductions in stocking rates in 1998 and 2005 (Jones and Bence 2009; Claramunt et al. 2012), alewife abundance has remained low. Thus, concerns about the risk of overstocking remained.

The hatchery-supported Lake Michigan fish community provides a unique opportunity to consider the importance of predator-prey interactions for fisheries and ecosystem management. Indeed, there have been several attempts to examine the balance between the predator and prey communities of Lake Michigan. Early studies were based on comparisons of estimates of predatory consumption from bioenergetics models and estimates of lake-wide prey biomass from fall trawl surveys (Stewart et al. 1981; Stewart and Ibarra 1991). However, these studies neither assessed

prey population dynamics in light of salmonine predation nor dynamically linked predator consumption with prey abundance. Jones et al. (1993) recognized the need for a dynamic model of prey fish and salmonine populations to assess the effects of changes in stocking levels on the dynamics of the prey fish community. Subsequently, Koonce and Jones (1994) developed a multispecies dynamic model for Lake Michigan that incorporated dynamic links between predator and prey population through a functional feeding response model, but did not attempt to estimate functional response parameters from empirical data. Following the methods of Koonce and Jones (1994), Szalai (2003) assessed the dynamics of alewife and bloater (*Coregonus hoyi*) populations in Lake Michigan by fitting a multispecies age-structured model using relative abundance data for prey fish (from bottom trawl and hydroacoustic surveys) and estimates of salmonine consumption (from bioenergetics models), which allowed estimation of mortality rates stemming from predation.

While earlier studies have led to a better understanding of predator-prey interactions in Lake Michigan, several recent changes in the fish community and ecosystem necessitate a reexamination of predator-prey interactions in the lake. First, adult alewife abundances have been at very low levels since the mid-2000s (Warner et al. 2011). Second, although the salmonine community continues to be mainly dependent on hatchery-reared fish, a large proportion of the Chinook salmon population in Lake Michigan is now derived from natural reproduction (Williams 2012), which could have important implications for stocking decisions. Third, Szalai (2003) assessed the dynamics of bloater along with alewife because age-composition data were available only for these prey species at that time. However, rainbow smelt may be the second most important prey of salmonines, especially for medium-sized lake trout (Madenjian et al. 2002), but predator-prey interactions involving rainbow smelt remain largely unquantified for Lake Michigan. In light of the aforementioned changes, new information available, and past unmet needs, an updated and more rigorous analysis of the predator-prey interactions in Lake Michigan could be useful for informing future stocking decisions.

Materials and methods

Multispecies SCA model

Our multispecies assessment model was built using an SCA framework (Fournier and Archibald 1982; Deriso et al. 1985; Walters and Martell 2004), in which salmonine consumption was included as a source of mortality for prey fishes. The model incorporated a population submodel, which projected abundances-at-age of alewife and rainbow smelt based on estimates of recruitment, natural mortality, and salmonine predation, and an observation submodel, which predicted observable quantities (trawl and hydroacoustic prey abundance indices, salmonine consumption, etc.) from the projected abundances. The model projected prey abundances and salmonine consumption over the time period 1962–2008 for ages 0–6 for alewife and ages 0–5 for rainbow smelt, with the last age class being an aggregate of all fish age 6 and older for alewife and age 5 and older for rainbow smelt. Three additional species, bloater, slimy sculpin (*Cottus cognatus*), and deepwater sculpin, were included as alternative prey for predators, but were not modeled dynamically. Rather, their abundances were treated as known quantities based on trawl survey estimates (Table A1). Although trawl abundance estimates for these species may be biased, salmonine consumption estimates suggest that these species play a minor role as diet for major Lake Michigan predators. Abundances-at-age of predators (Chinook salmon, lake trout, coho salmon, brown trout, and steelhead trout) over time were assumed to be known and were obtained from single-species assessment models for Lake Michigan (Tsehaye et al. 2014). In our multispecies assessment model, mortalities of alewife and rainbow smelt caused by these predators were determined by the input predator abundances (and associated demographic information), prey abun-

Table 1. List of parameters and variables used in the assessment model.

Symbol	Description
Index variables	
y	Year
m	Month
i	Prey species
j	Predator species
a	Prey age
a'	Predator age
k	Age category
Parameters and derived quantities	
N	Abundance at the beginning of the year
\bar{N}	Mean abundance during a time interval
M	Instantaneous natural mortality rate (year ⁻¹)
P	Instantaneous total predation mortality rate
Z	Total instantaneous mortality rate (year ⁻¹)
C	Annual consumption
A	Annual consumption rate per predator
α	Instantaneous attack rate of predator
h	Handling time of predator
\hat{C}	Predicted consumption (kg) of prey by predator
Mass	Mass (kg) of predator or prey fish
C_{\max}	Per-predator maximum consumption
G	Predator instantaneous growth rate
γ	Length-based scalar for a predator's effective search area
l	Length of predator (cm) at the beginning of the month
F	Size preference of predator for prey
HO	Habitat overlap of predator and prey
T	Observed trawl survey index
\hat{T}	Predicted trawl survey index
H	Observed hydroacoustic survey index
\hat{H}	Predicted hydroacoustic survey index
q	Catchability coefficient for trawl survey
Q	Catchability coefficient for hydroacoustic survey
B	Biomass at time of hydroacoustic survey
effn	Effective sample size
p	Observed proportion of consumption
\hat{p}	Predicted proportion of consumption
σ	Standard deviation
S	Spawning stock
R	Recruitment
α	Recruits per spawner at low stock size
β	Degree of compensation
ε	Error term

dances, and functional responses (relating per-predator consumption to prey abundance). Thus, our assessment model provides an assessment of the dynamics of two key prey species (alewife and rainbow smelt) and the linkages among these species, other prey fishes, and predators mediated by the predators' functional responses. The multispecies assessment model estimates annual recruitments of alewife and rainbow smelt as parameters. Stock-recruitment functions were then derived for both species based on the estimated recruitments and adult abundances in a separate step after the assessment model was fit. Individual model components are described in the sections "Population submodel" and "Observation submodel" below, and definitions of parameters and variables used in the population and observation submodels are presented in Table 1.

Input data

Several types of data were used as model input in our integrated analysis (Maunder 2003), including relative abundance of alewife, rainbow smelt, and alternative prey fishes (Table A1), size-at-age of prey fishes, and abundance, size-at-age, and consumption of predatory fishes. Relative abundance data on prey fishes were obtained from fall bottom trawl (1962–2008) and hydroacoustic surveys

(1992–1996; 2001–2008) conducted by the US Geological Survey Great Lakes Science Center (USGS-GLSC). Since 1962, USGS-GLSC has sampled the prey fish community in Lake Michigan each fall using bottom trawls at fixed locations. Between 1962 and 1966, sampling was conducted along a single transect off Saugatuck, Michigan. Starting in 1967, sampling was expanded to four transects. Since 1973, sampling has been conducted lake-wide (Hatch et al. 1981; Krause 1999). Fish caught in bottom trawls were sorted by species, counted, and weighed in aggregate. When total catch exceeded 20 kg, a random sample of roughly 10–15 kg was sorted by species, counted, and weighed; the remainder of the catch was assumed to have the same species composition and mass to count ratio. A subsample of alewife and rainbow smelt were aged using scales (1984–2002) and otoliths (2002–2008). Thus, trawl surveys provided information on age-specific relative abundance and biomass of alewife and rainbow smelt, along with overall abundance and biomass of bloater, slimy sculpin, and deepwater sculpin. Age-1 and age-2 alewives are not closely associated with the bottom, and thus catches for these age classes in trawl surveys are not considered to accurately reflect abundances levels. As a result, we only utilized relative indices of abundance of age-0 and age-3 and older alewife for model fitting. From 1992 to 1996 and 2001 to 2008, the Lake Michigan prey fish community was also assessed by the USGS-GLSC using fall hydroacoustic surveys. In these surveys, both alewife and rainbow smelt biomass estimates were divided into two age classes (age 0 and age 1 and older). For a description of the Lake Michigan hydroacoustic survey program and associated analyses, see Warner et al. (2011).

Mass (Table A2) and length-at-age of prey fish were included as input data for the estimation of functional response parameters. For alewife, mass-at-age data were obtained by dividing age-specific biomasses by abundances from the fall bottom trawl survey data. For rainbow smelt, we used mass-at-age data from Lantry and Stewart (1993), adjusted based on the biomass to abundance ratio of age-0 and age-1 and older fish from the trawl surveys. For all other prey species, mean masses were calculated by dividing total biomasses by total abundances obtained from the trawl surveys. For all species, length-at-age data were generated based on mass-at-age data using length–mass relationships provided in Szalai (2003).

Estimates of age-specific abundance at the beginning of the year for lake trout, Chinook salmon, coho salmon, brown trout, and steelhead trout were obtained from predator assessment models (Tsehaye et al. 2014; Table A3). Estimates of natural and fishing mortality and maturity schedules from the predator assessment models were also used as model inputs (Tables A4 and A5). Annual predator consumption estimates by prey type, categorized as small (age 1 and younger) alewife, large (age 2 and older) alewife, and all other prey fishes (a combination of rainbow smelt, bloater, deepwater sculpin, and slimy sculpin) were also drawn from these predator assessment models and treated as observed data for the assessment model. These time series of consumption estimates were obtained based on age-specific abundance estimates, mortality rates, and growth data using a production–conversion efficiency method in Ney (1990), which was also described in Tsehaye et al. (2014). Predator mass-at-age data were derived from biological samples collected from recreational fishers as part of a creel survey program conducted by the Michigan Department of Natural Resources (MDNR) (Tables A6 and A7). Chinook salmon and lake trout mass-at-age varied over time, whereas the other predators were assumed to have constant mass-at-age in all years based on available mass-at-age data.

Population submodel

The population submodel projected alewife and rainbow smelt abundances forward over time for each cohort using an exponential population model, with total mortality for each species assumed to consist of a background natural mortality component and a predation mortality component. We chose to use a monthly time step,

rather than annual, to account for monthly variations in predation mortality and to obtain more accurate analytic approximations for predation mortalities (see below for explanation).

$$(1) \quad N_{i,a,y,m+1} = N_{i,a,y,m} e^{-(M_{i,a,y,m} + P_{i,a,y,m})}$$

Age-0 abundances (recruitments) were estimated as model parameters, and abundances of older age classes at the beginning of the year were calculated as

$$(2) \quad N_{i,a+1,y+1,1} = N_{i,a,y,12}$$

for all but the last age class and as

$$(3) \quad N_{i,a,y+1,1} = N_{i,a,y,12} + N_{i,a-1,y,12}$$

for the last age group.

Background natural mortality rates were assumed to be known for both species and were obtained using Pauly’s (1980) equation. Natural mortality was also assumed to remain constant over time for all ages, but an additional source of natural mortality was applied to age-1 and older alewife in 1967 to account for a large die-off of alewife that occurred that year. The magnitude of this secondary natural mortality component was estimated as a model parameter.

Total predation mortality-at-age of each prey species was calculated based on per-predator consumption rates and predator and prey abundances-at-age.

$$(4) \quad P_{i,a,y,m} = \sum_j \sum_{a'} \frac{A_{i,a,j,a',y,m} N_{j,a',y,m}}{N_{i,a,y,m}}$$

For these calculations, monthly predator abundances were generated for each of the salmonine species based on the input data on annual abundance and mortality rates from the predator assessment models. Monthly predator numbers were calculated by accounting for monthly natural mortality ($M/12$) and fishing mortality (based on monthly proportions of fishing) and a pulse of spawning mortality (applicable for all salmonines except lake trout). To be exact, the calculation of predation mortality (eq. 4) should be based on mean prey and predator abundance over a given time step rather than abundance at the beginning of the time step. However, because the calculation of mean prey abundance based on abundance at the beginning of the time step requires an estimate of predation mortality, i.e.,

$$\bar{N} = \frac{N}{M + P} [1 - e^{-(M+P)}]$$

eq. 4 is transcendental and can only be solved iteratively (e.g., Szalai 2003; Jurado-Molina et al. 2005). Nevertheless, because we used a monthly time step, changes in abundance between time steps was expected to be modest; thus, \bar{N} could be approximated by N , which allowed predation mortality to be estimated analytically (e.g., Van Kirk et al. 2010).

