Title: Balancing prey availability and predator consumption: a multispecies stock assessment for Lake Ontario

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**Abstract**:

Trophic interactions are drivers of ecosystem change and stability, yet are often excluded from fishery assessment models, despite their potential capacity to improve estimates of species dynamics and future fishery sustainability. In Lake Ontario, recreational salmonine fisheries, including Chinook salmon (*Oncorhynchus tshawytscha*) and lake trout (*Salvelinus namaycush*), depend on a single prey species, alewife (*Alosa pseudoharengus*). To accommodate strong trophic interactions among species, we developed a multispecies statistical catch-at-age assessment (MSCAA) model that links the dynamics of the salmonine fisheries and alewife via prey consumption and predator growth. We found that prey availability had declined since 2015 due to decreased alewife recruitment and increased Chinook salmon biomass, leading to higher alewife mortality rates and lower predator growth rates. Forward projections of predator-prey dynamics suggest that Chinook salmon stocking reductions may improve the probability for alewife population growth, but could be counteracted by increased natural Chinook salmon recruitment. Combined with predator and prey monitoring efforts, multispecies assessments show promise as models of intermediate complexity to support a transition to ecosystem-based approaches to fisheries management.

**Keywords:** Recreational fisheries, Great Lakes, trophic interactions, Chinook salmon, predator-prey interaction, stock assessment

## 1. Introduction

Ecosystem-based approaches to fisheries management are becoming increasingly common as the complex effects ecosystem interactions can have on management and conservation outcomes becomes increasingly apparent (Pauly et al. 2002, Travis et al. 2014). A growing number of analytical tools for fisheries management explicitly incorporate trophic interactions, as predation mortality, competition, or reductions in prey availability can affect fishery productivity or even drive fishery collapse (Hollowed et al. 2000a, Garrison et al. 2010, Christensen and Walters 2004, Audzijonyte et al. 2019). Notably, when the continued stability of a fishery is dependent on the availability of a single prey item or where the harvested species is the primary prey for another species, future management decisions may benefit from replacing single-species models with multispecies analyses that incorporate trophic linkages and explicitly model predator-prey dynamics (Gislason 1999, Matsuda and Abrams 2004, Collie et al. 2016).

Fisheries models of intermediate complexity that incorporate several relevant species strike a balance between the demographic data included in single-species models (i.e., age and length structure) and the extensive information on community dynamics required for ecosystem models (e.g., Ecosim with Ecopath; Plagányi et al. 2014, Collie et al. 2016). Multispecies statistical catch-at-age (MSCAA) models are a group of models of intermediate complexity that simultaneously estimate the population dynamics and interactions of multiple species using the statistical framework of a statistical catch-at-age (SCAA) model (Holsman et al. 2016). In contrast to single-species models where species interactions, such as predation, are included as external and known drivers (e.g. constant natural mortality; Hollowed et al. 2000b, Brenden et al. 2011), MSCAA models allow these interactions to be estimated directly within an assessment model (van Kirk et al. 2010). This is accomplished by linking multiple SCAA models through trophic interaction models that capture relevant predator and prey dynamics. Thus, MSCAA models can replicate and quantify trophic interactions while maintaining the strengths of SCAA models, such as age-structure, to track cohort dynamics and likelihood-based statistical inference (Jurado-Molina et al. 2005). These models may be particularly useful in fisheries dominated by a few species whose joint population dynamics are driven by strong trophic linkages.

Across the Laurentian Great Lakes, many culturally and economically important salmonine fisheries depend on the availability of a small set of prey fish (Jones et al. 1993, Murry et al. 2010, Tsehaye et al. 2014, He et al. 2016). Fisheries managers have sought to balance predation pressure from stocked and naturally reproduced salmonine populations with fluctuating prey availability by adjusting stocking levels in response to shifts in prey fish biomass or production (Eshenroder et al. 1995, Stewart et al. 2017). Central to these management decisions are the population dynamics of two dominant predators, Chinook salmon (*Oncorhynchus tshawytscha*) and lake trout (*Salvelinus namaycush*), and the predation pressure they exert on their primary prey species, alewife (*Alosa pseudoharengus*; Mumby et al. 2018, Nawrocki et al. 2020). In Lake Ontario, the trophic interactions between these three species are drivers of fishery sustainability as alewife make up 90% of the offshore prey fish biomass and Chinook salmon and lake trout are critical drivers of alewife mortality due to their large population sizes and high prey fish demand (Jones et al. 1993, Murry et al. 2010, Weidel et al. 2020). Due to these strong predator-prey linkages, all three species are the focus of Lake Ontario management objectives that seek to jointly maintain salmonine sport fisheries, restore native fish species diversity, and maintain a stable prey fish base (Fish Community Objectives for Lake Ontario; Stewart et al. 2017). Thus, a MSCAA approach that incorporates the strong ecological linkages between predator species and alewife can both provide information on the status of the salmonine fisheries and the predator-prey balance in Lake Ontario.

A potential imbalance between prey abundance and predation pressure threatens the sustainability of the salmonine fisheries in Lake Ontario due to their heavy dependence on alewife. Population surveys of alewife indicate that lake-wide biomass has recently declined following successive years of low recruitment (Weidel et al. 2020), while surveys of Chinook salmon smolt abundance suggest that natural recruitment of Chinook salmon may be substantial and potentially increasing (Bishop et al. 2020). This has resulted in concerns that predation could exceed prey availability and lead to declines or even collapse of the salmonine fisheries in Lake Ontario. Similar trends were observed in other Great Lakes, where alewife population declines have prompted reductions in Chinook salmon stocking in Lake Michigan (Tsehaye et al. 2014) and a severe decline in alewife biomass in the early 2000s in Lake Huron led to significant declines in Chinook salmon abundance and recreational fishery harvest (Brenden et al. 2011, He et al. 2016, O'Keefe et al. 2015). Better understanding of the joint predator-prey dynamics for Chinook salmon, lake trout, and alewife, and quantifying the amount of pressure these predators exert on alewife could help identify destabilizing levels of predation pressure and provide information on the potential effect of future predator recruitment on both predator and prey populations in Lake Ontario.

Traditional single-species fisheries models fail to capture the key predator-prey dynamics that inform management decision-making in Lake Ontario. Although fisheries in Lake Ontario have had a long history of ecosystem-based management and the use of predator-prey models (Jones et al. 1993, Murry et al. 2010), a formal modeling framework that links assessments of key predator and prey species while simultaneously estimating species dynamics does not exist. Based on management objectives for maintaining the salmonine fisheries and prey fish biomass, we developed a MSCAA for Lake Ontario for the Chinook salmon and lake trout fisheries and their primary prey species, alewife (Stewart et al. 2017). We fit the model to a suite of survey and fishery data from Lake Ontario to characterize the joint population dynamics of these three species from 2001-2019 and to quantify predator-prey interactions. We then used the fitted model estimates to explore scenarios of predator-prey balance under different predator stocking levels and natural Chinook salmon recruitment. We show that by sharing information across predator and prey populations, the MSCAA model performed well in reconstructing the joint population dynamics of all three species and demonstrated how the output of the MSCAA model can provide insight into future predator-prey dynamics.

## 2. Methods

### *2.1 Lake Ontario MSCAA overview*

The MSCAA model is structured as three SCAA submodels for Chinook salmon, lake trout, and alewife linked via predation interactions. All submodels are simultaneously estimated, such that the population dynamics of one species are influenced by the dynamics of the other two. We allowed the Chinook salmon and lake trout submodels to exert predation pressure on alewife via a type-II functional response (see eq. 13; Holling 1959), which produced estimates of monthly alewife consumption by the predator species based on prey availability and accounted for satiation effects on predator consumption rate when alewife densities were high. To represent the effects of prey availability on predator dynamics, we used predator-specific bioenergetic models to convert alewife consumption into predator growth while accounting for metabolic energetic needs, generating estimates of predator weight-at-age, and creating a feedback loop between predation pressure and prey availability (see section 2.5; Kitchell et al. 1977, Deslauriers et al. 2017). Thus, predator biomass can only increase if a sufficient amount of prey biomass is available. In turn, an increase in predator consumption of alewife may result in higher alewife mortality rates and a decline in prey biomass. In this way, the MSCAA approach allows information to be shared between the SCAA submodels, with each submodel customized to include species-specific characteristics.

The species-specific SCAA submodels for Chinook salmon, lake trout, and alewife differed from one another based on life history and fishery characteristics; however, all followed classic SCAA model structure, where populations are age-structured, forward-projected, and demographics are governed by changes in mortality and recruitment (Quinn and Deriso, 1999). Modeled populations were indexed by species ($s$; Table 1), age ($a$), and, when relevant, groups within species (i.e. natal origin or length class). Additionally, the model runs on a monthly time step ($m$) from 2001-2019 (years, $y$), allowing for the representation of discrete events such as spawning, changes in bioenergetic factors (e.g., temperature), and differences in survey timing to be incorporated into the model structure.

We incorporated eight different datasets collected by the New York State Department of Environmental Conservation (NYSDEC), the Ontario Ministry of Natural Resources and Forestry (OMNRF), the United States Geological Survey (USGS) Great Lakes Science Center, and the United States Fish and Wildlife Service (USFWS) including harvest estimates, tagging data, and scientific surveys in Lake Ontario (Fig. S1, Table S1). We also included monthly data on predator temperature preferences (Raby et al. 2020) and prey energy density (Rand et al. 1994) in the bioenergetics submodels. The MSCAA model was programmed in ADMB (v.12.0; Fournier et al. 2012) and run in R using the R2ADMB package (v. 4.0.3; R Core Team 2020, Bolker et al. 2020). Result summarizations and simulation analyses using the MSCAA model were also conducted in R. Below we first describe each species submodel, followed by an explanation of the bioenergetics submodel, and finally a description of the multispecies short-term future simulations using the fitted model.

### *2.2.1 Chinook Salmon Population Submodel*

The Chinook salmon submodel included two sources of recruitment (i.e., stocked and natural recruitment), and accounts for fishing, natural, and spawning mortality. Although Chinook salmon is the most popular sport fishery in Lake Ontario, fishing effort has been relatively stable even as angler success (catch-per-unit-effort; CPUE) has generally increased over the last two decades (Connerton et al. 2020). For controlling the predator-prey balance, management actions focused solely on increasing fishing mortality (e.g. increasing angler harvest limits) are generally considered ineffective for reducing lake-wide Chinook salmon abundance because relatively few angling trips (<10%) meet current harvest limits (Connerton et al. 2020). Instead, stocking is the primary management approach to regulating the Chinook salmon population; however, reductions in stocking may be offset by increases in natural Chinook salmon recruitment. Previous studies have found that natural reproduction can vary annually, with the proportion of naturally reproduced age-3 Chinook salmon in Lake Ontario ranging from 30-70% (Connerton et al. 2009, Connerton et al. 2016, Prindle and Bishop 2020). Furthermore, advancements in stocking practices have led to improved juvenile survival of stocked Chinook salmon. As much as 44% of NYSDEC and 49% of OMNRF Chinook salmon fingerlings are placed in floating pens prior to being released into the lake (“pen-stocked”) resulting in increased growth and survival rates when compared to fingerlings directly stocked into the lake (“direct-stocked”; Connerton 2020; Table S2, Fig. S2A). A potential increase in natural recruitment combined with better survival of stocked fish could lead to significant increases in adult Chinook salmon abundance.

Understanding the relative contribution of direct-stocked, pen-stocked, and naturally reproduced fish to the Chinook salmon population enables better predictions as to how changes in stocking or natural recruitment may affect future predation pressure on alewife. To capture these different dynamics within the model, we divided the Chinook salmon population into five natal origin categories; 1) naturally reproduced, 2) direct-stocked by NYSDEC, 3) pen-stocked by NYSDEC, 4) direct-stocked by OMNRF, and 5) pen-stocked by OMNRF. For simplicity, we also included fish held for an extended period at the New York hatchery (approximately 300,000 fingerlings per year) with the NYSDEC pen-stocked fish, as prior research found that these fish had similarly increased survival rates (Connerton et al. 2016). Dividing the population by stocking agency also allowed us to adjust for known biases in surveys of spawning adults resulting from natal-homing (S1.1).

For simplicity, stocked and naturally reproduced recruits were modeled as entering the population in January $(m = 1)$ of each year as the age-0 cohort (hereafter age-0 fish, $a = 0$) and we assumed that all Chinook salmon perished by the end of their fifth year in the lake $(a = 4)$. The number of stocked age-0 fish was assumed known based on stocking records (Connerton 2020, Lake 2020), while the number of age-0 naturally reproduced age-0 fish was estimated annually. Thus, lake-wide abundance ($N$; Table 2) for Chinook salmon $(s = CHK)$ was indexed by year ($y$; Table 1), month $(m)$, age $(a)$, and natal origin $(i)$ and followed:

$$N_{s=CHK,y,m+1,a,i} = N_{s=CHK,y,m,a,i} e^{-Z_{s=CHK,y,m,a,i}} \quad (1)$$

which was modified to at the end of the year $(m = 12)$ to account for changes in age composition based on annulus formation, by setting the left side of eq.1 to $N_{s=CHK,y+1,m=1,a+1,i}$. Total instantaneous mortality $(Z)$, was modeled as the sum of instantaneous natural $(M)$ and fishing mortality $(F)$:

(2) $$Z_{s=CHK,y,m,a,i} = \frac{M_{s=CHK,a,i}}{12} + \sum_{f} F_{s=CHK,f,y,m,a}$$

Annual natural mortality $(M)$ was assumed to be time-invariant, known, and represented additional sources of mortality not accounted for by harvest (Eq. 3) or spawning (Eq. 4), such as predation, disease, and hooking mortality. For adults $(a \geq 1)$, we set $M = 0.1$ and either 2.3 or 1.6 for age-0 fish depending on natal origin (Table S2; Connerton et al. 2016). In contrast, fishing mortality $(F)$ varied monthly to accommodate seasonal closures and was not dependent on natal origin. However, we separately modeled fishing mortality for New York and Ontario waters to capture differences in these two groups of recreational anglers (fisheries, $f$):

(3) $$F_{s=CHK,f,y,m,a} = q_{s=CHK,f} S_{s=CHK,f,a} E_{f,y,m}$$

Monthly fishing effort $(E)$ was assumed to be known and was based on estimates of fishing effort calculated from creel surveys conducted on each side of the lake (Robson and Jones 1989, Stewart et al. 2004, Yuille and Jakobi 2017, Connerton et al. 2020). In contrast, fishery-specific catchability $(q)$ and fishery-specific age-based selectivity $(S)$ were estimated. For both fisheries, we assumed age-3 and older fish were fully recruited to the fishery $(S = 1)$ and that age-0 fish were not selected $(S = 0)$. Thus, we estimated selectivity only for age-1 and age-2 fish, which were estimated independently for each age and each fishery.