For Chinook salmon and lake trout, per-predator consumption was calculated using a type II multispecies functional response, which allows mortality rates to respond to changes in predator and prey abundances:

$$(5) \quad A_{i,a,j,a',y,m} = \frac{\alpha_{i,a,j,a',y,m} N_{i,a,y,m}}{1 + \sum_{i=1}^5 \alpha_{i,a,j,a',y,m} h_{i,a,j,a'} N_{i,a,y,m}}$$

Type II functional responses account for satiation effects and have been judged more to be appropriate for actively searching fish (Hollowed et al. 2000; Moustahfid et al. 2010). Handling time (h) was calculated as the ratio of prey mass to maximum consumption per predator, which was calculated as a function of gross conversion efficiency and mass increment (Tables A6–A8). For brown trout, coho salmon, and steelhead trout, we initially estimated predation mortality assuming that consumption rates also followed a type II multispecies functional response. However, our results indicated that brown trout, coho salmon, and steelhead trout consumed at a constant rate, given that they had fairly constant mass-at-age over the modeled time period. Consequently, consumption per predator for these species was calculated assuming that these fishes were feeding at a constant (maximum) rate over the years:

$$(6) \quad A_{i,a,j,d',y,m} = \frac{C_{\max j',d'} \alpha_{i,a,j,d',y,m} N_{i,a,y,m}}{\text{Mass}_{i,a,m} \sum_{i=1}^5 \alpha_{i,a,j,d',y,m} N_{i,y,m}}$$

The instantaneous attack rate for each predator type and age class on each prey type and age class was a function of predator search efficiency, size preference of prey, habitat overlap with prey, and predator length at the beginning of the month (Jones et al. 1993):

$$(7) \quad \alpha_{i,a,j,d',y,m} = \gamma_{j,d',y,m}^i F_{i,a,j,d',y,m} \text{HO}_{ij}$$

Predator lengths at the beginning of the month were obtained based on masses at the beginning of the month, which were derived from masses at the beginning of the year using estimates of instantaneous growth rate:

$$(8) \quad G_{j,a,y} = \ln \left(\frac{\text{Mass}_{j,a+1,y}}{\text{Mass}_{j,a,y}} \right)$$

As in Jones et al. (1993), the size preference of a predator depended on its length relative to that of its prey and was modeled as a bell-shaped function with peak preference of 1 at a prey to predator length ratio of 0.25.

$$(9) \quad F_{i,a,j,d',y,m} = e^{\left[\frac{-(\ell_{i,a,j,d',y} - 0.25)^2}{0.01} \right]}$$

Habitat overlap between a prey and a predator, which ranged from zero to one, were set equal to the values used in Koonce and Jones (1994). The effective search efficiencies, which determine how fast consumption rates increase at low prey abundances, were estimated as model parameters.

Observation submodel

The observation submodel predicted trawl and hydroacoustic indices of abundance for alewife and rainbow smelt based on abundances-at-age at the beginning of the tenth month of the calendar year, when the annual trawl and hydroacoustic surveys are generally conducted. The model predicted trawl relative abundance for age-0 and age-3 and older alewife and age-0 and age-1 and older rainbow smelt:

$$(10) \quad \hat{T}_{i,k,y} = q_k N_{i,k,y,10}$$

The model also predicted hydroacoustic biomass for age-0 and age-1 and older alewife and rainbow smelt:

$$(11) \quad \hat{H}_{i,k,y} = Q_k B_{i,k,y,10}$$

Catchability coefficients were estimated as model parameters for each of the hydroacoustic and trawl surveys. As measures of relative abundance, the trawl and hydroacoustic indices provided information on trends in prey abundances, but not direct information on absolute prey abundance. Therefore, the model's estimates of absolute abundance were informed by the input data on annual consumption by predators, such that estimated prey numbers are large enough to support annual consumption rates.

The observation submodel predicted consumption in mass of each prey species by each predator species to match the input data on consumption using Baranov's catch equation based on estimated predation mortality rates.

$$(12) \quad \hat{C}_{i,j,y,m} = \frac{P_{i,j,y,m}}{Z_{i,y,m}} N_{i,y,m} (1 - e^{-Z_{i,y,m}}) \text{Mass}_{i,m}$$

Finally, the predicted consumption of each prey species by each predator species was used to calculate the proportion of consumption by prey and predator type.

Model fitting

Our multispecies SCA model was developed using AD Model Builder (Fournier et al. 2012). We adopted a Bayesian approach to model fitting, whereby parameter point estimates were obtained by minimizing the negative log-posterior probability of the estimates. This approach to estimation is also known as highest posterior density estimation, or penalized likelihood (Schnute 1994). Uniform priors (on the log_e scale) were specified for each parameter so that parameter estimates were mainly influenced by observed data. The objective function used in the optimization of model fits consisted of seven log-likelihood components (Table 2), one corresponding to each of the data sources. Each of the likelihood functions was selected based on the assumed error structure for the corresponding observed data. The errors associated with trawl and hydroacoustic abundance indices were assumed to have a log-normal distribution. The errors associated with the proportion of consumption by predator type and the proportion of consumption by prey type were assumed to follow a Dirichlet distribution. The effective sample size for the Dirichlet distribution for both the proportion of consumption by predator and the proportion of consumption by prey type was set at the same value (54) as in Szalai (2003), which was obtained based on McAllister and Ianelli's (1997) iterative method to find the appropriate effective sample size.

The fitted assessment model was considered to have converged on the highest posterior density of parameter estimates when the gradient of the objective function was less than 1.0×10^{-4} with respect to each parameter. In total, 112 parameters were estimated as part of the model-fitting process, including annual recruitment for alewife and rainbow smelt, the effective search efficiencies for the different predators, catchability coefficients for the trawl and hydroacoustic surveys, and the standard dispersions for all data sources with a log-normal distribution. To assess uncertainty in parameter estimates, posterior probability distributions of parameters were obtained using MCMC sampling. The Metropolis–Hastings algorithm within AD Model Builder (Fournier et al. 2012) was used to obtain MCMC samples from the joint posterior distribution of parameter estimates and derived quantities. The MCMC chain was run for 1.1 million samples, saving every hundredth sample, to produce a total saved sample size of 10 000 after 1000 samples were discarded as burn-in. For each parameter, MCMC chains were evaluated for adequacy (convergence and sufficient information) using (i) trace plots for each estimated parameter and derived variable as a visual check to ensure that the chain was well-

Table 2. Negative log-likelihood functions used in model fitting.

Component	Equation	Distribution
Assessment model		
Trawl survey	$L = \sum_y \sum_k \left\{ \ln(\sigma_T) + \frac{[\ln(\hat{T}_{i,k,y}) - \ln(T_{i,k,y})]^2}{2\sigma_{T,k}^2} \right\}$	Log-normal
Hydroacoustic	$L = \sum_y \sum_k \left\{ \ln(\sigma_H) + \frac{[\ln(\hat{H}_{i,k,y}) - \ln(H_{i,k,y})]^2}{2\sigma_{H,k}^2} \right\}$	Log-normal
Total consumption	$L = \sum_y \left\{ \ln(\sigma_C) + \frac{[\ln(\hat{C}_y) - \ln(C_y)]^2}{2\sigma_C^2} \right\}$	Log-normal
Proportion of consumption by predator type	$L = -\sum_y [\ln \Gamma(\text{effn}) - \sum_{j=1}^3 \ln \Gamma(\text{effn} \times \hat{p}_{j,y}) + \sum_{j=1}^3 (\text{effn} \times \hat{p}_{j,y} - 1) \ln p_{j,y}]$	Dirichlet
Proportion of consumption by prey type	$L = -\sum_y [\ln \Gamma(\text{effn}) - \sum_{i=1}^3 \ln \Gamma(\text{effn} \times \hat{p}_{i,y}) + \sum_{i=1}^3 (\text{effn} \times \hat{p}_{i,y} - 1) \ln p_{i,y}]$	Dirichlet
Stock–recruitment relationships	$L = \sum_y \left\{ \ln(\sigma_r) + \frac{[\ln(R_y/S_y) - \ln(\hat{R}_y/\hat{S}_y)]^2}{2\sigma_r^2} \right\}$	Log-normal

mixed and did not show “stickiness”, (ii) the effective sample size of the saved MCMC chains, and (iii) the similarity between the first 10% and last 50% of the saved chains was tested using a standard Z score test (Geweke 1992). All MCMC chain diagnostics were conducted in R (R Development Core Team 2010) using the CODA package (Plummer et al. 2010).

Stock–recruitment relationships for alewife and rainbow smelt

We estimated stock–recruitment relationships for alewife and rainbow smelt in a separate step outside the SCA model using the time series of abundances-at-age estimated by the SCA model. Point estimates of stock–recruitment parameters were obtained by fitting a stock–recruitment model to a time series of abundances-at-age derived from the highest posterior density model fit. Stock size was defined as the abundance of age-2 and older fish for alewife and age-1 and older fish for rainbow smelt, and recruitment was defined as the abundance of age-0 fish for both species. For each species, we fit a linearized form of the Ricker stock–recruitment function:

$$(13) \quad \log_e(R_y/S_y) = \log_e(\alpha) - \beta S_y + \varepsilon_y$$

where $\varepsilon_y \sim N(0, \sigma_r^2)$.

Just as with the assessment model, the stock–recruitment model was fit for each species by minimizing the negative log-posterior density of parameter estimates using AD Model Builder. Uniform priors (on the \log_e scale) were used for each parameter ($\log_e(\alpha)$, $\log_e(\beta)$, $\log_e(\sigma_r)$) so that the resulting posterior distributions would mainly be influenced by observed data. A log-normal likelihood function was used in model fitting based on the assumed distribution of observation error for R/S (Table 2).

Determination of uncertainty in the stock–recruitment relationships for alewife and rainbow smelt followed a three-stage approach described in Haeseker et al. (2003) and Szalai (2003), which was based on a method developed for sampling from the joint posterior probability distribution for hierarchical models (Gelman et al. 2004). In the first stage, the MCMC procedure described above was used to obtain 10 000 time series of recruit and spawning stock abundances for each species. In the second stage, a linearized Ricker stock–recruitment function was fit to each of these plausible time series of recruitment and stock abundances using the same methods described above for obtaining point estimates. For each time series, this yielded highest posterior density estimates of the parameters of the stock–recruitment function ($\log_e(\alpha)$, $\log_e(\beta)$, $\log_e(\sigma_r)$) as well as the variance–covariance matrix

for $\log_e(\alpha)$ and $\log_e(\beta)$. While these were the most plausible stock–recruitment parameters for each time series, they did not capture all the uncertainty, because other stock–recruitment parameters could also have produced each time series. The third stage was intended to capture this additional uncertainty, in which a single random sample of stock–recruitment relationship parameters was drawn for each time series based on the stage 2 results. For $\log_e(\alpha)$ and $\log_e(\beta)$, the sample was drawn from a bivariate normal distribution, with the vector of means and variance–covariance matrix obtained in stage 2. For σ_r^2 , a scaled inverse χ^2 distribution was used with a scale parameter equal to the highest posterior density estimate of σ_r^2 and degrees of freedom equal to two less than the number of years of stock–recruitment observations. The end result of this three-stage process was one set of stock–recruitment parameters for each MCMC sample. Finally, MCMC chain diagnostics were performed for the stock–recruitment parameters using the same approaches previously described.

Results

Model fits

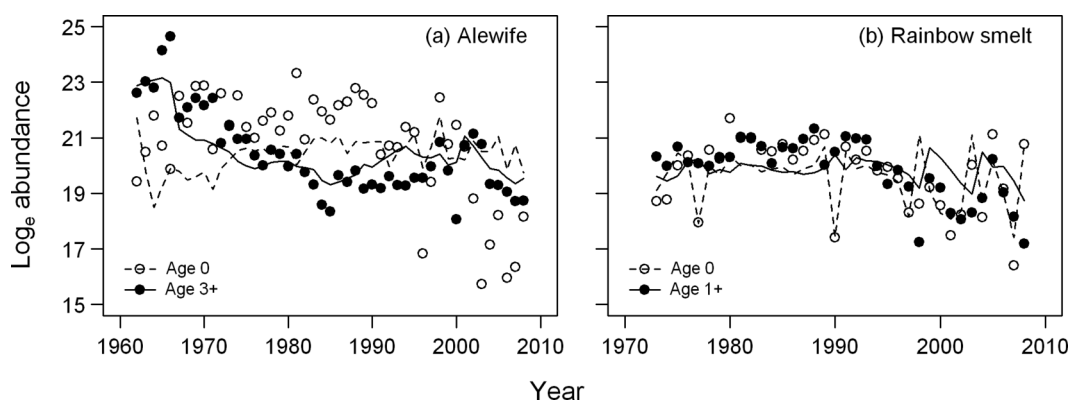
The assessment model successfully converged on a solution, with the maximum gradient of the objective function less than 1.0×10^{-4} . Based on all criteria used to evaluate convergence, the MCMC chain for each of the parameter estimates was also judged to have converged to the underlying posterior probability distributions and to contain enough information to characterize uncertainty in parameter estimates. Trace plots showed no “stickiness”, effective sample sizes were similar to actual number of saved MCMC samples, and the means of the first 10% and last 50% of the saved samples were similar, with Geweke’s (1992) Z score values of the differences between the means of the first 10% and last 50% having absolute values less than two for almost all parameters (Table 3).

Predicted values generally matched observed data quite well for age-3 and older alewife trawl abundance indices, with the mean absolute percent error between observed and predicted values being approximately 3.2% (Fig. 1). However, predicted age-3 and older alewife abundance indices were consistently above the observed for the most recent years. Model fits to observed age-0 alewife relative abundances were worse than those for age-3 and older, and the mean absolute percent error between observed and predicted values was approximately 8.3%. By contrast, model fits closely matched rainbow smelt trawl abundance indices for both age groups, with a mean absolute percent error between observed

Table 3. Highest posterior density estimates (HPD) and lower and upper 95% Bayesian credible limits of catchability, survival during the 1967 die-off (S_{67}), functional response and stock–recruitment parameters, and coefficients of variation (CV) and Geweke's (1992) Z score of the posterior probability distributions of these parameters.

Parameter	Species	Age	HPD	Lower 95% limit	Upper 95% limit	CV (%)	Z score
q	Alewife	0	0.13	0.07	0.19	24.70	0.59
		3+	0.29	0.15	0.37	22.16	0.16
	Rainbow smelt	0	0.09	0.06	0.17	23.93	-1.61
		1+	0.08	0.05	0.11	20.31	-0.24
Q	Alewife	0	0.68	0.32	1.58	29.14	-0.24
		1+	0.24	0.08	0.40	28.30	-0.75
	Rainbow smelt	0	0.42	0.16	1.10	52.42	-1.04
		1+	0.54	0.16	0.97	42.47	-1.95
S_{67}		1+	0.26	0.14	0.43	34.20	0.03
γ	Chinook salmon		1.73×10^{-6}	1.43×10^{-6}	2.03×10^{-6}	11.03	0.53
	Lake trout		2.13×10^{-6}	1.23×10^{-6}	3.63×10^{-6}	29.54	-1.57
σ_T	Alewife		2.59	2.14	3.12	7.53	-1.24
	Rainbow smelt		1.12	0.87	1.36	11.34	-1.95
σ_H	Alewife		0.80	0.60	1.44	23.02	-0.25
	Rainbow smelt		1.11	0.87	1.81	18.79	-1.78
σ_C			0.53	0.44	0.66	14.61	0.36
$\ln(\alpha)$	Alewife		1.27	0.80	1.66	22.11	0.29
	Rainbow smelt		1.54	0.30	2.61	48.30	2.70
β	Alewife		8.23×10^{-11}	3.43×10^{-11}	10.13×10^{-11}	36.10	-0.02
	Rainbow smelt		1.85×10^{-10}	0.95×10^{-10}	3.80×10^{-10}	37.02	-0.01
σ_r	Alewife		0.71	0.48	1.08	28.26	-2.06
	Rainbow smelt		1.12	0.74	1.60	19.56	2.20

Fig. 1. Observed (symbols) and predicted (lines) fall bottom trawl survey indices for age-0 and age-3+ alewife and age-0 and age-1+ rainbow smelt.



and predicted values of approximately 3.5%. However, the model slightly underestimated the relative abundance of age-1 and older rainbow smelt during the 1980s and overestimated their relative abundance during the late 1990s and 2000s. Even though the hydroacoustic surveys sampled a larger proportion of the population than the trawl surveys (as indicated by the respective catchability estimates), model fits for the hydroacoustic survey were in general worse than those for the trawl survey (Fig. 2), with the mean absolute percent error between observed and predicted values being greater than 60%. This indicates that the trawl estimates represented prey abundance more precisely in light of all the other data sets informing the integrated analysis (Maunder 2003). While the predicted hydroacoustic indices of abundance matched observed data quite well for the years 2001–2008, model predicted values did not fit observed data very well for earlier years. For both age-1 and older alewife and rainbow smelt, predicted values did not reflect the sharp increases observed in the hydroacoustic survey from 1992–1996.

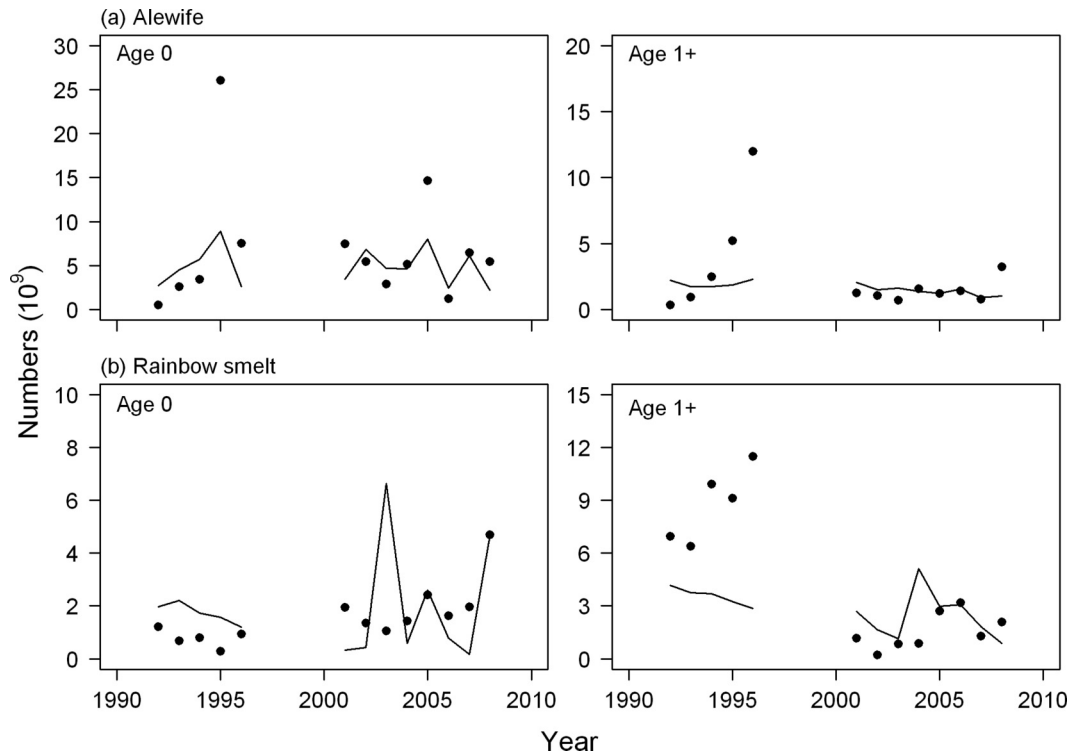
Model predictions of total consumption fit input data well (Fig. 3), with the mean absolute percent error between observed and predicted values being ~7.1%. Model predictions of proportion of consumption by the different salmonines also closely fit observed data, with a mean absolute percent error between ob-

served and predicted values of ~7.5%. Both observed and predicted values indicated that the proportion of consumption by Chinook salmon increased during the 1960s and 1970s, accounting for more than half the total consumption of all modeled predators thereafter, during which time the total consumption by the other salmonines remained almost constant (Fig. 3a). In contrast to total consumption, the model had difficulty matching the proportion of total consumption by prey type, with the mean absolute percent error between observed and predicted values being ~30%. In particular, predicted proportions of large alewife were slightly higher than observed values in later years, while predicted proportions of small alewife were lower than observed values.

Parameter estimates and uncertainty

Estimates of catchability coefficient were higher for the hydroacoustic survey than for the trawl survey, but they varied among age classes for both species. The steepness of the functional response at low prey densities was higher for lake trout than for Chinook salmon (Table 3; Fig. 4a). Because the other salmonine species showed no detectable variation in growth associated with changes in prey abundance, their functional response could be represented by a horizontal line (Fig. 4a). While

Fig. 2. Observed (symbols) and predicted (lines) fall hydroacoustic abundance estimates of age-0 and age-1+ alewife and age-0 and age-1+ rainbow smelt.



the same was the case with lake trout growth in the earlier years, which were included in the study by Szalai (2003), growth changes in later years of data (2000–2008) allowed us to estimate the search efficiency for this species. The Ricker model fit to time series of model-predicted prey numbers at age showed a stronger stock–recruitment relationship for alewife than for rainbow smelt, with similar production of recruits per spawner at low stock size (α) for both species, but a lower degree of compensatory density dependence (β) for alewife than for rainbow smelt (Table 3; Fig. 4b). Our comparisons of model-predicted changes in Chinook salmon and lake trout consumption and alewife recruitment in relation to prey abundance indicate that these predators appear to become food limited at about the same point where recruitment starts to decline with decreases in stock size (Figs. 4a and 4b).

The 95% Bayesian credible intervals of parameter estimates generally had narrow ranges, and the associated coefficients of variation (CV) indicate that most parameters were estimated with a low degree of uncertainty (Table 3), although there were some exceptions. Uncertainties in estimates of catchability coefficients were greater for rainbow smelt (CV range: 20%–52%) than for alewife (CV range: 22%–29%) depending on age and type of survey. For the length-based scalar of the effective search efficiency, uncertainty was greater for lake trout (CV = 30%) than for Chinook salmon (CV = 11%). The survival of age-1 and older alewife during the 1967 die-off was estimated with a CV of 34%.