In addition to instantaneous mortality sources, the other major source of mortality for Chinook salmon is spawning. To account for semelparity we modeled spawning as an instantaneous event occurring at the end of September $(m = 9)$, replacing eq.1 with the modified equation:

$$(4) \qquad N_{s=CHK,y,m=10,a,i} = \left(N_{s=CHK,y,m=9,a,i}e^{-Z_{s=CHK,y,m=9,a,i}}\right)(1.0 - \theta_a)$$

where $\theta_a$ is the age-specific probability of spawning. We estimated the probability of spawning for ages 1-3 and assumed that all age 4 fish spawned $(\theta = 1)$.

### *2.2.2 Chinook Salmon Likelihoods*

The majority of the assessment data for the Chinook salmon submodel came from creel surveys conducted by NYSDEC and OMNRF for the fisheries in New York and Ontario waters that provide estimates of the total annual harvest (Table S1; Yuille and Jakobi 2017, Connerton et al. 2020). We estimated annual harvest $(H)$ using a Baranov-type catch equation:

$$(5) \qquad H_{s=CHK,f,y,a} = \sum_{m}\sum_{i}\frac{F_{s=CHK,f,y,m,a,i}}{Z_{s=CHK,y,m,a,i}}(1.0 - e^{-Z_{s=Chk,y,m,a,i}})N_{s=CHK,y,m,a,i}$$

For each fishery, we included likelihoods for total annual harvest, which was assumed to follow a log-normal distribution (eq. ST4.1), and the age-distribution of harvested Chinook salmon, which we assumed followed a multinomial distribution (eq. ST4.2).

We supplemented data from creel surveys with scientific surveys that targeted or captured life history stages that are not well represented in the creel surveys. Specifically, we included data that targeted spawning Chinook salmon by including the age-distributions of spawners collected by NYSDEC and OMNRF as broodstock (Yuille 2019b, Prindle and Bishop 2020), which we assumed followed multinomial distributions (S1.1, eq. ST4.3). We also included an index of naturally reproduced age-0 smolts collected from the Salmon River, NY by NYSDEC (S1.2; Bishop et al. 2020) and an index of age-1 Chinook salmon abundance from the annual OMNRF community gillnet survey (S1.3; Yuille 2019a). Separate likelihoods were specified for the age-0 and age-1 indices and both were assumed to follow log-normal distributions (eqs. ST4.4 and ST4.5, respectively).

The final likelihood for the Chinook salmon submodel included the relative abundance of stocked and naturally reproduced Chinook salmon, the data for which came from four cohorts of adipose fin-clipped fish (Connerton et al. 2016). Between 2008 and 2011, the adipose fin of all stocked Chinook salmon across Lake Ontario was removed and extensive surveying was used to estimate the proportion of stocked-origin versus naturally reproduced fish. The deviations between the field-based estimates of the proportion of stocked fish from mass marking versus the model-based estimates of the relative abundance of stocked fish were assumed to follow a binomial distribution (S1.4; eqs. S7, ST4.6, and ST4.7).

### *2.3.1 Lake Trout Population Submodel*

Lake trout is an important contributor to alewife predation pressure due to its reliance on alewife as a prey item and large lake-wide population (Brenden et al. 2011 Jones et al. 1993, Mumby et al. 2018). In contrast to Chinook salmon, however, lake trout are long-lived, take 2 to 3 years to recruit to the recreational fishery, and do not switch to an alewife-dominated diet until about age 4 (Brenden et al. 2011, Metcalfe, OMNRF, pers. coms). As a result, stocking changes for lake trout will take longer to affect the prey fish community than stocking changes for Chinook salmon. Lake trout were extirpated from Lake Ontario in the 1950s due to overfishing, predation by sea lamprey, and habitat degradation (Christie 1973; Elrod et al. 1995); efforts to restore a self-sustaining lake trout population have been ongoing since the early 1970s. Although wild lake trout reproduction has been documented in Lake Ontario (Owens et al. 2003; Lantry et al. 2020), it is considered to be extremely limited. Thus, we assume all lake trout recruitment is via stocking in this species' submodel.

The lake trout submodel in the Lake Ontario MSCAA was adapted from an existing lake trout SCAA model from Brenden et al. (2011). Within the submodel, the lake trout population is both age and length structured, employing a length-at-age transition matrix to generate length class abundances (Quinn and Deriso 1999). This was necessary to account for both age and size-specific population dynamics, New York harvest regulations, and survey data. Length classes ($l$) were based on one-inch increments and ranged from 7 inches or less (<17.8 cm) to 37 inches or more (>94.0 cm). In contrast to the Chinook salmon and alewife submodels, the lake trout submodel was fit to seven additional years of data (1993-2000), allowing more cohorts to be tracked across all 15 age classes. Preliminarily analyses suggested that this improved estimates of lake trout abundance and key parameters such as juvenile mortality and selectivity. Population characteristics that were influenced by lake trout predation on alewife were only modeled from 2001-2019 (e.g. biomass, consumption) as those estimates were dependent on the Chinook salmon and alewife submodels.

To capture these population dynamics and survey logistics, lake trout abundance ($N$; $s = LKT$; Table 2) was indexed by year ($y$; Table 1), month ($m$), age ($a$), and length class ($l$):

(6)
$$N_{s=LKT,y,m+1,a,l} = N_{s=LKT,y,m,a,l}e^{-Z_{s=LKT,y,m,a,l}}$$

At the end of the year ($m = 12$) age increases and fish get redistributed among age-based length classes:

(7)
$$N_{s=LKT,y+1,m=1,a+1,l} = \gamma_{y,a,l}\sum_{l}(N_{s=LKT,y,m=12,a,l}\,e^{-Z_{s=LKT,y,m,=12a,l}})$$

where γ is the probability of a fish of age $a$ being in length class $l$. We assumed γ was known and based on length-at-age matrices developed outside of the MSCAA model. We allowed the length-at-age matrices to change over time to account for a small increase in lake trout length-at-age between 1993 and 2019, but due to limited sample sizes only used three matrices, each spanning one decade and based on aggregated samples from the annual USGS-NYSDEC-USFWS gillnet survey (e.g. 1993-1999, 2000-2009, 2010-2019; Lantry et al. 2020).

In addition to the natural and fishing mortality included in the Chinook salmon submodel, the lake trout submodel incorporated annual, age-specific sea lamprey predation mortality ($SL$), based on the sea lamprey marking rates observed in annual surveys (Brenden et al. 2011) into the estimates of total instantaneous mortality ($Z$):

$$(8) \qquad Z_{s=LKT,y,m,a,l} = \frac{1}{12}\left(M_{s=LKT,y,a} + SL_{y,a}\right) + \sum_{f} F_{s=LKT,f,y,m,l}$$

Annual instantaneous natural mortality ($M$) for age 2+ lake trout ($a \geq 2$) was set at 0.2 based on estimated mortality rates for other populations of lake trout in the Great Lakes (Linton et al. 2007, Jonas 2011), but was annually estimated for age-1 fish and modeled as a random walk to account for variable stocking and juvenile mortality. In contrast to the other sources of mortality, fishing mortality was length-based instead of age-based and, as with Chinook salmon, varied between New York and Ontario waters (fisheries, $f$). From 1992 through 2006, the harvest of lake trout within the size range of 25-30 inches (63.5-76.2 cm) was prohibited in New York waters, and then post-2007 only one fish per angler per day could be harvested from within this size range. To account for these regulations, we modeled fishing mortality as:

$$(9) \qquad F_{s=LKT,f,y,m,l} = E_{f=NY,y,m} q_{s=LKT,f,y} S_{s=LKT,y,l} \rho_{f,y,l}$$

where selectivity ($S$) is modeled as a length-based normalized gamma density function (Brenden et al. 2011, Quinn and Deriso 1999) and $\rho$ ranges from 0-1 and is a length-based adjustment for the New York regulations. We set $\rho = 1$ for all length classes that were excluded from the New York regulations (i.e. $l < 25$ or $l > 30$). Following Brenden et al. (2011), two values of $\rho$ were estimated for the 1992-2006 regulations, one for the two edges of the regulated length range (25 and 30-inch fish) and one for the rest of the range (26 to 29-inch fish). Due to the regulation changes in 2007, a single additional $\rho$ value was estimated for 2007-2019 and applied to all length classes within the regulated range (25 to 30-inch fish). Due to low samples sizes in recent Ontario creels surveys, a separate selectivity curve for lake trout caught in Ontario waters could not be reliably estimated. Instead, we used the selectivity curve estimated for New York fishing mortality; however, since there are no size restrictions for lake trout in Ontario waters, we set $\rho$ to 1 for all length classes. Catchability $(q)$ for lake trout for both fisheries was modeled as separate random walks following Brenden et al. (2011; S1.5) as species-specific estimates of fishing effort $(E)$ are unavailable and Lake Ontario anglers are known to spend less time targeting lake trout when catch rates for other salmonine fisheries, such as Chinook salmon, are high (Connerton et al. 2020).

### *2.3.2 Lake Trout Likelihoods*

As lake trout are both a recreational fishery and the focus of restoration efforts, data informing the lake trout submodel were available from creel surveys, multispecies surveys, and an annual USGS-NYSDEC-USFWS gillnet survey that specifically targets lake trout (Lantry et al. 2020). The most critical data for the lake trout submodel comes from the annual USGS-NYSDEC-USFWS survey, as it is the only consistent source of age-based data from lake trout marked with coded wire tags (S1.6). Four likelihoods were included based on data from this survey: the catch-per-unit effort (CPUE) for the annual number of fish caught in the survey, the CPUE of just coded wire-tagged fish, the length composition of all fish, and the age composition of just coded wire-tagged fish (eqs. ST5.1-4). An additional trawl survey conducted by USGS-

NYSDEC-USFWS also provides an index of juvenile (age-2) lake trout survival, which was included to improve estimates of changes in age-1 lake trout natural mortality. Specifically, this was modeled as the catch per 500,000 stocked yearlings from an annual trawl survey by USGS, NYSDEC, and USFWS (Lantry et al. 2020; eq. ST5.5). We also included an index of abundance from the annual OMNRF fish community survey, incorporating likelihoods for the CPUE and length composition for these data (S1.3; eqs. ST5.6 and ST5.7)

The lake trout survey data are supplemented by creel surveys conducted by both NYSDEC and OMNRF (Yuille and Jakobi 2017, Connerton et al. 2020). As with the Chinook salmon submodel, lake trout harvest $(H)$ was modeled using a Baranov catch equation:

$$H_{s=LKT,f,y,i} = \sum_{m}\sum_{a}\frac{F_{s=LKT,f,y,m,i}}{Z_{s=LKT,y,m,a,i}}(1.0 - e^{-Z_{s=LKT,y,m,a,i}})N_{s=LKT,y,m,a,i} \tag{10}$$

Total harvest $(H)$ for each fishery was assumed to follow a log-normal distribution (eqs. ST5.8 and ST5.9), while a multinomial distribution was used to model the length composition from the NYSDEC creel survey (eq. ST5.10). Due to low sample sizes, we did not fit a likelihood for length composition for the OMNRF creel survey. To account for known variability in angler behavior over time (e.g. higher catch and release rates, targeting other species), we modeled catchability for each fishery as a random walk and assumed the deviations followed a log-normal distribution (S1.5; ST5.11 and ST5.12).

### *2.4.1 Alewife Population Submodel*

Introduced in the mid-1800s, alewife populations rapidly increased in Lake Ontario while several native fish species declined or collapsed, including lake trout. Alewife are thought to have been instrumental to the successful introduction of Chinook salmon and other Pacific salmonines in 1968 (Smith 1970), providing a large prey fish biomass for these top predators. Currently, alewife still dominate the offshore prey fish biomass and are the primary diet item for Lake Ontario salmonines (Hoyle et al. 2017, Weidel et al. 2020).

As with Chinook salmon and lake trout, alewife abundance ($N$; Table 2) was indexed by year ($y$; Table 1), month ($m$), and age ($b$; 1-5+):

(11) $$N_{s=ALE,y,m+1,b} = N_{s=ALE,y,m,b}e^{-Z_{s=ALE,y,m,b}}$$

which was modified to allow for aging to occur at the end of the year ($m = 12$), by setting the left side of eq.1 to $N_{s=ALE,y+1,m=1,b+1}$. All alewife age five or older were grouped into a single plus age group ($b = 5+$). We freely estimated the annual abundance of age-1 alewife ($N_{y,m=1,b=1}$, hereafter "annual alewife recruitment"). We did not include age-0 alewife in the model, as there is a lack of data on the annual dynamics of age-0 alewife and due to their small size, they are not a common prey item for adult Chinook salmon or lake trout. To include time-varying predation mortality, alewife total instantaneous morality ($Z$) was modeled as the sum of annual natural (or "residual", van Kirk et al. 2010) mortality ($M$) and monthly predation mortality ($P$) from Chinook salmon and lake trout:

(12) $$Z_{s=ALE,y,m,b} = \frac{1}{12}M_{s=ALE} + \sum_{a} P_{s=CHK,p=ALE,y,m,a,b} + \sum_{a} P_{s=LKT,p=ALE,y,m,a,b}$$

We assumed that alewife natural mortality was time and age invariant, and known at 0.41 (Weidel et al. 2021). Predation mortality varied with both predator and prey age, and thus mortality was indexed by both alewife age $(b)$ and predator age $(a)$. For parameters that represent predation interactions, we use $s$ to denote the predator species (either $s = CHK$ or $s = LKT$) and $p$ to denote the prey species (i.e. $p = ALE$). We modeled predation mortality through a type-II multispecies functional response, which accounts for predator satiation at high levels of prey availability (Holling 1959, Murdoch 1973). Thus, alewife consumption varied with prey availability, predator abundance, and predator size:

$$(13) \qquad P_{s,p=ALEy,m,a,b} = \frac{N_{s,y,m,a}}{B_{s=ALE,y,m,b}} \left( \frac{\phi_s L_{s,y,m,a} V_{s,p=ALE,y,m,a,b}}{1 + \phi_s h_{s,y,m,a} \sum_a V_{s,p=ALE,y,m,a,b} \left(1 + \frac{\sum_{k \neq ALE} D_k}{D_{k=ALE}}\right)} \right)$$

where $\phi_s$ is an estimated predator-specific scalar multiplied by predator length $\left(L_{s,y,m,a}\right)$ to calculate the effective search area of the predator (Tsehaye et al. 2014), $h$ is predator-specific handling time, and $V$ is the age-specific alewife biomass vulnerable to predation, which varied between species and among predator ages. Alewife biomass $(B)$ was calculated as:

$$(14) \qquad B_{s=ALE,y,m,b} = N_{s=ALE,y,m,b} W_{s=ALE,y,m,b}$$

where monthly weight-at-age estimates $\left(W_{s=ALE,y,m,b}\right)$ were assumed known and calculated by interpolating weight data from the annual trawl survey (conducted in April). While we assumed that Chinook salmon only consumed alewife, lake trout have a more diverse diet, though still dominated by alewife (Jude et al. 1987, Nawrocki et al. 2020). We used $D$ to represent the proportion of each prey species (indexed by $k$; Table 1) in the lake trout diet (alewife, round goby, *Neogobius melanostomus*; rainbow smelt, *Osmerus mordax*; and sculpin *Cottidae sp.*). While ideally diet data would be used to fit the model and incorporate the population dynamics of other prey species (Trijoulet et al. 2019), there was not sufficient data on the other three prey species to reliably estimate the amount of biomass vulnerable to predation. However, alewife dominate Lake Ontario lake trout diets, comprising 63% to 97% of lake trout diets from 2001-2019 (Holden et al. 2017, Metcalfe, OMNRF, pers. comms). Thus, we did not model the dynamics of any other prey species and assumed that lake trout diets were known. To incorporate this assumption into the functional response equation, we set the amount of non-alewife vulnerable biomass equal to $\sum_a V_{s,p=ALE,y,m,a,b}\left(\frac{\sum_{k\neq ALE} D_k}{D_{k=ALE}}\right)$ and assumed that handling time did not vary by prey species (Murdoch 1973).

To allow predation pressure to vary with predator size, we approximated handling time $(h)$ as $1/Cmax$, where $Cmax$ is the age-specific maximum amount of total prey biomass an individual predator could consume in a given month based on our estimates of predator weight-at-age and water temperature preferences $(Temp)$ based on pop-off temperature loggers from Raby et al. (2020):

$$Cmax_{s,y,m,a} = 30W_{s,y,m,a}\left(CA_s W_{s,y,m,a}^{CB_s}\right) f\left(Temp_{s,m}\right)_s \tag{15}$$

where $CA$ and $CB$ are species-specific bioenergetics constants and $f(Temp)$ represents the temperature functions originally derived by Thornton and Lessem (1978) and parameterized for Chinook salmon (Stewart and Ibarra 1991, Plumb and Moffit 2015) and lake trout (Stewart et al. 1983). The temperature functions also allowed maximum consumption to vary seasonally, with the least amount of consumption occurring during colder winter months (S1.7; eqs. S15-18). Similarly, the amount of alewife biomass vulnerable to predation varied with predator size and age. The portion of the alewife biomass vulnerable $(V)$ to predation is based on the spatial and temporal overlap in habitat use by predator and prey $(O)$ and the relative length $(L)$ of the prey compared to that of the predator (Jones et al. 1993, Tsehaye et al. 2014):

$$(16) \qquad V_{s,p=ALE,y,m,a,b} = B_{s=ALE,y,m,b} O_{s,p=ALE,a,b} e^{-\frac{1}{100}\left(\frac{L_{s=ALE,y,m,b}}{L_{s,y,m,a}} - 0.25\right)^2}$$

This allowed predator consumption to reflect a size-based preference for prey fish and was maximized when prey were one-quarter the length of the predator. Thus, we are able to represent prey selectivity by older, larger predators for the largest alewife available, and prey selection by younger, smaller predators for smaller alewife (Jacobs et al. 2013). The habitat usage matrix $(O)$ reflects the overlap in the spatial and temporal distributions of the predator and prey species and was assumed known and adapted from Jones et al. (1993; Table S6).

### *2.4.2 Alewife Likelihoods*

In the absence of harvest data, the primary data source for alewife came from annual trawl surveys that provided estimates of lake-wide alewife abundance and biomass (Weidel et al. 2020). We assumed that the surveys provide an accurate representation of the magnitude of lake-wide abundance $(T)$ and followed:

$$(17) \qquad \hat{T}_{y,b} = N_{s=ALE,y,m=4,b} q_{s=ALE,y,b} S_{s=ALE,b}$$

However, we allowed for annual deviations in catchability ($q$; i.e. “white noise” catchability; Wilberg and Bence 2006; S1.5). This accounted for known biases in the trawl survey population estimates, due to annual changes in the spatial distribution of the alewife population across the lake (Weidel et. al. 2020). The trawl survey was conducted in New York waters only until 2015, and trawling in both New York and Ontario waters beginning in 2016 suggested biases in trawl survey population estimates due to the annual changes in the spatial distribution of the alewife population across the lake (Weidel et al. 2020). The white noise model for catchability allowed us to account for over or underestimates in the trawl survey population estimates due to the spatial distribution of alewife. Preliminary analyses of catchability curves suggested that annual deviations in catchability varied between adult (age-2+) and age-1 alewife, and thus we estimated separate time-varying catchabilities for these two age groups. We also estimated a time-invariant selectivity parameter for age-1 alewife, as they are not fully recruited to the trawl gear, while we assumed adult alewife were fully recruited and did not estimate a selectivity parameter $\left(S_{s=ALE,b=2+}\right)$. Total survey abundance $\left(\sum_b \hat{T}_{y,b}\right)$ was assumed to have a lognormal distribution (eq. ST7.1) while the survey age distribution $\left(\hat{T}_{y,b}/\sum_b \hat{T}_{y,b}\right)$ was assumed to follow a multinomial distribution (eq. ST7.2). Deviations in catchability for both age-1 and adult alewife were also assumed to follow a lognormal distribution (eqs. ST7.3 and ST7.4).

### *2.5 Predator Bioenergetics Submodel*

The final submodel in the MSCAA linked prey availability to predator growth through a Wisconsin-style bioenergetics model (Stewart et al. 1983, Stewart and Ibarra 1991, Deslauriers et al. 2017). Briefly, predator growth was estimated as a function of prey consumption relative to the maximum amount of consumption possible given water temperature and estimated predator size (eq. 15). Consumed prey biomass was converted into energy based on seasonal prey energy densities. Energy was then lost via waste products or allocated to meet metabolic demands. Any remaining energy was converted into predator growth, or weight loss if prey consumption did not satisfy metabolic needs:

$$Growth = Consumption - (Metabolism + Waste) \tag{18}$$

The detailed model structure for the Wisconsin bioenergetics model and parameters for both Chinook salmon and lake trout have been well described elsewhere in the literature (Deslauriers et al. 2017, Stewart et al. 1983, Stewart and Ibarra 1991) and parameters and model inputs for seasonal prey energy density estimates are summarized in Table S8. The outputs of the bioenergetics submodel were estimates of predator weight-at-age, which were used to generate monthly estimates of predator biomass $(B)$:

$$B_{s=CHK,y,m,a,i} = N_{s=CHK,y,m,a,i} W_{s=CHK,y,m,a} \tag{19}$$

$$B_{s=LKT,y,m,a,l} = N_{s=LKT,y,m,a,l} W_{s=LKT,y,m,a} \tag{20}$$

We calculated alewife consumption for each predator species using a Baranov-type catch equation, which allowed consumption ($C$; Table 2) to vary by species ($s$; Table 1), year $(y)$, month $(m)$, and predator age$(a)$ based on predation ($P$; eq. 13) and total mortality ($Z$; eq. 12):

$$C_{s,p=ALE,y,m,a} = \sum_{b} \left(B_{s=ALE,y,m,b}\right) \left(\frac{P_{s,p=ALE,y,m,a,b}}{Z_{s=ALE,y,m,b}}\right) \left(1 - e^{-Z_{s=ALE,y,m,b}}\right) \tag{21}$$

Subsequently, we used alewife consumption per predator $(C_{s,p=ALE,y,m,a}/N_{s,y,ma})$ as an input into the bioenergetics model to estimate predator growth rates (Eq. 18). As alewife are the primary prey item for Chinook salmon and lake trout, changes in alewife consumption are a driver of predator growth rates. Due to this predator-prey relationship, we were able to compare model estimates of predator weight-at-age to survey data. For Chinook salmon, we compared monthly weight-at-age estimates to fish age-1 and older collected during the NYSDEC creel survey in June and July. As age-0 Chinook salmon have a more diverse diet and drivers of growth are poorly understood, we did not model age-0 growth rates and instead estimated age-1 weight at the beginning of the year as a random walk (ST4.8). Similarly, for lake trout we fit age-4 and older weight-at-age estimates to data from the USGS-NYSDEC-USFWS annual gillnet survey and estimated age-4 weight in January as a random walk. All four of these likelihoods were assumed to follow log-normal distributions (eqs. ST4.9, ST4.10, ST5.13, ST5.14).

### *2.6 Annual Surplus Production*

We evaluated the annual predator-prey balance in Lake Ontario by comparing total annual alewife consumption by Chinook salmon and lake trout to annual alewife surplus production (ASP). Although ASP is typically calculated as the change in population biomass plus harvested biomass (Quinn and Deriso 1999), to understand the balance between predator consumption and alewife biomass we calculated ASP as:

$$ASP_y = \left(\sum_{b=2}^{5} B_{s=ALE,y,m=1,b} - B_{s=ALE,y-1,m=1,b}\right) + \sum_s \sum_m \sum_a C_{s,y,m,a} \qquad (22)$$

replacing harvested biomass with biomass consumed by predators. Annual surplus production reflects interannual changes in the alewife population biomass net of recruitment and growth (biomass addition), loss to natural mortality sources, and loss to predator consumption. Positive ASP values indicate potential alewife biomass gains as annual biomass additions exceeded the amount of alewife biomass to natural mortality sources. Alewife biomass will only increase when predator consumption is less than the net of biomass additions and biomass lost to natural mortality, in all other cases alewife biomass will decline. Years with negative ASP may result in the greatest declines in alewife biomass as biomass additions are unable to offset the biomass lost to natural mortality sources much less biomass lost to predation.

### *2.7 Future Predator-Prey Scenarios*

We used the fitted MSCAA model to explore the potential effect of future stocking decisions on the predator-prey dynamics in Lake Ontario. We focused our simulations on short-term predator-prey dynamics to explore the probability that alewife densities would increase in the next five years or whether they were likely to continue to decline under different Chinook salmon stocking and natural recruitment scenarios. Due to their shorter lifespan, reductions in Chinook salmon stocking can quickly reduce adult Chinook salmon abundance and lessen predation pressure on alewife, whereas increases in salmon natural recruitment can quickly increase predation pressure or negate the impact of stocking reductions.

To demonstrate the potential effect of stocking adjustments on the predator-prey balance, we explored three scenarios of annual Chinook salmon stocking: 1) no stocking cuts - Chinook salmon annual stocking levels reflect previous baseline levels implemented up to 2016 (2.4 million age-0 salmon/yr; Connerton 2020, Lake 2020), 2) recent stocking cuts - stocking levels reflect a stocking adjustment implemented in 2019 reflecting managers' concern over potentially declining alewife abundances (1.4 million), and 3) no stocking - a hypothetical scenario to explore the implications of ceasing hatchery stocking. As an increase in natural Chinook salmon can potentially offset the effect of stocking reductions, we also considered a range of natural recruitment levels across scenarios. Since drivers of natural Chinook salmon recruitment are understudied and due to poor fits of stock-recruitment relationships to our estimates of spawning stock biomass and natural recruitment (Fig. S3.), we used the estimated values of annual natural recruitment from the fitted model to produce a range of realistic future scenarios. We held natural recruitment constant across the five simulated years and ran separate sets of simulations for each of the estimated values of annual natural recruitment from the fitted model (n=18;

natural recruitment in the terminal year cannot be reliably estimated). We did not explore changes in lake trout stocking, as lake trout take several years post-stocking to switch to a primarily alewife diet and thus any simulated stocking cuts would have limited influence on short-term trends in predation pressure. Instead, we assumed that lake trout stocking and juvenile survival remained equal to 2019 values.