The posterior probability distributions of the stock–recruitment parameters generally suggested a higher degree of uncertainty for rainbow smelt than for alewife, particularly about the production of recruits per spawner at low stock size (Table 3). For alewife, the CV of $\log_e(\alpha)$ and σ was relatively low (22% and 29%, respectively), while the CV of β was larger (36%). Although there was fairly high uncertainty in the parameters of the stock–recruitment relationships of both species, the relatively low level of σ (0.71) for alewife indicates a relatively stronger stock–recruitment relationship for alewife than for rainbow smelt, for which $\sigma = 1.12$. Besides allowing us to estimate the search

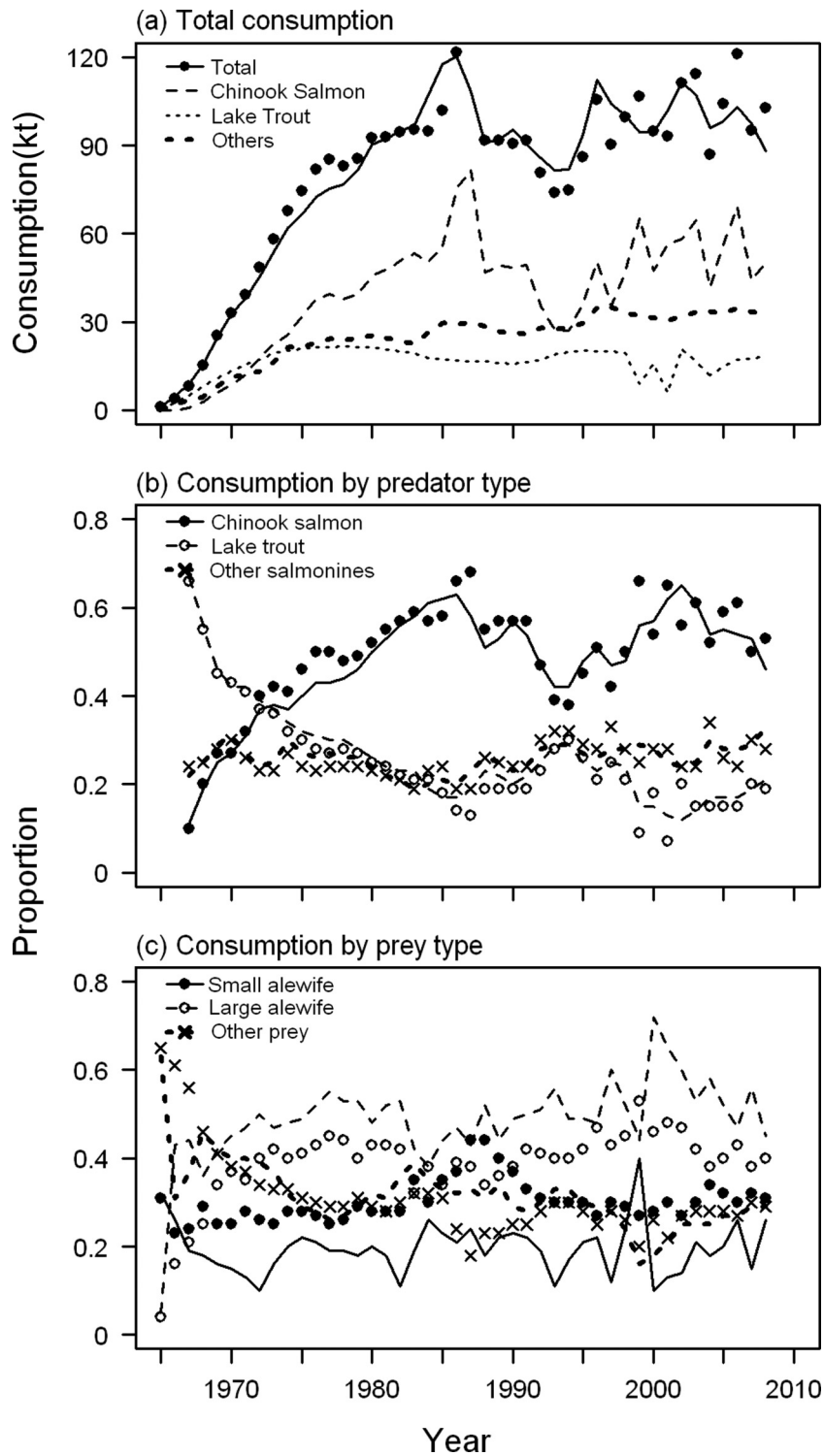
efficiency for lake trout, the additional data from 2000–2008 resulted in less uncertainty in parameter estimates than in Szalai (2003), where the effective search efficiency for Chinook salmon and $\log_e(\alpha)$ and β for alewife were estimated with higher CVs of 17%, 24%, and 65.4% versus CVs of 11%, 22%, and 36%, respectively, in this study.

Changes in prey abundance, predation mortality, and salmonine consumption

While observed data indicated a steep decline in alewife recruitment since the late 1990s (Fig. 1a), the decline in model-predicted recruitment was less clear, although there were several instances of lower recruitment levels in recent years (Fig. 5a). For the years prior to 1990, neither model estimates nor observed data indicated a clear temporal pattern in alewife recruitment (Fig. 5). Compared with alewife, rainbow smelt showed more variable recruitment, but, just as with alewife, occurrences of lower rainbow smelt recruitment were more frequent in recent years. In contrast to the variations in recruitment, model estimates as well as observed data indicated a clear decline in age-3 and older alewife abundances during the 1970s and early 1980s (Fig. 5a). This was followed by an increase in abundance of age-3 and older alewife during the late 1980s and 1990s, with a peak abundance in 2001 resulting from a strong year-class in 1998. Since the early 2000s, there has been a consistent decline in abundance of age-3 and older alewife. By contrast, estimates of age-1 and older rainbow smelt abundance showed no clear temporal patterns, although there was a slight decline in the most recent years (Fig. 5a).

Predation rates on alewife and rainbow smelt followed broadly similar temporal patterns, but the changes in predation mortality were larger for alewife (Fig. 5a). Predation mortality estimates for age-1 and older fish steadily increased until the mid-1980s for both species, followed by a decline in the late 1980s. Predation mortality rates for these age classes remained relatively constant throughout much of the 1990s, with a slight decline in the late 1990s prior to a

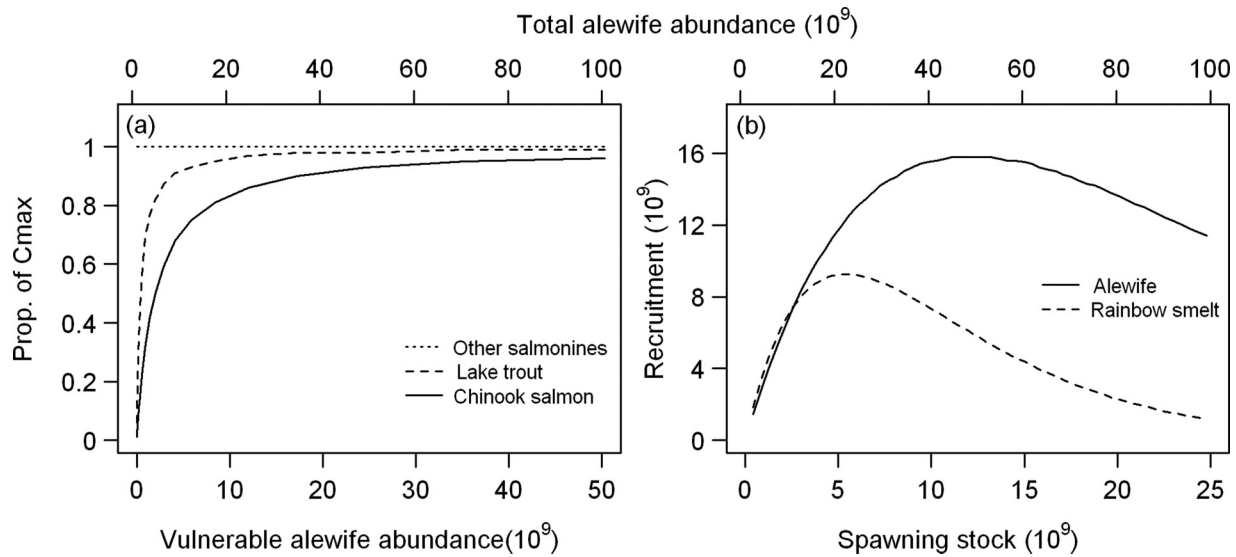
Fig. 3. “Observed” (symbols) and predicted (lines) (a) total consumption; (b) proportion of consumption by Chinook salmon, lake trout, and coho salmon, brown trout, steelhead trout combined; and (c) proportion of large alewife, small alewife, and rainbow smelt and other prey in total salmonine consumption.



rapid increase that began in the early 2000s. In contrast, age-0 predation mortality rates exhibited considerable interannual variability for both alewife and rainbow smelt, with no clear increasing or decreasing trend. Predation mortality of age-1 and older alewife followed opposite trends to age-3 and older alewife abundance, but there was no clear relationship between age-0 predation mortality and their abundance (Fig. 5a). There was a slight negative relation-

ship between age-1 and older rainbow smelt predation mortality and abundance, but generally there was no clear inverse relationship between trends in predation mortality and abundance of age-1 and older rainbow smelt. From these results, predation by salmonines had a strong negative effect on age-1 and older alewife abundance in Lake Michigan, whereas the predation effect on age-1 and older rainbow smelt was relatively weak.

Fig. 4. Relative changes in predatory consumption and prey productivity based on our highest posterior density parameter estimates, expressed as (a) functional response curves for Chinook salmon, lake trout, and all other salmonines showing changes in consumption per predator (averaged over ages) in response to changes in total prey abundance (sum of alewife and rainbow smelt), but plotted against the corresponding total and vulnerable alewife abundance, and (b) stock–recruitment relationships for alewife and rainbow smelt. (Note: vulnerable alewife abundance was calculated using estimates of age-specific size preferences obtained from the model; both vulnerable alewife abundance and spawning stock were calculated assuming a stable age distribution with known recruitments and age-specific total mortalities set at means of model estimates; x axes were scaled assuming that total alewife abundance accounted for 60% of total prey abundance based on mean annual abundance estimates; upper x axis does not apply to the rainbow smelt stock–recruitment curve.)



Consumption per predator of Chinook salmon followed similar temporal patterns to those for age-3 and older alewife abundance, showing a decline until the mid-1980s and an increase in the 1990s, followed by a steady decline in the most recent years (Fig. 5b). Consumption per predator of lake trout showed little annual variation. These results are consistent with our predator-prey habitat overlap data, which suggest heavier reliance of Chinook salmon on alewife and more diverse prey for the other salmonines. These are also reflected in the differences in estimated functional responses between the two species, with lake trout consumption suggesting a near-maximum per-predator consumption unless alewife abundance was very low (Fig. 4a). Total prey consumption by all salmonines increased as salmonine abundance increased from the mid-1960s until 1985 (Fig. 3). From 1985 to 1995, both predicted and observed prey consumption declined (Fig. 3) in concert with the declines in consumption per predator of Chinook salmon. In line with the functional response estimates, this decline was modest compared with the decline in alewife abundance. Just as in the 1980s, total consumption in recent years remained relatively high, although alewife abundance was low.