To capture the stochastic nature of alewife recruitment during simulations, alewife annual recruitment outcomes were randomly drawn with replacement from the estimated values of age-1 abundance for 2015 to 2019 (Fig. 2F). These recent years may best represent short-term future trends in alewife recruitment. Ranging from 92 to 1196 million age-1 alewife per year, this time series includes one year of strong recruitment and four of relatively poor recruitment. To account for the variability in alewife recruitment, ten thousand iterations were run for each combination of stocked and natural recruitment Chinook salmon simulation scenarios.

The predator-prey balance for each simulation iteration was evaluated based on the change in alewife biomass over the five simulated years. A decline in alewife biomass suggests a predator-prey imbalance as prey production is unable to offset biomass losses to predation and natural mortality sources. In contrast, iterations where alewife biomass increased over the simulation indicate that alewife production via growth and recruitment are able to offset predator demand. We also calculated the average alewife biomass present at the end of five years (terminal biomass) across simulation iterations to evaluate if potential population growth would result in a substantial change in alewife biomass after five years.

## 3. Results

The fitted Lake Ontario MSCAA model successfully converged, achieving estimates for all 239 parameters (objective function maximum gradient $< 1 \times 10^{-4}$; Table S9). Fitted estimates of the primary indices of Chinook salmon, lake trout, and alewife abundance closely tracked with the observed values from annual surveys (Figs. 1, S4, S5). Furthermore, a retrospective analysis, sequentially increasing the length of the fitted time series, found no systematic change in abundance or biomass estimates for Chinook salmon, lake trout, or alewife indicating the model lacked structural deficiencies (Fig. S6; Mohn 1999).

Our results confirmed that the total biomass of predators, though variable, has increased over the last 20 years, while alewife biomass has declined. The biomass of Chinook salmon and lake trout within the lake peaked in 2018 (3.2 kg/ha; Fig. 2G) and 2012 (1.7 kg/ha Fig. 2H), respectively, while alewife biomass was at its lowest level in 2019 (46.3 kg/ha; Fig. 2I). Due to differences in life-history characteristics between the predators, Chinook salmon population abundance was more variable than for lake trout. Chinook salmon have a relatively short lifespan as the majority of fish only spend 3-4 years at large in the lake prior to spawning. Thus, the lake-wide Chinook salmon abundance quickly shifts in response to changes in stocking or natural reproduction (Fig 2.A, Fig. S2). For example, Chinook salmon abundance nearly doubled in just 3 years between 2014 and 2017 due to a large cohort of naturally reproduced smolts in 2016 (Fig. 2D). Likewise, abnormally low water flows and high water temperatures in 2008 resulted in both low natural recruitment and reduced hatchery egg take (Connerton 2009), producing a weak cohort and lower Chinook salmon abundance that persisted from 2009-2012. In contrast, Lake Ontario lake trout are a relatively long-lived species (>25 years maximum age). As a result, the lake trout population was generally less variable, although lake-wide abundance doubled between 2009 and 2012 due to a combination of changes in sea lamprey mortality and age-1 mortality (Fig. S7).

Due to differences in population dynamics among top predators, alewife consumption by the lake trout population has been relatively consistent, whereas the stochastic nature of Chinook salmon recruitment has resulted in bursts of short-term increases in alewife consumption. Importantly, while predator abundances and associated prey demand were high over the fitted time series, alewife abundance and biomass remained relatively consistent until 2015 (Fig. 2C) owing to periodic strong alewife recruitment pulses (Fig. 2F). However, alewife biomass began to decline in 2015 due to back-to-back weak alewife recruitment in 2013 and 2014, decreasing by approximately 50% between 2015 (86.5 kg/ha) and 2019 (46.3 kg/ha).

In addition to capturing the individual dynamics of each species, the MSCAA model allowed us to quantify how the trophic linkages between species influenced the dynamics of the alewife population and the two salmonine fisheries. Including a functional response relationship between the predator and prey species allowed alewife mortality to be driven by Chinook salmon and lake trout prey consumption. Overall, Chinook salmon exerted greater predation pressure on alewife than lake trout, and annually the Chinook salmon population consumed between 3 and 12 times more alewife biomass per year than the lake trout population (Fig. 3). In addition to having greater biomass than lake trout (Fig 2), Chinook salmon have higher annual growth rates and temperature preferences that result in greater annual bioenergetic needs than lake trout (Raby et al. 2020, Stewart et al. 1981). Combined with their high reliance on alewife, our bioenergetics model predicted changes in Chinook salmon weight-at-age associated with declines or increases in alewife availability that tracked well with survey data, indicating that the bioenergetic link between species provided a reasonable representation of trophic interactions between predator and prey (Fig. 4). For example, Chinook salmon sizes were predicted to increase over the 2010-2013 period of high alewife biomass (Fig. 2I), which matched well with weight-at-age creel survey data over these years (Fig. 4). While overall our estimates of lake trout weight-at-age also matched well with survey data, discrepancies in 2018 may be due to changes in the spatial distribution of lake trout and the fish that are included in the annual surveys or changes in diet that were not reflected in available datasets, highlighting the need for annual diet surveys.

Our estimation of annual alewife surplus production (ASP) highlighted that the alewife population is largely sustained by sporadic years of strong recruitment. In-between these strong year classes, the alewife population declined and ASP was often negative (Fig. 3), suggesting that growth and recruitment could not replace biomass lost to other mortality sources, much less offset the biomass consumed by Chinook salmon and lake trout. Thus, due to their dependence on alewife, the two salmonine fisheries are also largely supported by these sporadic alewife recruitment pulses. Periods of high predator demand that coincide with extended periods between strong alewife recruitment events, can result in rapid declines of alewife biomass (2015-2017) as the biomass lost to predation and other sources of mortality ate not replaced through the recruitment and growth of young alewife. Similarly, inflated prey demand associated with high predator abundance may mitigate the potential alewife population growth resulting from a strong year class, such as occurred following the large 2017 age-1 cohort, which only resulted in a small increase in adult alewife abundance in 2018.

Simulation analyses based on the estimates from the fitted MSCAA model provided insight into short-term future states of predator-prey dynamics in Lake Ontario (Fig. 5). Results suggest that because the current regime of alewife recruitment has been weak since 2015 (Fig. 2F), alewife population growth is possible over the next 5 years, but heavily dependent on Chinook salmon stocking and natural recruitment levels. Our simulations indicate that alewife biomass is particularly vulnerable to high levels of natural Chinook salmon recruitment. Alewife population growth was most likely to occur under scenarios with no stocking and the lowest amount of natural Chinook salmon recruitment (0.05 million age-0s/yr; Fig. 5). In this case, alewife biomass only decreased in 4.7% of simulation iterations. As this scenario had the lowest amount of Chinook salmon recruitment, this represented a "best case" scenario for an increase in alewife biomass, whereby the average alewife biomass after five years (terminal biomass) for this scenario was strong at 97.0 kg/ha. Although any amount of stocking increased the probability of a decline in alewife biomass, for this scenario of low natural Chinook salmon reproduction 88.7% of simulation iterations with reduced stocking and 83.6% with full stocking resulted in increased alewife biomass. However, Chinook salmon recruitment under this scenario may be artificially low given the average estimate of natural salmon recruitment from the model was 2.4 million age-0s/yr (Fig. S2).

Alewife biomass was particularly vulnerable to extremely high ("run-away") levels of natural reproduction and simulation iterations with sustained, high natural reproduction (10 million age-0s/yr) typically resulted in further declines in alewife biomass (Fig. 5). Without stocking reductions, alewife biomass declined in 61.6% of run-away natural recruitment simulations and the average terminal biomass after five simulated years was 47.0 kg/ha (Fig. 5). Although stocking reductions released some predation pressure on the simulated alewife population, alewife biomass still declined in 55.6% of run-away simulation iterations with reduced stocking and 41.2% of simulation iterations with no stocking. Although our fitted MSCAA model indicated that this level of natural Chinook salmon recruitment has only occurred once in Lake Ontario over the time period we examined (2016; Fig. S2), high levels of natural Chinook salmon recruitment are thought to have contributed to the decline of the alewife population and Pacific salmonine fisheries in other Great Lakes (Brenden et al. 2012).

## Discussion:

The MSCAA framework allowed us to simultaneously model the population dynamics and trophic interactions of two popular fisheries and their shared primary prey species in Lake Ontario, providing the opportunity to understand how future changes in predator or prey populations may influence the sustainability of the salmon and trout fisheries. Currently, alewife prey availability for top predators is lower than at any other point in the last 20 years (Fig. 2I). Our model estimates of predator-prey dynamics suggest that this was driven by consecutive years of low alewife recruitment in 2013 and 2014, combined with record-breaking Chinook salmon natural recruitment in 2016, which resulted in high levels of alewife mortality (Fig. 2L). In turn, declines in alewife availability may have contributed to declines in predator weight-at-age, particularly for Chinook salmon (Fig 4).

Simulations using the fitted MSCAA model for Lake Ontario suggest that alewife population growth and a return to pre-2015 levels may be possible even with current trends in lower average alewife recruitment, as long as they are offset by periodic high alewife recruitment pulses. On the other hand, a substantial increase in natural Chinook salmon recruitment or increased survival of stocked Chinook salmon (e.g. increased pen-stocking) could impede alewife population growth or contribute to further population decline. Scenario testing results indicate that current management efforts to reduce Chinook salmon stocking increase the probability of alewife population growth over the next five years, although outcomes depend heavily on the state of natural Chinook salmon recruitment. Sustained high levels of Chinook salmon natural recruitment are predicted to result in a high probability of alewife decline even if salmon stocking were ceased altogether. Combined, these results emphasize the importance of natural Chinook salmon recruitment in influencing the future dynamics of the alewife population, and thus the future stability of the salmonine fisheries. While a decline in prey availability may affect the natural recruitment of Chinook salmon, a lack of data on the dynamics of stocked versus naturally reproduced Chinook salmon makes it difficult to distinguish environmental and ecological drivers from changes in the stocking program. Annual monitoring of natural recruitment via a mass marking program for stocked Chinook salmon could improve estimates of Chinook salmon abundance and facilitate research into drivers of natural Chinook salmon recruitment. Greater understanding of these processes may help inform future stocking decisions and support management efforts to maintain the predator-prey balance in Lake Ontario.

Our inclusion of a bioenergetics submodel serves as a feedback mechanism for prey dynamics to directly influence predator growth and, ultimately, predation mortality. Since the bioenergetics submodel transforms prey consumption into predator growth rates, declines in alewife biomass can result in lower weight-at-age estimates for Chinook salmon and lake trout. In turn, smaller predators have lower maximum consumption rates and decreased individual predation rates on alewife. For Lake Ontario, this feedback is evident post-2016, where low alewife biomass combined with an increase in predators has resulted in lower weights, particularly for Chinook salmon (Fig. 4). Integrating bioenergetics with the population dynamics model allowed us to compare the consumption rates of both predator species without requiring annual weight-at-age estimates for all age groups. This was particularly useful for estimating the consumption rates of younger predator cohorts that contribute to predation pressure but are not well represented in current surveys, as they are not yet fully recruited into the recreational fisheries or to some survey gear. While integrating bioenergetics into population models can provide an important trophic feedback mechanism, these models do require detailed biological and ecological data that may not yet be available for some fisheries. Although more complex models, such as the Wisconsin-style bioenergetics model implemented herein may provide better weight-at-age estimates and can incorporate changes in environmental and ecological factors such as temperature or prey energy density, the inclusion of a simpler bioenergetics model may be sufficient for incorporating the impacts of prey dynamics on the predator population for some systems (Ney 1990).

The strong predator-prey linkages in the Lake Ontario food web indicate that future growth of the alewife population may largely depend on reducing predation pressure to allow the population to rebuild or prevent further decline should there be additional alewife recruitment failures. Of the two predator species in the MSCAA model, Chinook salmon were the largest contributor to predation pressure and annually consumed 3-12 times as much alewife biomass as lake trout (Fig. 3A). Although lake trout still exert considerable predation pressure on alewife, they do not switch to an alewife-dominated diet until age four, meaning that it would take three years for reduced lake trout stocking to have any impact on alewife predation. Due to their comparatively longer lifespan, lake trout predation pressure is also less likely to rapidly change as adult lake trout abundance is less variable than Chinook salmon. Thus, a decline in Chinook salmon abundance will have the greatest short-term impact on reducing predation pressure, recognizing that reducing Chinook salmon abundance will depend on both stocking and natural recruitment.