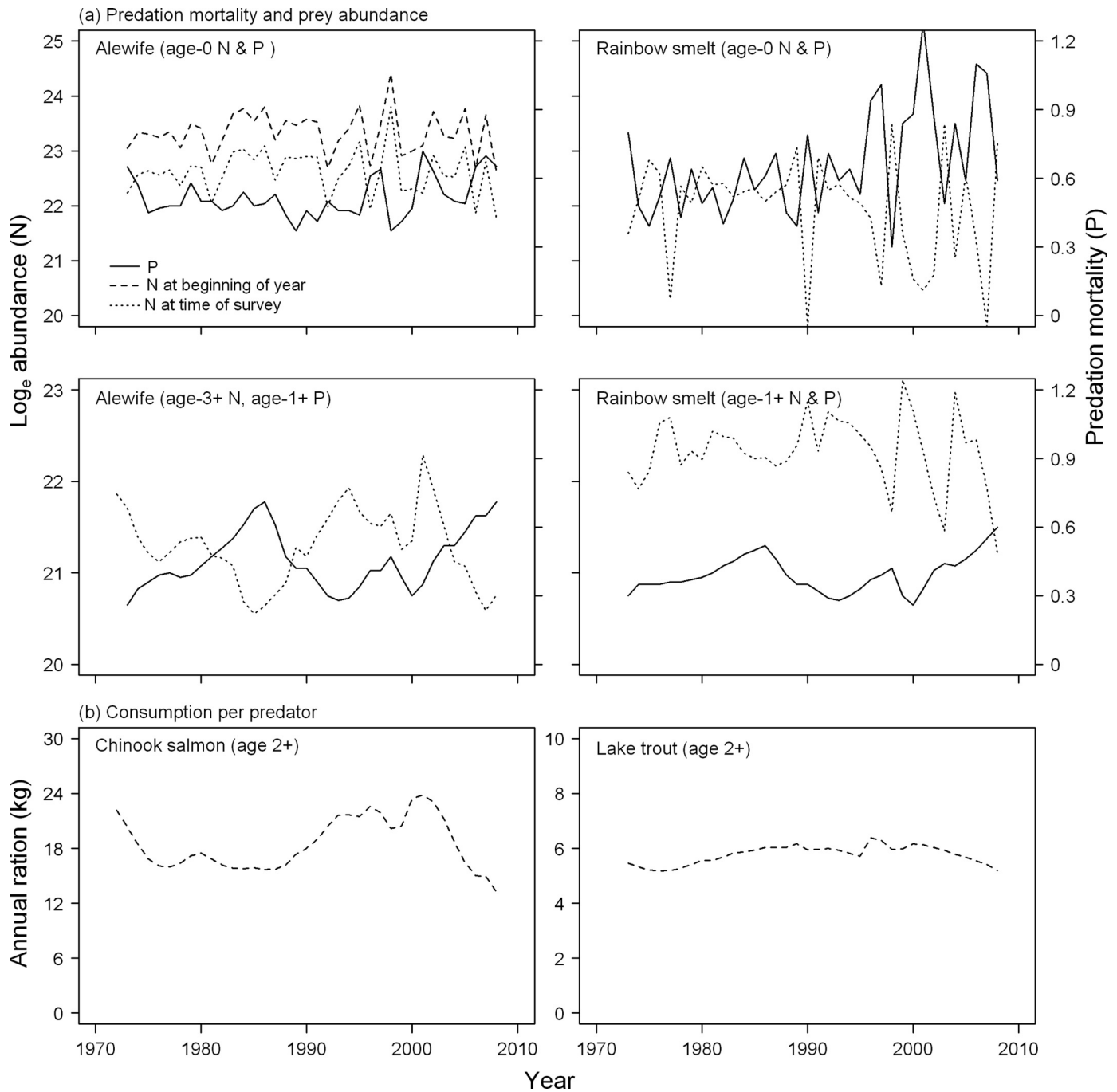
Discussion

Using a Bayesian modeling approach, we developed a multispecies SCA model to assess trade-offs between consumptive demands of predatory species and productivity of forage fishes, focusing on the Lake Michigan pelagic fish community, where the effect of top predators on prey species is an important management consideration. Based on historical reconstruction of changes in prey abundance and predator consumption, we estimated several parameters governing these trade-offs, including the steepness of salmonine functional responses, prey mortalities caused by salmonine predation, as mediated by functional responses, and parameters of Ricker stock-recruitment relationships for prey fish. These parameters and their posterior probability distributions can subsequently be used as inputs toward formal development of a decision model to compare the performance of alternative predator management policies in terms

of both their direct effect on predator abundance and their indirect effect on prey fishes. As such, our multispecies modeling approach provides the basis for both tactical decision-making and strategic evaluation of management policies (Plagányi et al. 2012). The lack of long time series of observational data on predator and prey populations has been one of the main obstacles for the development of such multispecies assessment models elsewhere, where attempts at estimating parameters governing prey-predator interactions have generally been limited and uncertainties associated with estimated parameters mostly remained unquantified (Eby et al. 1995; Cox et al. 2002). In this study, the availability of historical data from both current predator stock assessments (Tsehaye et al. 2014) and prey fish trawl and hydroacoustic surveys allowed us to develop a multispecies SCA model that explicitly included predator-prey feedbacks.

In estimating predation mortalities and productivities of prey fishes and the corresponding functional feeding responses of predatory species, this modeling approach allowed us to explore the importance of each of these ecological processes in structuring fish communities for the Lake Michigan pelagic fish community. First, estimating mortalities stemming from salmonine predation and associated changes in alewife and rainbow smelt abundance and recruitment enabled us to gauge the sensitivity of Lake Michigan's forage base to fluctuating predator abundances. Based on the inverse relationship between our estimates of predation mortality and alewife abundances (Fig. 5a), salmonine consumption appeared to play an important role in driving historical population dynamics of alewife in Lake Michigan, which supports the contention by Stewart and Ibarra (1991) and Madenjian et al. (2002). Thus, the high predation mortality estimates associated with the sharp declines in alewife abundance prior to the Chinook salmon mass mortality event in the 1980s are suggestive of salmonine consumption exceeding prey productivity during these years. Similarly, the estimated increases in predation mortality coincident with the continuous decline in alewife abundance and recruitment in recent years signal excessive salmonine abundance relative to prey supply, suggesting that the risk of a mass mortality event still remained under current salmonine stocking rates.

Fig. 5. Temporal changes in (a) alewife and rainbow smelt abundance in relation to predation mortality rates and (b) consumption per predator of age-2 and older Chinook salmon and lake trout.



Second, estimating the steepness of multispecies functional response curves for major salmonine predators allowed us to explore the relationship between predator consumption and lake-wide prey availability. The steepness of the functional response curves indicated that salmonine consumption rate will remain relatively high (Fig. 4a) even at low prey densities (Fig. 4b), with Chinook salmon (and to a lesser extent lake trout) experiencing a decline in consumption per predator only at the lowest prey densities and the other salmonines consuming at an almost maximum rate across the entire range of observed prey densities (Fig. 4a). These findings suggested that feedback mechanisms between predators and prey fish are unlikely to help maintain a balance between predator consumption and prey productivity and prevent large declines in prey availability

in Lake Michigan. Therefore, major increases in abundance of Lake Michigan salmonines, be it as a result of higher stocking rates, increased natural reproduction (Williams 2012), or higher survival rates (Tsehaye et al. 2014), could lead to a major decline in forage availability. This could in turn have serious consequences for the salmonine populations, potentially in the form of a mass mortality event as happened in the late 1980s (Stewart and Ibarra 1991; Holey et al. 1998). Because the mass mortality event in the late 1980s occurred following a marked decline in alewife numbers and subsequent food limitation and diet shifts (Stewart and Ibarra 1991; Madenjian et al. 2002), increased dependency of Chinook salmon on alewife from the 1990s to the 2000s (Jacobs et al. 2013; Tsehaye et al. 2014) suggest that the Lake Michigan fish

pelagic community faces considerable risk of predator–prey imbalance under current stocking rates. Though it has also been argued that the Chinook mass mortality in the past stemmed from poor hatchery practices (Claramunt et al. 2012), the low mass-at-age of Chinook salmon in the years leading up to the mass mortality event suggested that Chinook salmon faced food limitation. Furthermore, similar changes in Chinook salmon feeding habits occurred in Lake Huron prior to the alewife collapse in 2004 (Riley et al. 2008; Roseman et al. 2008; Roseman and Riley 2009), including increased incidence of cannibalism (J. Schaeffer, USGS, personal communication), supporting the contention that increased salmonine abundance could eventually lead to prey depletion and serious food limitations for the predatory salmonines. Although no Chinook salmon mass mortality event of the magnitude observed in Lake Michigan in the 1980s has occurred in Lake Huron after the alewife populations collapsed, annual mortality rates for some age classes actually increased considerably in the early 2000s (Brenden et al. 2012).

Fishing may be expected to help stabilize the predator–prey communities if a feedback mechanism exists whereby Chinook salmon become more vulnerable to fishing when alewife are scarce. Such feedback mechanisms could arise from Chinook salmon and the other salmonines either being more likely to strike a fishing lure when experiencing food limitation or being more concentrated in a smaller geographic area of high alewife abundance. In the stock assessment model for Chinook salmon in Tsehaye et al. (2014), catchability, which was estimated as a time-varying parameter following a random walk (Wilberg and Bence 2006), increased from 1986 through 2008. However, this change did not imply a clear feedback that would help stabilize the predator–prey balance, because the temporal change in catchability was a steady one and did not obviously track fluctuations in alewife abundance or Chinook mass-at-age. In addition, the level of exploitation was relatively modest and did not appreciably reduce cohort consumption rates, in part because fishing tended to concentrate on larger fish, which have already consumed a substantial amount and would soon die due to maturation, even in the absence of fishing (Tsehaye et al. 2014).

Our multispecies modeling approach incorporating predator–prey interactions can be used to explore the importance of top-down regulation in a large aquatic ecosystem. Assessing the contributions of this key driver versus bottom-up control may be difficult in large ecosystems, where the spatial scale and high complexity of the food webs often limit our ability to run experiments that can be more easily conducted in small freshwater systems (Vander Zanden et al. 2005; Bunnell et al. 2014). In this study, the availability of long-term, lake-wide monitoring data on hatchery-supported salmonines and their prey allowed us to assess the importance of prey–predator interactions in regulating the trophic structure of the pelagic community in Lake Michigan. Although our results suggested that salmonine predation did not have a strong influence on rainbow smelt abundance, the changes in the abundance of the most dominant prey (alewife) in relation to salmonine consumption and the associated functional feeding responses of predators highlight the importance of top-down regulation in the Lake Michigan pelagic fish community, which is in agreement with suggestions by Madenjian et al. (2002), Madenjian et al. (2005), and Bence et al. (2008). In this regard, our study adds to the growing list of studies on large aquatic systems, such as the Baltic Sea, the Northwest Atlantic, and the Black Sea, in which top predators have been found to exert top-down control on prey fish populations (Schindler et al. 2002; Daskalov 2002; Harvey et al. 2003). Together with these studies, our study demonstrates the significant role that predators could play in structuring fish communities and why it is important to understand predator–prey linkages for determining ecosystem-level consequences of fisheries management (Cox et al. 2002; Link 2002; Essington et al. 2002). However, in contrast to these studies, which generally examined

the effects on the aquatic food web of decreases in predator abundances through fishing (Pauly et al. 1998; Schindler et al. 2002), our study examined the importance of top-down structuring in a situation of increasing predator abundances through stocking. Thus, the introduction of salmonine predators in Lake Michigan for ecological and socioeconomic reasons has also afforded an opportunity to learn about large-scale impacts of predator introductions on previously unexploited prey populations, giving an added perspective to ecosystem-wide effects of fishery management decisions.

Finally, while the posterior probability distributions of parameter estimates reflect the relative degree of uncertainty associated with the corresponding life history or fishery characteristics, pointing to future research and monitoring needs, our multispecies model fits can also be used to identify areas of uncertainty regarding our choices of observation and population submodels. In this regard, though most parameters in our model were estimated with a relatively low degree of uncertainty (Table 3), our analysis revealed some discrepancies between trawl survey indices of abundance of alewife and model-predicted values in some years. Especially for the most recent years, our model estimates of alewife abundance were higher than was suggested by observed trawl data. It may be argued that these discrepancies are due to inconsistencies between some of the data sets used in the “integrated analysis” (Mauder 2003), with the trawl survey data in recent years suggesting lower alewife abundance than did the input data on total consumption. Another possible explanation for these discrepancies is that there might be alternative prey that we did not consider in the model that helped sustain the level of “observed” consumption. However, there was no evidence of alternative prey species found in sufficient quantities in Lake Michigan to explain these inconsistencies (Jacobs et al. 2013). Alternatively, these discrepancies could be because of our assumption of a time-invariant catchability while there may actually be changes in trawl catchabilities in the later years (e.g., due to shifts in the timing of the USGS annual prey surveys and (or) dreissenid mussel effects (Madenjian et al. 2006)), suggesting the need to consider alternative observation model hypotheses. In fact, inappropriate observation model hypotheses, particularly those assuming a constant proportionality between relative and actual abundance, have been blamed for many failures in fish stock assessments (Walters and Martell 2004).

In addition to the specific observation model uncertainties pertaining to our model, there have generally been uncertainties about using a saturating functional response to model consumption given that fish are rarely captured with full stomachs, and proportions of maximum consumption estimated through bioenergetics modeling are often quite low (Walters 2000; Walters and Martell 2004). Walters (2000) and Walters and Martell (2004) suggest that the phenomenon of satiation and the trade-offs between time spent handling prey and time spent searching for prey may not be applicable to some aquatic ecosystems, with the amount of consumption instead determined by the balance between the energy state of the predator and its predation risk avoidance behavior during foraging activities. Nevertheless, because the only source of predation risk for large salmonines in Lake Michigan is attacks by the parasitic sea lamprey and fishing, the use of a saturating functional response model seems reasonable for modeling Lake Michigan salmonine predation (Szalai 2003). Yet, alternative population (e.g., other functional response forms), as well as observation (e.g., time varying catchability), model hypotheses can be considered in future research as knowledge improves of underlying ecological and biological processes (e.g., risk avoidance behavior of salmonines with respect to fishing) in the Lake Michigan fish community, and the best models can be identified using model selection methods, such as the Akaike information criterion (Burnham and Anderson 2000). Overall, the ability to detect inconsistencies among multiple data sets and (or) identify uncertainties in observation and population model hypotheses

points to the advantages of multispecies modeling approaches over single-species and existing whole-ecosystem modeling approaches.

Acknowledgements

Funding for this project was provided by the Great Lakes Fishery Trust (Project No. 2007.950). Additional funding was provided through the US Fish and Wildlife Service Sportfish Restoration Program, Federal Aid in Sport Fish Restoration, and the Michigan Department of Natural Resources (MDNR) Game and Fish Protection Fund. We thank all staff at the US Geological Survey (USGS) Great Lakes Science Center who have contributed to the trawl and hydroacoustic prey fish assessments as well as the MDNR staff for their contributions to the acoustic surveys. We also thank Brian Irwin (University of Georgia – USGS Georgia Cooperative Fish and Wildlife Research Unit) for providing helpful comments on the manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US government. This is manuscript 2014-05 of the Quantitative Fisheries Center at Michigan State University and contribution 1813 of the USGS Great Lakes Science Center.

References

- Bax, N.J. 1998. The significance and prediction of predation in marine fisheries. *ICES J. Mar. Sci.* 55: 997–1030. doi:10.1006/jmsc.1998.0350.
- Bence, J.R., Dobiesz, N.E., Madenjian, C.P., Argyle, R., Barbiero, R., Bowlby, J.N., Claramunt, R.M., O’Gorman, R., and Schaner, T. 2008. Top-down effects of open-water salmonine predators in the Great Lakes. Quantitative Fisheries Center Technical Report T2008-7, East Lansing, Mich.
- Benjamin, D.M., and Bence, J.R. 2003. Statistical catch-at-age framework for Chinook salmon in Lake Michigan, 1985–1996. Michigan Department of Natural Resources, Ann Arbor, Mich.
- Brenden, T.O., Bence, J.R., and Szalai, E.B. 2012. An age-structured integrated assessment of Chinook salmon population dynamics in Lake Huron’s main basin since 1968. *Trans. Am. Fish. Soc.* 141: 919–933.
- Bunnell, D.B., Barbiero, R., Ludsin, S.A., Madenjian, C.P., Croley, I.L., Thomas, E., Warren, G.J., Dolan, D.D., Brenden, T.O., Briland, R., Gorman, O.T., He, J.X., Johengen, T.H., Lantry, B.F., Lesht, B.M., Nalepa, T.F., Riley, S.C., Riseng, C.M., Treska, T.J., Tsehaye, I., Warner, D.M., Walsh, M.G., and Weidel, B.C. 2014. Ecosystem-level trends within the Laurentian Great Lakes: implications for the stability of the world’s inland seas. *Bioscience*. 64: 26–39.
- Bunnell, D.B., Madenjian, C.P., and Claramunt, R.M. 2006. Long-term changes of the Lake Michigan fish community following the reduction of exotic alewife (*Alosa pseudoharengus*). *Can. J. Fish. Aquat. Sci.* 63: 2434–2446. doi:10.1139/f06-132.
- Burnham, K.P., and Anderson, D.R. 2000. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Carpenter, S.R., Kitchell, J.F., and Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity. *BioScience*, 35: 634–639. doi:10.2307/1309989.
- Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., D’Antonio, C., Francis, R., Franklin, J.F., MacMahon, J.A., Noss, R.F., Parsons, D.J., Peterson, C.H., Turner, M.G., and Woodmansee, R.G. 1996. The report of the Ecological Society of America Committee on the scientific basis for ecosystem management. *Ecol. Appl.* 6: 665–691. doi:10.2307/2269460.
- Christensen, V. 1996. Managing fisheries involving predator and prey species. *Rev. Fish. Biol. Fish.* 6: 417–442. doi:10.1007/BF00164324.
- Christensen, V., and Pauly, D. 2004. Placing fisheries in their ecosystem context, an introduction. *Ecol. Model.* 172: 103–107. doi:10.1016/j.ecolmodel.2003.09.002.
- Claramunt, R.M., Madenjian, C.P., and Clapp, D.F. 2012. Pacific salmonines in the Great Lakes basin. In *Great Lakes fisheries policy and management: a binational perspective*. 2nd ed. Edited by W.W. Taylor, A.J. Lynch, and N.J. Leonard. Michigan State University Press, East Lansing, Mich. pp. 609–650.
- Cox, S.P., Essington, T.E., Kitchell, J.F., Martell, S.J.D., Walters, C.J., Boggs, C., and Kaplan, I. 2002. Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. II. A preliminary assessment of the trophic impacts of fishing and effects on tuna dynamics. *Can. J. Fish. Aquat. Sci.* 59(11): 1736–1747. doi:10.1139/f02-138.
- Danielsson, A., Stefánsson, G., Baldrússon, F.M., and Thorarinnsson, K. 1997. Utilization of the Icelandic cod stock in a multispecies context. *Mar. Resour. Econ.* 12: 329–344.
- Daskalov, G.M. 2002. Overfishing drives a trophic cascade in the Black Sea. *Mar. Ecol. Prog. Ser.* 225: 53–63. doi:10.3354/meps225053.
- Deriso, R.B., Quinn, T.J., II, and Neal, P.R. 1985. Catch-age analysis with auxiliary information. *Can. J. Fish. Aquat. Sci.* 42: 815–824. doi:10.1139/f85-104.
- Dettmers, J.M., Goddard, C.I., and Smith, K.D. 2012. Management of alewife using Pacific salmon in the Great Lakes: whether to manage for economics or the ecosystem? *Fisheries*, 37: 495–501. doi:10.1080/03632415.2012.731875.
- Eby, L.A., Rudstam, L.G., and Kitchell, J.F. 1995. Predator responses to prey population dynamics: an empirical analysis based on lake trout growth rates. *Can. J. Fish. Aquat. Sci.* 52(7): 1564–1571. doi:10.1139/f95-149.
- Eshenroder, R.L., and Burnham-Curtis, M.K. 1999. Species succession and sustainability of the Great Lakes fish community. In *Great Lakes fisheries policy and management: a binational perspective*. Edited by W.W. Taylor and C.P. Ferreri. Michigan State University Press, East Lansing, Mich. pp. 489–513.
- Essington, T.E., Schindler, D.E., Olson, R.J., Kitchell, J.F., Boggs, C., and Hilborn, R. 2002. Alternative fisheries and the predation rate of yellowfin tuna in the Eastern Pacific Ocean. *Ecol. Appl.* 12: 724–734. doi:10.1890/1051-0761(2002)012[0724:AFATPR]2.0.CO;2.
- Fenichel, E.P., Horan, R.D., and Bence, J.R. 2010. Indirect management of invasive species through bio-controls: a bioeconomic model of salmon and alewife in Lake Michigan. *Resour. Energy Econ.* 32: 500–518. doi:10.1016/j.reseneeco.2010.04.002.
- Fournier, D.A., and Archibald, C.P. 2011. A general theory for analyzing catch at age data. *Can. J. Fish. Aquat. Sci.* 39: 1195–1207. doi:10.1139/f82-157.
- Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., Nielsen, A., and Sibert, J. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, 27: 233–249. doi:10.1080/10556788.2011.597854.
- Gelman, A., Carlin, J.B., Stern, H.S., and Rubin, D.B. 2004. Bayesian data analysis. 2nd ed. Chapman and Hall/CRC, Boca Raton, Fla.
- Geweke, J. 1992. Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. In *Bayesian statistics*. Edited by J.M. Bernardo, J.O. Berger, A.P. Dawid, and A.F.M. Smith. Oxford University Press, Oxford, UK. pp. 169–193.
- Haeseker, S.L., Jones, M.L., and Bence, J.R. 2003. Estimating uncertainty in the stock-recruitment relationship for St. Marys River sea lampreys. *J. Great Lakes Res.*, 29(Suppl. 1): 728–741.
- Hansen, M.J., and Holey, M.E. 2002. Ecological factors affecting sustainability of Chinook and coho salmon populations in the Great Lakes. In *Sustaining North American salmon: perspectives across regions and disciplines*. Edited by K.D. Lynch, M.L. Jones, and W.W. Taylor. American Fisheries Society, Bethesda, Md. pp. 155–179.
- Harvey, C.J., Cox, S.P., Essington, T.E., Hansson, S., and Kitchell, J.F. 2003. An ecosystem model of food web and fisheries interactions in the Baltic Sea. *ICES J. Mar. Sci.* 60: 939–950. doi:10.1016/S1054-3139(03)00098-5.
- Hatch, R.W., Haack, P.M., and Brown, E.H., Jr. 1981. Estimation of alewife biomass in Lake Michigan, 1967–1978. *Trans. Am. Fish. Soc.* 110: 575–584.
- Holey, M.E., Elliott, R.F., Marcquenski, S.V., Hnath, J.G., and Smith, K.D. 1998. Chinook salmon epizootics in Lake Michigan: possible contributing factors and management implications. *J. Aquat. Anim. Health*, 10: 202–210. doi:10.1577/2F1548-8667%281998%2910%3C0202%3ACSEILM%3E2.0.CO%3B2.
- Hollowed, A.B., Ianelli, J.N., and Livingston, P.A. 2000. Including predation mortality in stock assessments: a case study for Gulf of Alaska walleye pollock. *ICES J. Mar. Sci.* 57: 279–293. doi:10.1006/jmsc.1999.0637.
- ICES. 2000. Ecosystem effects of fishing. *ICES J. Mar. Sci.* 57: 791.
- Jacobs, G.R., Madenjian, C.P., Bunnell, D.B., Warner, D.M., and Claramunt, R.M. 2013. Chinook salmon foraging patterns in a changing Lake Michigan. *Trans. Am. Fish. Soc.* 142: 362–372. doi:10.1080/2F00028487.2012.739981.
- Jennings, S., and Kaiser, M.J. 1998. The effects of fishing on marine ecosystems. *Adv. Mar. Biol.* 34: 201–352. doi:10.1016/2F00065-2881%2808%2960212-6.
- Jonas, J. 2011. Statistical catch-at-age models used to describe the status of lean Lake Trout populations in the 1836-Treaty ceded waters of lakes Michigan, Huron, and Superior at the inception of the 2000 Consent Decree. A report completed by the Modeling Subcommittee to the Technical Fisheries Committee, Michigan Department of Natural Resources, Sault Ste. Marie, Mich. pp. 23–70.
- Jones, M.L., and Bence, J.R. 2009. Uncertainty and fishery management in the North American Great Lakes: lessons from applications of decision analysis. In *Pacific salmon: ecology and management of western Alaska’s populations*. Edited by C.C. Krueger and C.E. Zimmerman. American Fisheries Society, Bethesda, Md. pp. 1059–1082.
- Jones, M.L., Koonce, J.F., and O’Gorman, R. 1993. Sustainability of hatchery-dependent salmonine fisheries in Lake Ontario: the conflict between predator demand and prey supply. *Trans. Am. Fish. Soc.* 122: 1002–1018.
- Jurado-Molina, J., Livingston, P.A., and Ianelli, J.N. 2005. Incorporating predation interactions in a statistical catch-at-age model for a predator-prey system in the eastern Bering Sea. *Can. J. Fish. Aquat. Sci.* 62(8): 1865–1873. doi:10.1139/f05-110.
- Koonce, J.F., and Jones, M.L. 1994. Sustainability of the intensively managed fisheries of Lake Michigan and Lake Ontario. Final report of the SIMPLE Task Group, Board of Technical Experts, Great Lakes Fishery Commission, Ann Arbor, Mich.
- Kotchen, M.J., Moore, M.R., Lupi, F., and Rutherford, E.S. 2006. Environmental constraints on hydropower: an ex post benefit-cost analysis of dam relicensing in Michigan. *Land Econ.* 82: 384–403.
- Krause, A.E. 1999. Sampling variability of ten fish species and population dynamics of alewife (*Alosa pseudoharengus*) and bloater (*Coregonus hoyi*) in Lake Michigan. M.Sc. thesis, Michigan State University, East Lansing.
- Lantry, B.F., and Stewart, D.J. 1993. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: an interlake comparison. *Trans. Am. Fish. Soc.* 122: 951–976. doi:10.1577/1548-8659(1993)122<0951:EEORSI>2.3.CO;2.