Longer-term forecasting of Lake Ontario predator-prey dynamics will likely require consideration of trends in nutrient availability, environmental conditions, and system productivity to assess how unfolding lake changes may affect future fishery dynamics. Should phosphorus and lower trophic level productivity continue to decline (Dove and Chapra 2015), alewife may become trapped between a decline in planktonic prey availability and an increase in predation pressure, both of which may have contributed to the collapse of alewife in Lake Huron (Kao et al. 2016). Similarly, long-term climatic shifts may impact the long-term stability of predator and prey populations by altering recruitment rates, growth rates, and the availability of optimal thermal habitats (Lynch et al. 2010, Collingsworth et al. 2017). While Chinook salmon would likely decline in the event that alewife biomass collapses, the lake trout population may be more successful at adjusting to more a diverse prey fish diet (Jacobs et al. 2013, Nawrocki et al. 2020). Long-term monitoring of lake trout diets could both improve model estimates of lake trout predation pressure and provide insights into the stability of the lake trout fishery in the event of an alewife collapse. Thus, simultaneous consideration of the portfolio of predator species and the interactions among predators and prey may improve opportunities to forecast and support broader fisheries sustainability.

As fisheries management becomes more ecosystem-based, we envision continued interest in integrating species interactions into stock assessment models. In conjunction with other ecological and environmental models, MSCAA models may improve stock assessments by providing a mechanistic link to connect species dynamics (Hollowed et al. 2000a). Thus far, applications of MSCAA models have largely focused on representing predation-based trophic interactions, however future work to incorporate other species interactions such as resource competition within trophic levels may further improve the utility of these assessment frameworks (Travis et al. 2014). Ultimately, stock assessment models are constrained by the availability of data; while models of intermediate complexity such as MSCAA show great promise in transitioning towards ecosystem-based fisheries management, realizing their benefits will require investments into sustained data collection on the ecological and biological processes that govern species' population dynamics and which facilitate species interactions (Trijoulet et al. 2019).

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## Competing interests statement

The authors declare there are no competing interests.

## Contributors' statement

All authors contributed to the development of this manuscript. Conceptualization – KBF, SAS, SRL. Data curation – KBF, BCW, MJC, JRL, JPH, MJY, BL. Methodology and Formal Analyses – KBF, SAS, TOB, PJS, LGR. Funding acquisition – SAS, SRL. Supervision – SAS, LGR, PJS, BCW, SRL. Validation – KBF, BCW, MJC, JRL, JPH, MJY, BL, SRL, LGR. Visualization and writing original draft – KBF and SAS. Reviewing and editing – all authors.

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## Data availability statement

The datasets used in these analyses are either available from the freely accessible, referenced sources (Table S1) or can be provided by the specified agency upon reasonable request.

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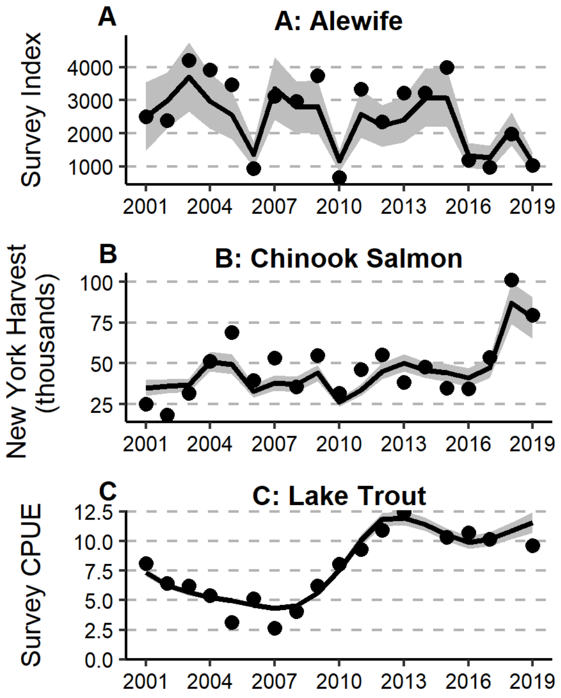

Figure 1: The Lake Ontario multispecies statistical catch-at-age (MSCAA) model captured historical trends in species abundances well, as demonstrated by model fits (solid line, ±1SE grey polygon) to annual surveys (points) for (A) the index of adult alewife abundance from the annual USGS-NYSDEC-OMNRF-USFWS trawl survey, (B) creel survey estimates of the number of Chinook salmon harvested by New York anglers, and (C) the catch-per-unit effort (CPUE) for coded wire tagged lake trout collected during the annual USGS-NYSDEC-USFWS survey.

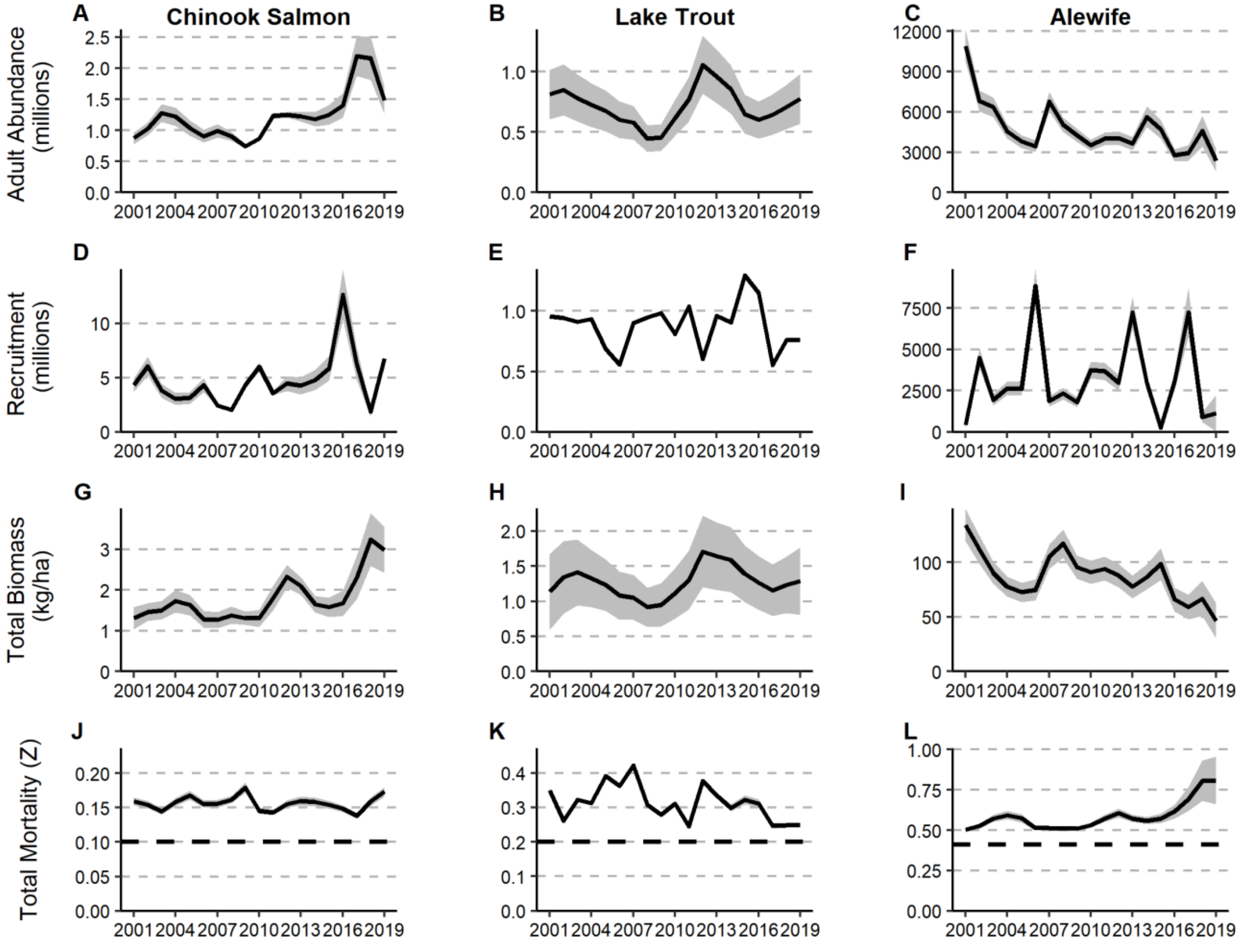

Figure 2: Multispecies statistical catch-at-age model estimates of species dynamics for Lake Ontario predators (Chinook salmon and lake trout) and prey (alewife) from 2001 to 2019. Adult abundance includes Chinook salmon age 1+ (A, solid line, ±1SE grey polygon), lake trout age 4+ (B), and alewife age 2+ (C), while annual recruitment was based on stocked and naturally reproduced age-0 Chinook salmon (age 0; D), stocked age-1 lake trout (assumed known; E), and age-1 alewife (no stocking; F). Based on the adult abundance estimates and estimated weight-at-age for predators and annual trawl survey estimates of weight-at-age for alewife, we modeled the total biomass (kg) of each species relative to the area of Lake Ontario (1,896,000 ha; G, H, I). We also modeled average adult total instantaneous mortality per year for each species ($Z$; J, K, L); which does not include spawning mortality for Chinook salmon. Annual adult natural

mortality was assumed known for all species ($M$; dashed black line; J, K, L). (Note variable y-axes.)

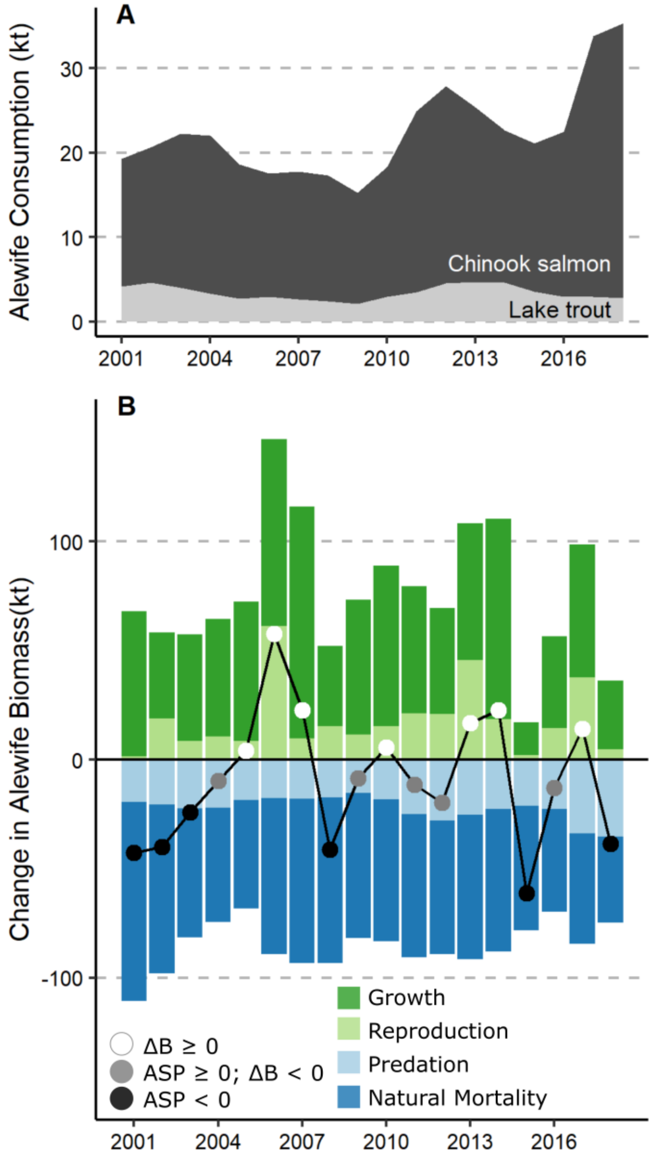

Figure 3: To quantify the amount of predation pressure placed on alewife by Chinook salmon and lake trout, we used the fitted results from the multispecies statistical catch-at-age model for Lake Ontario to estimate alewife annual surplus production (ASP). ASP indicates potential alewife population growth and was calculated as the sum of alewife biomass consumed by Chinook salmon and lake trout (A) and the annual change in alewife biomass (B). Positive ASP values occurred in years when biomass additions via growth (dark green) and recruitment (light

green) offset biomass lost natural mortality sources (dark blue), excluding predation by Chinook salmon and lake trout (light blue). However, positive ASP values only corresponded to an increase in alewife biomass in years when ASP was greater than the alewife biomass consumed by Chinook salmon and lake trout (white points). Positive ASP and a negative change in alewife biomass indicate years when potential alewife population growth was eliminated due to Chinook salmon and lake trout consumption (grey points). When ASP was negative, biomass lost to natural morality exceeded biomass additions and consumption by predators only intensified the decline in alewife biomass (black points).

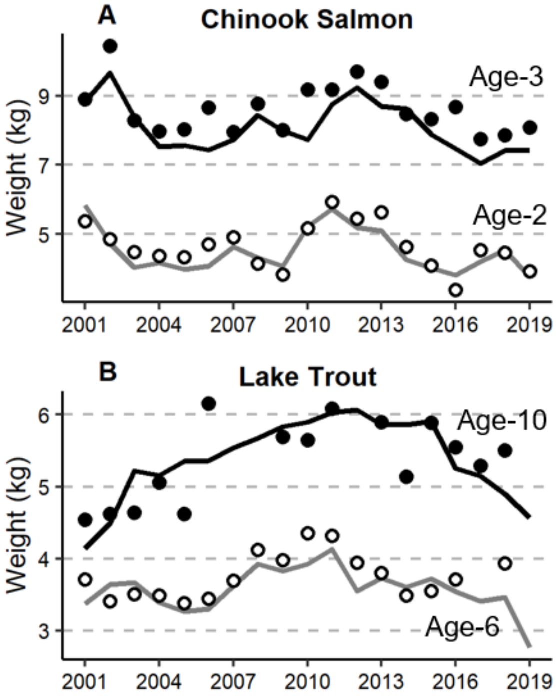

Figure 4: Within the Lake Ontario multispecies statistical catch-at-age framework, predator weight-at-age was estimated using a bioenergetics submodel and varied with prey fish (alewife) availability. Chinook salmon (A; age-2 grey line, age-3 black line) and lake trout (B; age-6 grey line, age-10 black line) weight-at-age estimates were fit to the average weight-at-age for fish collected during the NYSDEC creel survey (age-2 white points, age-3 black points) and the USGS-NYSDEC-USFWS gillnet survey (age-6 white points, age-10 black points), respectively.

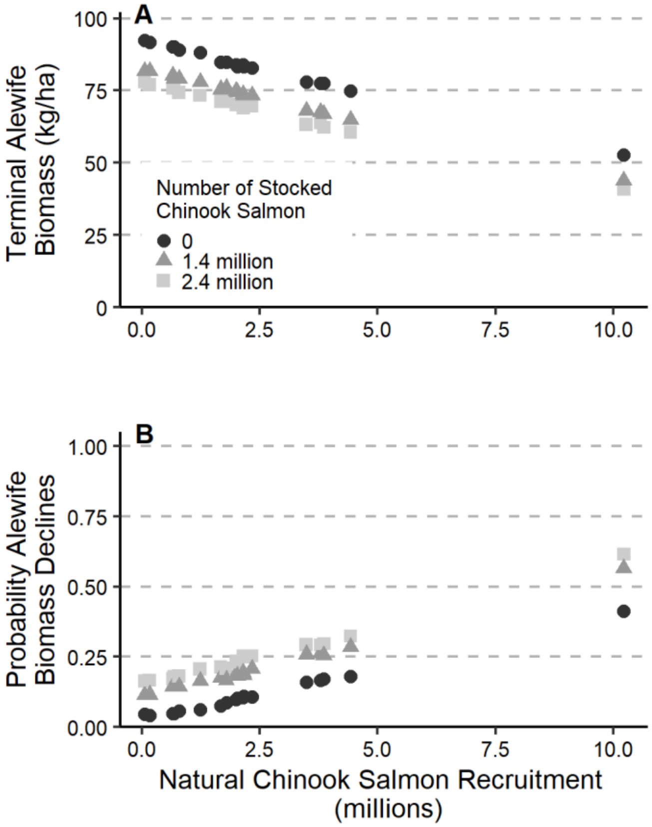

Figure 5: Impact of predation pressure on the probability of continued alewife decline over a five-year forward projection period under scenarios of Chinook salmon stocking and natural recruitment rates (x-axis). Using the fitted parameters from the Lake Ontario multispecies statistical catch-at-age model we simulated alewife, Chinook salmon, and lake trout dynamics under three stocking scenarios; Chinook salmon stocking prior to 2017 reductions (2.4 million age-0 salmon, grey triangles), 2019 stocking levels post-reductions (1.4 million age-0 salmon, light grey squares), and no stocking (black circles). A total of 10,000 simulations iterations were conducted for each combination of Chinook salmon stocking and natural recruitment rates. For each simulation iteration, annual alewife recruitments were drawn randomly from the set of model estimated recruitments from 2015-2019. For each scenario, we estimated the average alewife biomass (kg/ha) for at the end of the five-year simulation (terminal biomass, A) and the

probability that the terminal biomass would be less than the estimated biomass of alewife in 2019 (46.3 kg/ha; B).

Table 1: Descriptions of indexing variables for the Lake Ontario multispecies statistical catch-at-age model. “NA” = not applicable, “+” represents a plus age or length class.

| | | Species | | |
|---|---|---|---|---|
| Symbol | Definition | Alewife | Chinook Salmon | Lake Trout |
| $s$ | species (or predator species) | ALE | CHK | LKT |
| $p$ | prey species | ALE | NA | NA |
| $y$ | year | 2001-2019 | 2001-2019 | 1993-2019 |
| $m$ | month | 1 (Jan)-12 (Dec) | 1-12 | 1-12 |
| $a$ | predator age | NA | 0-4 | 1-15+ |
| $b$ | prey age | 1-5+ | NA | NA |
| $i$ | natal origin | NA | Stocking agency and method, or naturally reproduced | NA |
| $l$ | length class | NA | NA | 7-37+ (length class, inches) |
| $f$ | fishery | NA | New York (NY) or Ontario (Ont) | New York (NY) or Ontario (Ont) |
| $k$ | prey item | NA | NA | alewife, rainbow smelt, round goby, sculpin |

Table 2: Mathematical notation for the Lake Ontario multispecies statistical catch-at-age model. Due to differing life-history characteristics, not all quantities are applicable to all three species (“NA” = not applicable). Values are either estimated (E), assumed known from data or literature (K), or derived from a combination of the two (D). For clarity, symbols are presented here without indexing. Parameter estimates that are not available in the text are presented in Table S9.

| | | Species | | |
|---|---|---|---|---|
| Symbol | Description | Alewife | Chinook salmon | Lake trout |
| $N$ | Abundance | D | D | D |
| $Z$ | Total mortality | D | D | D |
| $B$ | Biomass | D | D | D |
| $W$ | Weight | K (Weidel et al. 2020) | K($a = 0$; Connerton 2020, Lake 2020),<br>E ($a = 1, m = 1$),<br>D ($a = 1 +$) | K($a < 4$; Connerton 2020, Lake 2020)<br>E ($a = 4, m = 1$),<br>D ($a = 4 +$) |
| $R$ | Recruitment | E | K (stocked; Connerton 2020, Lake 2020)<br>E (naturally reproduced) | K (Connerton 2020, Lake 2020) |
| $F$ | Fishing mortality | NA | D | D |
| $P$ | Predation mortality | D | NA | NA |
| $M$ | Annual natural morality | K ($M = 0.41$) | K($M = 0.1$) | E ($a = 1$),<br>K($a = 2+; M = 0.2$) |
| $q$ | Catchability | E | E | E |
| $S$ | Selectivity | E | E | E |
| $E$ | Fishing effort | NA | K (Connerton et al. 2020; Yuille and Jakobi 2017) | K(Connerton et al. 2020; Yuille and Jakobi 2017) |
| $\rho$ | Length-based selectivity adjustment | NA | NA | K($l < 25$ $or$ $l > 30$)<br>E($25 \leq l \leq 30$) |
| $\theta$ | Probability of spawning | NA | E | NA |
| $L$ | Average length-at-age | K (Weidel et al. 2020) | D | K (Lantry et al. 2020) |
| $V$ | Vulnerable prey biomass | D | D | D |
| $O$ | Habitat overlap | K (Table S6) | K (Table S6) | K (Table S6) |
| $\phi$ | Length-based scalar | NA | E | E |
| $h$ | Handling time | NA | D | D |
| $\gamma$ | Length-at-age matrix | NA | NA | K (Lantry et al. 2020) |
| $SL$ | Sea lamprey predation mortality | NA | NA | K (Brenden et al. 2011) |
| $H$ | Harvest | NA | D | D |
| $D$ | Predator diet | NA | NA | K (Holden et al. 2017) |

|  |  |  |  |  |
|---|---|---|---|---|
| $Cmax$ | Temperature and size-dependent total maximum consumption | NA | D | D |
| $CA$ | Bioenergetic constant | NA | K (Plumb and Moffitt, 2015) | K (Stewart et al. 1983) |
| $CB$ | Bioenergetic constant | NA | K (Plumb and Moffit, 2015) | K (Stewart et al. 1983) |
| $f(Temp)$ | Temperature function for estimating maximum consumption | NA | K (S1.7) | K(S1.7) |
| $T$ | Estimated alewife abundance from annual trawl survey | D | NA | NA |
| $C$ | Predator consumption of alewife | NA | D | D |
| $ASP$ | Annual surplus production | D | NA | NA |

Balancing prey availability and predator consumption: a multispecies stock assessment for Lake Ontario

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## Supplementary Materials

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### *Tables*

Table S1: Data sets used in the likelihoods for multispecies statistical catch-at-age model. All data sets were collected by the New York State Department of Environmental Conservation (NYSDEC), the Ontario Ministry of Natural Resources and Forestry (OMNRF), and/or the United States Fish and Wildlife Service (USFWS).

Table S2: Instantaneous annual natural mortality rates for Chinook Salmon based on natal origin and age.

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### *References*

## S1. Survey information and likelihoods

*S1.1 Annual surveys of spawners*

We included two likelihoods based on annual surveys of the age distribution of spawning Chinook salmon conducted by NYSDEC and OMNRF, which were based on the spawning fish used as broodstock for hatcheries. We modeled the number of spawners ($Spawn$; Table S3) as:

$$Spawn_{s=CHK,y,a,i} = N_{s=CHK,y,m=9,a,i} e^{-Z_{s=CHK,y,m=9,a,i}}(\theta_a) \tag{S1}$$

which was structured by natal origin $(i)$ so that we could account for the impacts of natal homing on the age distribution of spawners, as prior research found that the vast majority of fish collected during the surveys were stocked by the respective agency. As the relative amount of fish from different natal origins varies by cohort, separating the fish by natal origin allowed us to best represent the demographics present in the surveys of spawning adults. To account for these biases, when comparing the model estimates of the age composition of spawning Chinook salmon to agency-specific $(f)$ survey data, we grouped spawners by their respective stocking agency:

$$\widehat{Spawn}_{f=NY,s=CHK,a} = Spawn_{s=CHK,y,a,i=NY(Direct)} + Spawn_{s=CHK,y,a,i=NY(Pen)} \tag{S2}$$

$$\widehat{Spawn}_{f=ONT,s=CHK,a} = Spawn_{s=CHK,y,a,i=ONT(Direct)} + Spawn_{s=CHK,y,a,i=ONT(Pen)} \tag{S3}$$

grouping together both direct and pen-stocked fish. As the number of fish collected during these spawner surveys depends on egg collection targets for hatchery production, this survey does not provide an index of the number of spawners and only includes age composition data which are included in the likelihoods (eq. ST4.3). Further information on these surveys can be found in Prindle and Bishop (2020) and Yuille (2019b).

*S1.2 Salmon River young-of-year survey*

Since 2001, seine surveys of naturally reproduced young-of-year Chinook salmon have taken been conducted weekly at four sites on the Salmon River, NY in May and June. The Salmon River is thought to be the largest single source of natural Chinook salmon production in Lake Ontario. To characterize the peak of Chinook salmon movement within the river, the timing of which varies annually, the “mean peak catch” is used as the index of natural production and is calculated as the average number of young-of-year fish collected during the three consecutive weeks with the highest catches for a given year. For the model, we calculated this index as:

$$\hat{I}_{j=NY(Seine),y} = \beta N_{s=CHK,y,m=1,a=0,i=Nat} \quad \text{(S4)}$$

where $N_{s=CHK,y,m=1,a=0,i=Nat}$ is the model estimated number of naturally reproduced Chinook salmon for a given year and $\beta$ (Table S3) is a time-invariant parameter representing the proportion of naturally reproduced fish sampled by the survey. We assumed that this index followed a log-normal distribution (eq. ST4.4). More information on this survey can be found in Prindle and Bishop (2020).

*S1.3 OMNRF community gillnet survey*

The community gillnet survey conducted by OMNRF provides an index of lake trout abundance (CPUE) in Ontario waters ($j = ONT(Gill)$; Table S3):

(S5) $$\hat{I}_{j=ONT(Gill),s=LKT,y,a} = \alpha_{s=LKT} S_{j=ONT(Gill),s=LKT,l} \sum_{a} N_{s=CHK,y,m=8,a,i}$$

where $S$ is modeled as a logistic function based on length as lake trout collected during this survey are not aged. In the model, we included likelihoods for both the annual CPUE and the length composition of lake trout caught in the survey (eqs. ST5.6 and ST5.7). While Chinook salmon are not targeted by the survey, young Chinook salmon are included in the gillnet survey and we include the CPUE in the model as an index of age-1 Chinook salmon abundance:

(S6) $$\hat{I}_{j=ONT(Gill),s=CHK,y} = \alpha_{s=CHK} \sum_{i} N_{s=CHK,y,m=7,a=1,i}$$

as a likelihood in the model (eq. ST4.5). Additional information on the OMNRF community gillnet survey can be found in Yuille (2019b) and Holden (2019).

### *S1.4 Proportion of stocked Chinook salmon*

From 2008 to 2011 all stocked Chinook salmon were adipose fin-clipped to distinguish stocked from naturally reproduced Chinook salmon and a subset had coded wire tags implanted to provide empirical data on differences between stocked populations. From 2010 to 2016, massive field efforts were undertaken to recover marked fish (Connerton et al. 2016), which provided an estimate of the proportion of the Chinook salmon population of a given age that was stocked ($Stock_{y,a}$; Table S3). In the MSCAA model, we estimated the proportion of stocked fish in the population as:

(S7) $$\widehat{Stock}_{y,a} = 1 - \frac{N_{s=CHK,y,m=1,a,i=Nat}}{\sum_i N_{s=CHK,y,m=1,a,i}}$$

where $i = Nat$ represents naturally reproduced Chinook salmon. We used different weightings for age-1 and age-4 fish versus age-2 and age-3, since the sample sizes were much greater for ages 2 and 3 as they compose the majority of the recreational harvest (eqs. ST4.6 and ST4.7).