- Link, J.S. 2002. Ecological considerations in fisheries management: When does it matter? *Fisheries*, **27**: 10–17. doi:10.1577/2F1548-8446%282002%29027%3C0010%3AECIFM%3E2.0.CO%3B2.
- Link, J.S., and Garrison, L.P. 2002. Changes in piscivory associated with fishing induced changes to the finfish community on Georges Bank. *Fish. Res.* **55**: 71–86. doi:10.1016/S0165-7836(01)00300-9.
- Livingston, P.A., and Jurado-Molina, J. 2000. A multispecies virtual population analysis of the eastern Bering Sea. *ICES J. Mar. Sci.* **57**: 294–299. doi:10.1006/jmsc.1999.0524.
- Livingston, P.A., and Methot, R.D. 1998. Incorporation of predation into a population assessment model of eastern Bering Sea walleye pollock. *Edited by T.J. Funk, T.J. Quinn, II, J. Heifetz, J.N. Ianelli, J.E. Powers, J.F. Schweigert, P.J. Sullivan, and C.I. Zhang. Alaska Sea Grant College Program Publication AK-SG-98-01, Fairbanks, Alaska.* pp. 663–678.
- Madenjian, C.P., Fahnenstiel, G.L., Johengen, T.H., Nalepa, T.F., Vanderploeg, H.A., Fleischer, G.W., Schneeberger, P.J., Benjamin, D.M., Smith, E.B., Bence, J.R., Rutherford, E.S., Lavis, D.S., Robertson, D.M., Jude, D.J., and Ebener, M.P. 2002. Dynamics of the Lake Michigan food web, 1970–2000. *Can. J. Fish. Aquat. Sci.* **59**(4): 736–753. doi:10.1139/f02-044.
- Madenjian, C.P., Höök, T.O., Rutherford, E.S., Mason, D.M., Croley, T.E., II, Szalai, E.B., and Bence, J.R. 2005. Recruitment variability of alewives in Lake Michigan. *Trans. Am. Fish. Soc.* **134**: 218–230. doi:10.1577/FT03-222.1.
- Madenjian, C.P., Pothoven, S.A., Dettmers, J.M., and Holuszko, J.D. 2006. Changes in seasonal energy dynamics of alewife (*Alosa pseudoharengus*) in Lake Michigan after invasion of dreissenid mussels. *Can. J. Fish. Aquat. Sci.* **63**(4): 891–902. doi:10.1139/f06-017.
- Maunder, M.N. 2003. Paradigm shifts in fisheries stock assessment: from integrated analysis to Bayesian analysis and back again. *Nat. Resour. Model.* **16**: 465–475. doi:10.1111%2Fj.1939-7445.2003.tb00123.x.
- McAllister, M.K., and Ianelli, J.N. 1997. Bayesian stock assessment using catch-at-age data and the sampling – importance resampling algorithm. *Can. J. Fish. Aquat. Sci.* **54**(2): 284–300. doi:10.1139/f96-285.
- Mills, E.L., Leach, J.H., Carlton, J.T., and Secor, C.L. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *J. Gt. Lakes Res.* **19**: 1–54. doi:10.1016/S0380-1330(93)71197-1.
- Moustahfid, H., Tyrrell, M.C., Link, J.S., Nye, J.A., Smith, B.E., and Gamble, R.J. 2010. Functional feeding responses of piscivorous fishes from the northeast US continental shelf. *Oecologia*, **163**: 1059–1067. doi:10.1007/s00442-010-1596-2. PMID:20229244.
- Ney, J.J. 1990. Trophic economics in fisheries: assessment of demand-supply relationships between predators and prey. *Rev. Aquat. Sci.* **2**: 55–81.
- NRC. 1999. Sustaining marine fisheries. The National Academies Press, Washington, D.C.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. Int. Explor. Mer.* **39**: 175–192. doi:10.1093%2Ficesjms%2F39.2.175.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. 1998. Fishing down marine food webs. *Science*, **279**: 860–863. doi:10.1126/science.279.5352.860. PMID:9452385.
- Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., and Sainsbury, K.J. 2004. Ecosystem-based fishery management. *Science*, **305**: 346–347. doi:10.1126/science.1098222. PMID:15256658.
- Plagányi, É.E., and Butterworth, D.S. 2012. The Scotia Sea krill fishery and its possible impacts on dependent predators: modeling localized depletion of prey. *Ecol. Appl.* **22**: 748–761. doi:10.1890/11-0441.1. PMID:22645808.
- Plagányi, É.E., Punt, A.E., Hillary, R., Morello, E.B., Thébaud, O., Hutton, T., Pillans, R.D., Thorson, J.T., Fulton, E.A., Smith, A.D.M., Smith, F., Bayliss, P., Haywood, M., Lyne, V., and Rothlisberg, P.C. 2012. Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. *Fish. Fish.* **15**(1): 1–22. doi:10.1111%2Fj.1467-2979.2012.00488.x.
- Plummer, M., Best, N., Cowles, K., and Vines, K. 2010. Output analysis and diagnostics for MCMC [online]. R package version 0.14-2. Available from <http://cran.r-project.org/web/packages/coda/index.html>.
- Quinn, T.J., and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.
- R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Riley, S.C., Roseman, E.F., Nichols, S.J., O'Brien, T.P., Kiley, C.S., and Schaeffer, J.S. 2008. Deepwater demersal fish community collapse in Lake Huron. *Trans. Am. Fish. Soc.* **137**: 1879–1890. doi:10.1577/F07-141.1.
- Roseman, E.F., and Riley, S.C. 2009. Biomass of deepwater demersal forage fishes in Lake Huron, 1994–2007: implications for offshore predators. *Aquat. Ecosyst. Health Manage.* **12**: 29–36. doi:10.1080/14634980802711786.
- Roseman, E.F., O'Brien, T.P., Riley, S.C., Farha, S., and French, J.R.P., III. 2008. Status and trends of the Lake Huron deepwater demersal fish community, 2008. A report to the Great Lakes Fishery Commission, Great Lakes Fishery Commission, Ypsilanti, Mich.
- Rutherford, E.S. 1997. Evaluation of natural reproduction, stocking rates, and fishing regulations for Steelhead *Oncorhynchus mykiss*, Chinook salmon *O. tshawytscha*, and coho salmon *O. kisutch* in Lake Michigan. Federal Aid in Sport Fish Restoration, Project F-35-R-22, Final Report, Fisheries Division, Michigan Department of Natural Resources, Ann Arbor, Mich.
- Schindler, D.E., Essington, T.E., Kitchell, J.F., Boggs, C., and Hilborn, R. 2002. Sharks and tunas: Fisheries impacts on predators with contrasting life histories. *Ecol. Appl.* **12**: 735–748. doi:10.1890/1051-0761(2002)012[0735:SATFIO]2.0.CO;2.
- Schnute, J.T. 1994. A general framework for developing sequential fisheries models. *Can. J. Fish. Aquat. Sci.* **51**(8): 1676–1688. doi:10.1139/f94-168.
- Stewart, D.J., and Ibarra, M. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–88. *Can. J. Fish. Aquat. Sci.* **48**(5): 909–922. doi:10.1139/f91-107.
- Stewart, D.J., Kitchell, J.F., and Crowder, L.B. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Trans. Am. Fish. Soc.* **110**: 751–763. doi:10.1577/1548-8659(1981)110<751:FFATSP>2.0.CO;2.
- Szalai, E.B. 2003. Uncertainty in the population dynamics of alewife (*Alosa pseudoharengus*) and bloater (*Coregonus hoyi*) and its effects on salmonine stocking strategies in Lake Michigan. Doctoral dissertation, Michigan State University, East Lansing.
- Tsehaye, I., Jones, M.L., Brenden, T.O., Bence, J.R., and Claramunt, R.M. 2014. Changes in the salmonine community of Lake Michigan and their implications for predator–prey balance. *Trans. Am. Fish. Soc.*
- Tsou, T.-S., and Collie, J.S. 2001. Estimating predation mortality in the Georges Bank fish community. *Can. J. Fish. Aquat. Sci.* **58**(5): 908–922. doi:10.1139/f01-044.
- Van Kirk, K.F., Quinn, T.J., and Collie, J.S. 2010. A multispecies age-structured assessment model for the Gulf of Alaska. *Can. J. Fish. Aquat. Sci.* **67**(7): 1135–1148. doi:10.1139/F10-053.
- Vander Zanden, M.J., Essington, T.E., and Vadeboncoeur, Y. 2005. Is pelagic top-down control in lakes augmented by benthic energy pathways? *Can. J. Fish. Aquat. Sci.* **62**(6): 1422–1431. doi:10.1139/f05-042.
- Walters, C. 2000. Natural selection for predation avoidance tactics: implications for marine population and community dynamics. *Mar. Ecol. Prog. Ser.* **208**: 299–313.
- Walters, C.J., and Martell, S.J.D. 2004. Fisheries ecology and management. Princeton University Press, Princeton, N.J.
- Warner, D.M., Claramunt, R.M., Hansen, D., and Farha, S.A. 2011. Status of pelagic prey fishes in Lake Michigan, 2011. A report to the Great Lakes Fishery Commission, Great Lakes Fishery Commission, Windsor, Ont.
- Wilberg, M.J., and Bence, J.R. 2006. Performance of time-varying catchability estimators in statistical catch-at-age analysis. *Can. J. Fish. Aquat. Sci.* **63**(10): 2275–2285. doi:10.1139/f06-111.
- Williams, M. 2012. Spatial, temporal, and cohort-related patterns in the Contribution of wild Chinook salmon *Oncorhynchus tshawytscha* to total Chinook harvest in Lake Michigan. M.Sc. thesis, Michigan State University, East Lansing.

Appendix A

Appendix tables appear on the following pages.

Table A1. Trawl abundance estimates of bloater, slimy sculpin, and deepwater sculpin (10^9) from the US Geological Survey Great Lakes Science Center.

Year	Bloater	Slimy sculpin	Deepwater sculpin
1967	0.05	0.21	0.25
1968	0.05	0.21	0.25
1969	0.05	0.21	0.25
1970	0.05	0.21	0.25
1971	0.05	0.21	0.25
1972	0.05	0.21	0.25
1973	0.05	0.21	0.29
1974	0.02	0.41	0.57
1975	0.02	0.61	1.18
1976	0.01	0.85	1.46
1977	0.01	0.23	0.95
1978	0.07	0.15	0.90
1979	0.25	0.20	1.82
1980	0.40	0.19	2.91
1981	0.80	0.21	2.28
1982	0.81	0.07	1.35
1983	2.54	0.10	2.96
1984	4.04	0.03	2.32
1985	3.18	0.06	2.39
1986	4.20	0.04	1.87
1987	4.40	0.12	2.67
1988	5.62	0.09	1.66
1989	7.56	0.07	0.96
1990	3.92	0.02	0.90
1991	4.51	0.17	0.65
1992	5.07	0.15	1.99
1993	3.10	0.13	0.93
1994	2.53	0.21	0.69
1995	1.99	0.23	1.08
1996	2.65	0.44	1.82
1997	2.07	0.40	1.87
1998	0.83	0.18	0.22
1999	0.48	0.62	2.37
2000	0.36	0.56	1.07
2001	0.31	0.17	1.58
2002	0.25	0.23	1.35
2003	0.18	0.37	1.27
2004	0.31	0.72	1.67
2005	0.39	1.00	2.06
2006	0.26	1.92	1.65
2007	0.10	0.56	0.64
2008	0.08	0.81	0.36

Table A2. Mass-at-age of alewife and rainbow smelt (kg).