### *S1.5 Time-varying catchability*

We modeled fishery-specific catchability for lake trout harvest as a random walk,

(S8) $$q_{f,s=LKT,y} = q_{f,s=LKT,y} + \tau_{f,s=LKT,y}$$

as it is believed to vary annually with catch rates of other salmonine fisheries and assumed that the deviations ($\tau$; Table S3) were normally distributed (eqs. ST5.11 and ST5.12). As catchability was estimated annually, we interpolated lake trout harvest data for years when a creel survey was not conducted by OMNRF (Table S1). Additional information on the creel surveys can be found in Connerton et al. (2020) and Yuille and Jakobi (2017).

In contrast to lake trout, survey catchability for alewife was modeled using a “white noise” model (Wilberg and Bence, 2006). Recent research suggests that the spatial distribution of alewife varies annually (Weidel et al. 2020), but since the trawl survey was only conducted in New York waters until 2016, we assumed that annual catchability deviated from a constant average. Since we assumed that the abundance estimates from the trawl survey were an accurate representation of the magnitude of lake-wide adult alewife abundance, we assumed that the average catchability for adult alewife $(b = 2+)$ was 1.0 and thus annual catchability was:

(S9) $$q_{s=ALE,y,b=2+} = \exp\left(\tau_{s=ALE,y,b=2+}\right)$$

where the annual deviations $(\tau)$ were normally distributed (eqs. ST7.3 and ST7.4). Similarly, the annual catchability of age-1 alewife was:

(S10) $$q_{s=ALE,y,b=1} = \exp\left(\tau^{*}_{s=ALE,b=1} + \tau_{s=ALE,y,b=1}\right)$$

where $\exp(\tau^{*})$ is the estimated average catchability for age-1 alewife as age-l alewife are not fully recruited to the trawl survey gear.

*S1.6 USGS-NYSDEC-USFWS Gillnet survey*

The USGS-NYSDEC-USFWS gillnet survey of lake trout is an index of lake trout abundance for Lake Ontario and is the only survey that has consistent data on lake trout age composition by collecting coded-wire tag data. As not all stocked lake trout are marked, the survey has two indices of lake trout abundance, one based on all the fish caught in the survey ($j = Gill(NY)$; Table S3):

(S11) $$\hat{I}_{j=Gill(NY),s=LKT,y,l} = \sum_{a} S_{j=Gill(NY),s=LKT,y,a}\, q_{j=Gill(NY),y,a}\, N_{s=LKT,y,m=8,a,l}$$

and one based only on coded-wire tagged fish collected during the survey $\left(j = Gill(CWT)\right)$:

(S12) $$\hat{I}_{j=Gill(CWT),s=LKT,y,a} = \sum_{l}\left(S_{j=Gill(NY),s=LKT,y,a}\, q_{j=Gill(NY),a}\, N_{s=LKT,y,m=8,a,l}\right) cwt_{y,a}$$

where $cwt$ is the proportion of fish with coded wire tags in each age group, per year. Discrepancies between the two surveys may be due to post-stocking dispersal of lake trout, as only NYSDEC stocked fish are coded-wire tagged and the USGS-NYSDEC-USFWS survey is conducted in New York waters. Selectivity $(S)$ is age-based and modeled using a logistic function and catchability $(q)$ is time-invariant but estimated separately for age-1 $(a = 1)$ and age-2+ fish $(a >= 2)$. From this survey, we not only included likelihoods for both indices, but also the length composition of all fish and the age composition of coded-wire tagged fish (eqs ST5.1-4).

We also included an index of juvenile (age-2) lake trout survival to estimate changes in age-1 lake trout natural mortality. Specifically, this was modeled as the catch per 500,000 stocked yearlings from an annual trawl survey by USGS, NYSDEC, and USFWS (Lantry et al 2020; $j = juv$):

(S13) $$\hat{I}_{j=juv,s=LKT,y} = \psi_y N_{y,m=7a=2}\left(\frac{500{,}000}{N_{y-1,m=1,a=1}}\right)$$

and due to a survey design change, we estimated two values for $\psi$, one for pre-1997 and one for post-1997. To allow for variability in juvenile mortality, we also modeled age-1 lake trout natural mortality as a random walk:

(S14) $$M_{s=LKT,y,a} = M_{s=LKT,y-1,a}\eta_y$$

and assumed the annual deviations $(\eta)$ followed a log-normal distribution (eq. ST5.15).

*S1.7 Predator maximum consumption rates*

We modeled prey consumption rates for the predators as a function of ambient water temperature, as salmonine consumption and growth rates are sensitive to changes in water temperature (Brett et al. 1982). Maximum prey consumption $(Cmax_s)$ varied with ambient water temperatures, such that consumption was maximized when predators were exposed to optimal water temperature conditions. For lake trout this was modeled as:

(S15) $$f(Temp_{s=LKT,m}) = e^{0.123(Temp_{s=LKT,m})}$$

where consumption always increased with temperature (Steward et al. 1983). In contrast, Chinook salmon maximum consumption was represented by the product of two sigmoidal curves (Thornton and Lessem 1978, Stewart and Ibarra 1991, Plumb and Moffit 2015):

(S16) $$f(Temp_{s=CHK,m}) = K_A K_B$$

to characterize the increase in consumption as ambient water temperature approaches the optimal temperature ($K_A$; Table S3):

(S17) $$K_A = \frac{0.36 \cdot e^{0.447(Temp_{s=CHK,m} - 5)}}{1 + 0.36\left(e^{0.447(Temp_{s=CHK,m} - 5)} - 1\right)}$$

and the decrease in consumption as water temperature increases beyond the optimal temperature($K_B$):

(S18) $$K_B = \frac{0.53 \cdot e^{1.217(24 - Temp_{s=CHK,m})}}{1 + 0.53\left(e^{1.217(24 - Temp_{s=CHK,m})} - 1\right)}$$

## Supplemental Figures

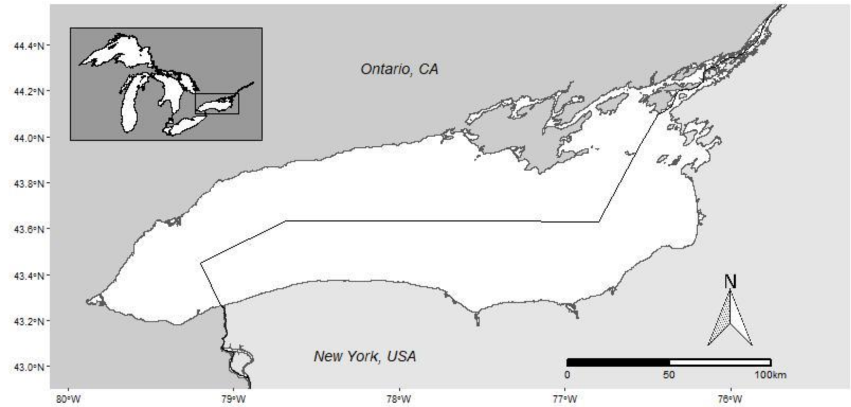

Figure S1: Lake Ontario is a binational, managed lake ecosystem (New York, US and Ontario, CA) and part of the Laurentian Great Lakes Basin (inset map). Fisheries in the US waters of Lake Ontario are primarily managed by the New York State Department of Environmental Conservation (NYSDEC) while the Ontario Ministry of Natural Resources and Forestry (OMNRF) manages fisheries in the CA waters. Spatial data sources: Laurentian Great Lakes shoreline from the Great Lakes Aquatic Habitat Framework (GLAHF; Wang et al. 2015), United States and Canadian boundaries from the Database of Global Administrative Areas (GADM 2018). The map coordinate system is based on the WGS84 datum.

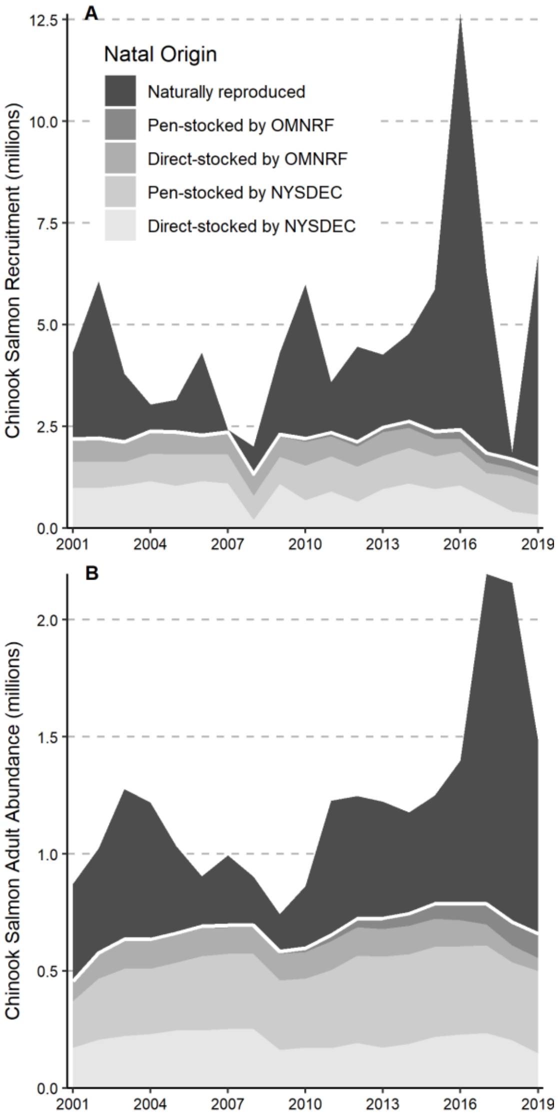

Figure S2: Natal origin of age-0 (A) and adult (B) Chinook salmon based on stocking agency, natural origin, and stocking method. Recruitment of direct-stocked and pen-stocked fish is assumed known and based on stocking records from NYSDEC and OMNRF, while natural Chinook salmon recruitment (dark grey) is estimated by the Lake Ontario multispecies statistical catch-at-age model, except for the terminal year (2019), which cannot be reliably estimated. Instead, we estimated naturalized recruitment in 2019 based on the data from the Salmon River, NY young-of-year survey and the fitted parameter. The survival rate of pen-stocked fish is twice that of direct stocked or naturally reproduced fish and thus, per age-0 fish, have a relatively large contribution to the adult Chinook salmon population. The total number of stocked fish (white line) has remained relatively constant while annual natural recruitment is more variable and is the primary driver behind the annual fluctuations in Chinook salmon adult abundance.

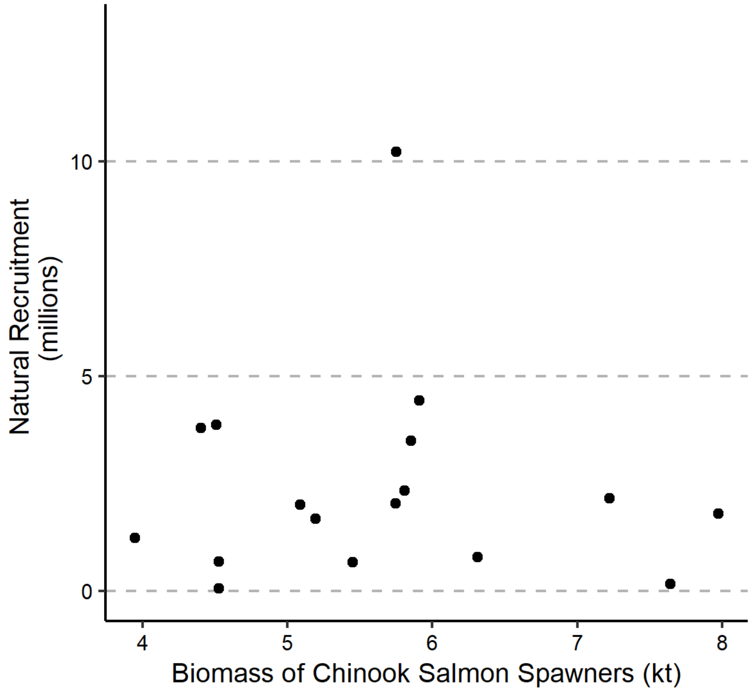

Figure S3: Chinook salmon spawning stock biomass and recruitment based on estimates from the multispecies statistical catch-at-age model for Lake Ontario. Spawning stock biomass is estimated as the biomass of adult spawners in September $(m = 9)$ of each year and recruitment is the number of naturally reproduced (wild) age-0s from the following year.

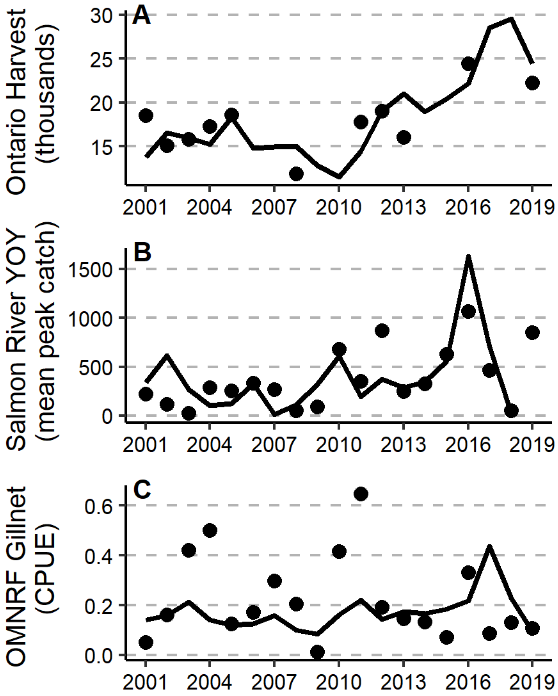

Figure S4: Model fits (solid lines) from the multispecies statistical catch-at-age model for Lake Ontario to indices of Chinook salmon abundance (points) in Lake Ontario from three distinct surveys; the estimated harvest of Chinook salmon in Ontario waters from the OMNRF creel survey (A), mean peak catch of young of year (YOY) naturalized Chinook salmon from seine surveys on Salmon River, NY (B; S1.6), and catch per unit effort (CPUE) of age-1 Chinook salmon from the annual OMNRF community gillnet survey (C).