Species	Age (years)							
	0	1	2	3	4	5	6	7
Alewife	0.0002	0.0028	0.0130	0.0220	0.0270	0.0320	0.0370	0.0410
Rainbow smelt	0.0001	0.0009	0.0034	0.0059	0.0181	0.0342	0.0473	—

Table A3. Time series of salmonine abundance estimates in Lake Michigan (Tsehaye et al. 2014).

Year	Abundance (10 ⁶)					Total
	Chinook salmon	Steelhead trout	Coho salmon	Brown trout	Lake trout	
1967	0.60	0.12	0.87	0.04	3.52	5.15
1968	0.81	0.40	1.10	0.11	4.53	6.96
1969	0.99	0.66	2.01	0.20	5.16	9.02
1970	1.98	0.80	2.77	0.26	5.62	11.45
1971	2.76	1.07	2.51	0.35	6.14	12.83
1972	3.01	1.35	2.25	0.54	6.95	14.10
1973	3.99	1.89	2.04	1.10	7.25	16.26
1974	4.84	2.07	2.65	1.37	7.39	18.32
1975	5.87	2.34	2.41	1.31	7.74	19.67
1976	5.80	2.73	2.35	1.36	7.96	20.20
1977	5.57	2.67	2.57	1.62	7.86	20.29
1978	7.24	2.47	2.38	1.65	7.93	21.67
1979	7.74	2.74	3.01	1.64	7.86	22.99
1980	9.13	2.87	2.86	1.59	7.96	24.40
1981	9.13	2.85	2.26	1.62	7.59	23.45
1982	10.41	2.60	1.96	1.65	7.41	24.02
1983	11.43	2.67	1.94	1.93	7.47	25.44
1984	12.96	3.29	2.34	2.12	6.11	26.81
1985	12.64	3.40	2.34	2.11	6.95	27.43
1986	12.53	3.70	2.03	2.09	7.42	27.76
1987	12.39	3.88	1.92	1.80	7.14	27.14
1988	10.50	3.42	2.42	1.86	6.67	24.86
1989	11.75	3.21	2.22	1.93	6.65	25.77
1990	13.97	3.10	1.96	2.06	6.97	28.05
1991	12.37	3.17	2.01	2.08	7.32	26.95
1992	10.66	3.30	2.18	2.10	7.61	25.84
1993	9.63	3.44	1.71	2.19	8.10	25.07
1994	9.36	3.65	1.29	2.31	7.97	24.58
1995	10.57	3.68	1.70	2.40	8.25	26.61
1996	11.84	3.64	2.35	2.50	7.46	27.79
1997	11.29	3.63	2.30	2.51	7.45	27.17
1998	11.33	3.50	1.86	2.47	7.34	26.51
1999	11.26	3.39	2.06	2.36	4.99	24.06
2000	10.53	3.06	2.13	2.40	5.03	23.16
2001	13.13	3.15	2.19	2.44	4.97	25.88
2002	12.62	3.26	2.23	2.41	5.14	25.66
2003	11.59	3.52	2.43	2.39	5.83	25.76
2004	10.85	3.47	1.81	2.40	6.00	24.54
2005	10.50	3.74	1.85	2.42	6.68	25.18
2006	10.93	3.67	2.04	2.47	7.06	26.18
2007	10.32	3.73	1.92	2.36	8.02	26.35
2008	9.65	3.65	1.74	2.40	8.18	25.63

Table A4. Estimates of natural mortality of Chinook salmon (Tsehaye et al. 2014).

Year	Age (years)					
	0	1	2	3	4	5
1967	0.70	0.30	0.10	0.10	0.10	0.10
1968	0.70	0.30	0.10	0.10	0.10	0.10
1969	0.70	0.30	0.10	0.10	0.10	0.10
1970	0.70	0.30	0.10	0.10	0.10	0.10
1971	0.70	0.30	0.10	0.10	0.10	0.10
1972	0.70	0.30	0.10	0.10	0.10	0.10
1973	0.70	0.30	0.10	0.10	0.10	0.10
1974	0.70	0.30	0.10	0.10	0.10	0.10
1975	0.70	0.30	0.10	0.10	0.10	0.10
1976	0.70	0.30	0.10	0.10	0.10	0.10
1977	0.70	0.30	0.10	0.10	0.10	0.10
1978	0.70	0.30	0.10	0.10	0.10	0.10
1979	0.70	0.30	0.10	0.10	0.10	0.10
1980	0.70	0.30	0.10	0.10	0.10	0.10
1981	0.70	0.30	0.10	0.10	0.10	0.10
1982	0.70	0.30	0.10	0.10	0.10	0.10
1983	0.70	0.30	0.10	0.10	0.10	0.10
1984	0.70	0.30	0.10	0.10	0.10	0.10
1985	0.70	0.30	0.10	0.10	0.10	0.10
1986	0.70	0.30	0.10	0.10	0.10	0.10
1987	0.70	0.84	0.42	0.86	0.86	0.86
1988	0.70	0.87	0.44	0.90	0.90	0.90
1989	0.70	0.61	0.29	0.53	0.53	0.53
1990	0.70	1.17	0.62	1.31	1.31	1.31
1991	0.70	1.33	0.71	1.53	1.53	1.53
1992	0.70	1.62	0.89	1.94	1.94	1.94
1993	0.70	1.45	0.78	1.70	1.70	1.70
1994	0.70	1.23	0.65	1.39	1.39	1.39
1995	0.70	0.54	0.24	0.44	0.44	0.44
1996	0.70	1.05	0.55	1.14	1.14	1.14
1997	0.70	1.24	0.66	1.41	1.41	1.41
1998	0.70	0.71	0.34	0.67	0.67	0.67
1999	0.70	1.20	0.64	1.36	1.36	1.36
2000	0.70	0.76	0.38	0.75	0.75	0.75
2001	0.70	0.71	0.35	0.68	0.68	0.68
2002	0.70	0.49	0.21	0.36	0.36	0.36
2003	0.70	1.06	0.55	1.16	1.16	1.16
2004	0.70	0.56	0.26	0.47	0.47	0.47
2005	0.70	0.36	0.14	0.19	0.19	0.19
2006	0.70	0.57	0.26	0.48	0.48	0.48
2007	0.70	0.53	0.24	0.43	0.43	0.43
2008	0.70	0.87	0.44	0.89	0.89	0.89

Table A5. Estimates of (a) background natural mortality and (b) spawning mortalities based on Rutherford (1997) and Jonas (2011).

(a) Natural mortality.										
Species	Age (years)									
	1	2	3	4	5	6	7	8	9	10+
Lake trout	0.62	0.23	0.24	0.25	0.26	0.27	0.27	0.27	0.27	0.27
Steelhead trout	0.10	0.10	0.10	0.50	1.00					
Brown trout	0.30	0.10	0.10	0.10	0.10					
Coho salmon	0.500	0.1								

(b) Spawning mortality.							
Species	Age (years)						
	0	1	2	3	4	5	
Chinook salmon*	0.00	0.12	0.33	0.99	0.99	0.99	0.99
Steelhead trout		0.04	0.14	0.42	0.62	0.62	0.62
Brown trout		0.05	0.50	0.65	0.70	0.99	0.99
Coho salmon		0.05	0.99				

*For years prior to 1981.

Table A6. Mass-at-age (kg) at annulus formation of Chinook salmon based on creel survey data from the Michigan Department of Natural Resources.

Year	Age (years)					
	0	1	2	3	4	5
1967	0.005	0.586	3.176	8.193	9.830	11.800
1968	0.005	0.586	3.176	7.485	9.300	11.560
1969	0.005	0.586	3.176	7.485	9.630	12.400
1970	0.005	0.586	3.176	7.485	9.630	12.400
1971	0.005	0.586	3.176	7.485	9.630	12.400
1972	0.005	0.586	3.176	7.485	9.630	12.400
1973	0.005	0.586	3.176	7.485	9.630	12.400
1974	0.005	0.586	3.176	7.485	9.630	12.400
1975	0.005	0.586	3.176	7.485	9.630	12.400
1976	0.005	0.586	3.176	7.485	9.630	12.400
1977	0.005	0.586	3.176	7.485	9.630	12.400
1978	0.005	0.586	3.176	7.485	9.630	12.400
1979	0.005	0.586	3.063	7.200	9.270	11.930
1980	0.005	0.586	2.936	6.766	8.650	11.070
1981	0.005	0.586	2.810	6.332	8.110	10.400
1982	0.005	0.586	2.683	5.898	7.570	9.730
1983	0.005	0.586	2.557	5.463	7.030	9.050
1984	0.005	0.586	2.430	5.029	6.490	8.380
1985	0.005	0.650	2.640	2.830	5.950	7.850
1986	0.005	0.770	1.730	4.260	4.470	7.670
1987	0.005	0.760	2.160	3.510	6.400	6.630
1988	0.005	0.750	2.230	4.260	5.920	9.100
1989	0.005	0.710	2.020	4.010	6.290	7.990
1990	0.005	0.780	2.110	4.080	6.590	9.170
1991	0.005	0.810	2.250	4.140	6.490	9.150
1992	0.005	0.890	2.610	4.880	7.350	10.100
1993	0.005	0.800	2.600	5.010	7.630	10.210
1994	0.005	0.770	2.240	4.700	7.420	10.100
1995	0.005	0.820	2.210	4.330	7.220	10.080
1996	0.005	0.840	2.380	4.330	6.810	9.790
1997	0.005	0.720	2.290	4.380	6.600	9.130
1998	0.005	0.730	1.850	3.820	5.990	8.090
1999	0.005	0.840	2.220	3.900	6.320	8.690
2000	0.005	0.870	2.850	5.160	7.500	10.530
2001	0.005	0.800	2.400	5.010	7.510	9.820
2002	0.005	0.780	2.240	4.460	7.450	10.020
2003	0.005	0.830	2.180	4.140	6.620	9.570
2004	0.005	0.760	2.330	4.200	6.480	9.060
2005	0.005	0.720	1.920	3.840	5.750	7.870
2006	0.005	0.780	2.110	3.840	6.140	8.200
2007	0.005	0.740	2.250	4.180	6.300	8.850
2008	0.005	0.740	1.870	3.730	5.710	7.690

Table A7. Mean mass-at-age (kg) of other salmonines at annulus formation based on creel survey data from the Michigan Department of Natural Resources.

Species	Age (years)									
	1	2	3	4	5	6	7	8	9	10+
Lake trout	0.05	0.26	0.81	1.42	2.06	2.74	3.32	3.91	4.39	5.33
Steelhead trout	0.08	1.45	3.16	4.69	5.44					
Brown trout	0.48	1.50	3.03	3.72	3.72					
Coho salmon	0.23	1.61								

Table A8. Gross conversion efficiency values by age used in the estimation of consumption for the years before and after dreissenid invasion (1995 was used as the cutoff year) (Tsehaye et al. 2014).

	Age (years)										
	0	1	2	3	4	5	6	7	8	9	10
Chinook salmon											
Before	0.271	0.277	0.186	0.092	0.037	0.037					
After	0.243	0.224	0.152	0.075	0.030	0.030					
Lake trout											
Before	0.205	0.192	0.162	0.144	0.144	0.128	0.116	0.105	0.095	0.085	0.205
After	0.199	0.180	0.148	0.132	0.131	0.116	0.105	0.095	0.087	0.077	0.199
Steelhead trout											
Before		0.238	0.221	0.213	0.154	0.144					
After		0.222	0.196	0.185	0.134	0.125					
Brown trout											
Before		0.231	0.221	0.213	0.154	0.154					
After		0.216	0.196	0.185	0.134	0.134					
Coho salmon											
Before		0.302	0.234								
After		0.285	0.199								