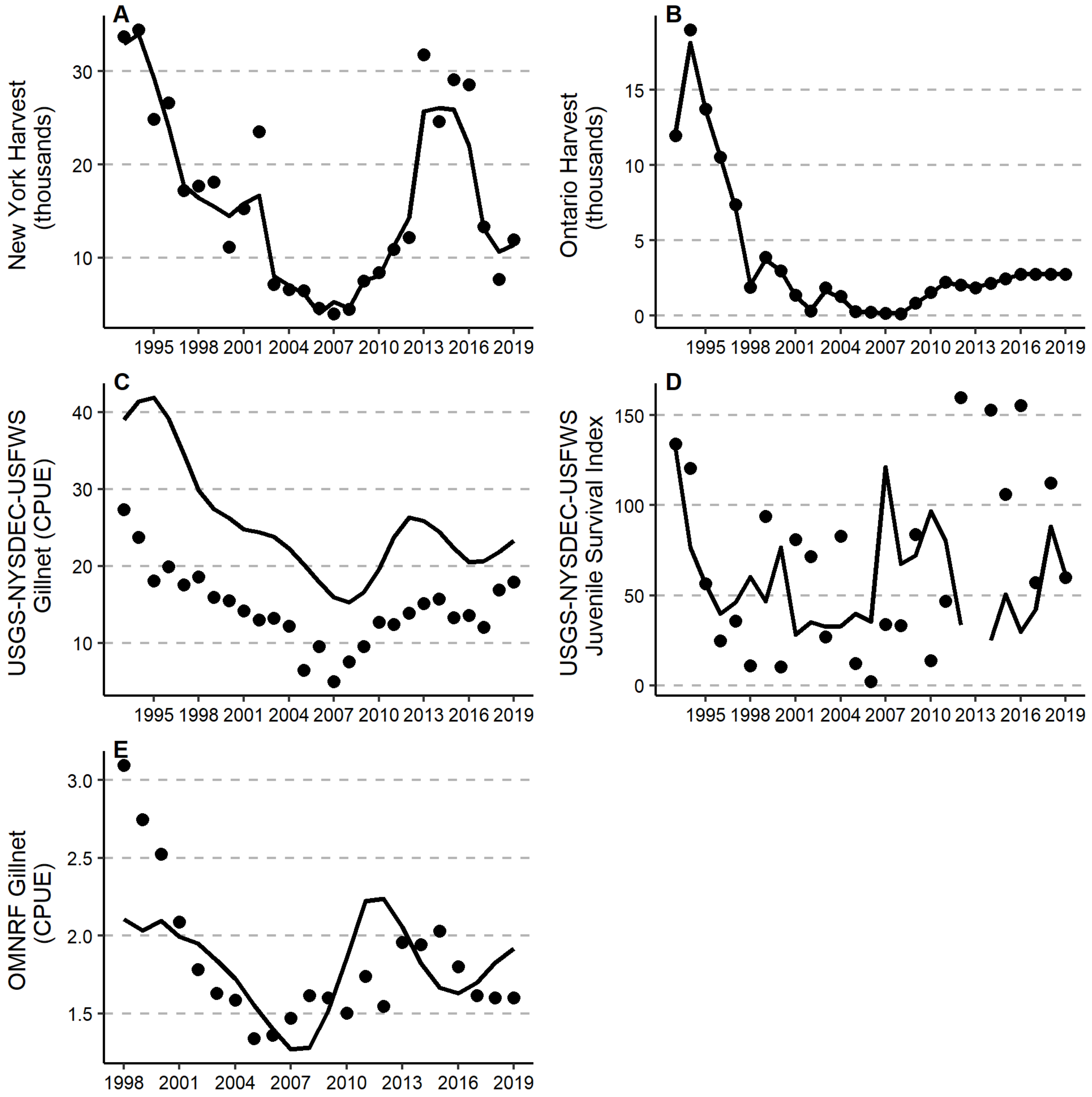

Figure S5: Model fits (solid lines) from the multispecies statistical catch-at-age model to indices of lake trout abundance (points) in Lake Ontario from five annual surveys. Estimates of lake trout harvest are from annual creel surveys conducted by NYSDEC and OMNFR for fishing in New York (A) and Ontario (B) waters, respectively (S1.3). The USGS-NYSDEC-USFWS surveys specifically target lake trout (S1.4), the gillnet survey provides an index of total adult lake trout abundance (C) while the trawl survey provides an index of juvenile (age-1) survival (D). The final survey is an index of lake trout abundance based on the catch-per-unit effort from the annual community gillnet survey (E; S1.5; note different x-axis).

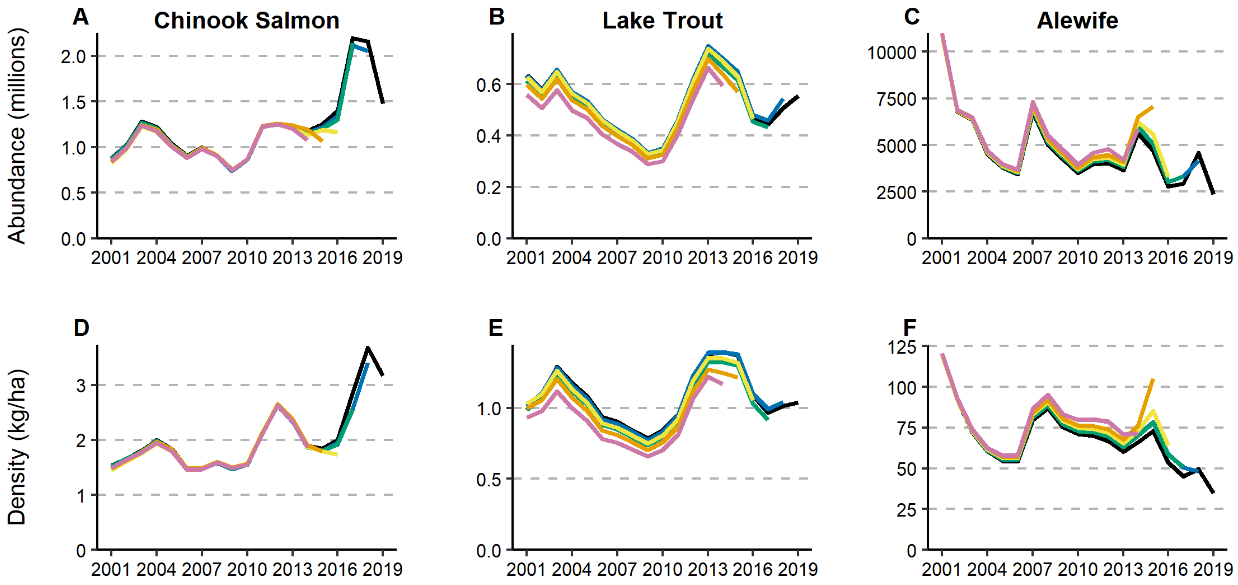

Figure S6: The retrospective patterns for Chinook salmon, lake trout, and alewife in Lake Ontario indicate relative stability in estimated abundance and density from the Lake Ontario multispecies statistical catch-at-age model. To obtain the retrospective patterns, all input data for the final year was systematically removed and the model was fitted to the reduced data set, this was repeated until 2014 became the terminal year (5 peels; Mohn 1999). Each line represents a different terminal year (pink 2014, orange 2015, yellow 2016, green 2017, blue 2018, black 2019); the lack of a distinctive pattern when data is removed suggests a lack of systematic bias in the model.

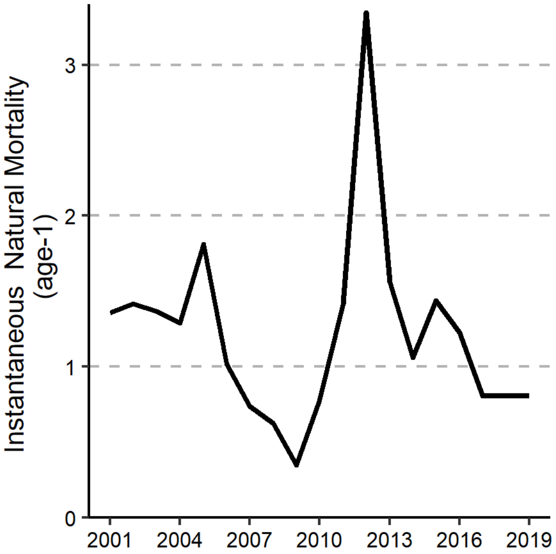

Figure S7: Estimates of annual instantaneous natural mortality $(M)$ for age-1 lake trout from the Lake Ontario multispecies statistical catch-at-age model for 2001-2019. Natural mortality was modeled as a random walk except for in the terminal year (2019), which could not be reliably estimated and was set equal to the previous year (2018). The average estimated instantaneous natural mortality rate for age-1 lake trout was 1.22.

## Supplemental Tables

Table S1: Data sets used in the likelihoods for multispecies statistical catch-at-age model. All data sets were collected by the New York State Department of Environmental Conservation (NYSDEC), the Ontario Ministry of Natural Resources and Forestry (OMNRF), and/or the United States Fish and Wildlife Service (USFWS).

| Species | Data Set | Years | Cooperating Agencies (source) |
|---|---|---|---|
| Chinook Salmon | Annual harvest in New York waters | 2001-2019 | NYSDEC (Connerton et al. 2020) |
| | Age-distribution of fish harvested in New York waters | 2001-2019 | NYSDEC (Connerton et al. 2020) |
| | Weight-at-age of fish harvested in New York waters | 2001-2019 | NYSDEC (Connerton et al. 2020) |
| | Proportion of stocked fish in the population at-large based on adipose fin clips | 2008-2015 | NYSDEC (Connerton et al. 2016) |
| | Annual harvest in Ontario waters | 2001-2005, 2008, 2011-2013, 2016 | OMNRF (Yuille and Jakobi 2017) |
| | Age-distribution of fish harvested in Ontario waters | 2001-2005, 2008, 2011-2013, 2016 | OMNRF (Yuille and Jakobi 2017) |
| | Age-distribution of spawners collected at the Salmon River Hatchery, NY | 2001-2019 | NYSDEC (Prindle and Bishop 2020) |
| | Age-distribution of spawners collected from the Credit River, Ontario | 2001-2019 | OMNRF (Yuille 2019b) |
| | Index of age-0 smolt abundance in the Salmon River | 2003-2019 | NYSDEC (Bishop and Prindle 2020) |
| | CPUE of age-1 fish collected during community gillnet survey | 2001-2019 | OMNRF (Yuille 2019a) |
| Lake Trout | Annual harvest in New York waters | 2001-2019 | NYSDEC (Connerton et al. 2020) |
| | Length-distribution of fish harvested in New York waters | 2001-2019 | NYSDEC (Connerton et al. 2020) |
| | Annual harvest in Ontario waters | 2001-2005, 2008, 2011-2013, 2016 | OMNRF (Yuille and Jakobi 2017) |
| | CPUE for all fish collected in USGS-NYSDEC-USFWS gillnet survey | 1993-2019 | USGS, NYSDEC, USFWS (Lantry et al. 2020) |
| | Length distribution for all fish collected in USGS-NYSDEC-USFWS gillnet survey | 1993-2019 | USGS, NYSDEC, USFWS (Lantry et al. 2020) |

| | | | |
|---|---|---|---|
| | CPUE for coded-wire tagged fish collected in USGS-NYSDEC-USFWS gillnet survey | 1993-2019 | USGS, NYSDEC, USFWS (Lantry et al. 2020) |
| | Age distribution for all fish collected in USGS-NYSDEC-USFWS gillnet survey | 1993-2019 | USGS, NYSDEC, USFWS (Lantry et al. 2020) |
| | CPUE for fish collected during community gillnet survey | 1998-2019 | OMNRF (Holden 2019) |
| | Length distribution for fish collected during community gillnet survey | 1998-2019 | OMNRF (Holden 2019) |
| | Index of juvenile survival | 1993-2018 | USGS, NYSDEC, USFWS (Lantry et al. 2020) |
| Alewife | Lake-wide abundance from annual trawl survey | 2001-2019 | USGS, NYSDEC, OMNRF, USFWS (Weidel et al. 2020) |
| | Age distribution in annual trawl survey | 2001-2019 | USGS, NYSDEC, OMNRF, USFWS (Weidel et al. 2020) |

Table S2: Instantaneous annual natural mortality rates for Chinook Salmon based on natal origin and age. Pen-stocked fish are held in floating or fixed net pens in locations around Lake Ontario approximately one month prior to stocking. Pen-stocked fish have increased growth rates compared to fish that are directly stocked into the lake (“direct-stocked”), though both sets of fish are released into the lakes at the same time. Pen-stocked fish have shown to have better survival rates than direct-stocked fish (Connerton et al. 2016). As no survey targets both wild and stocked age-0 fish, we assumed that wild fish have the same mortality rate as direct-stocked fish.

| **Natal Origin** | **Age-0** | **Age-1+** |
|---|---|---|
| Naturally Reproduced | 2.3 | 0.1 |
| Direct-stocked | 2.3 | 0.1 |
| Pen-stocked | 1.6 | 0.1 |

Table S3: Indices and parameters used in supplemental equations.

| **Index** | **Description** |
|---|---|
| $j$ | Survey |
| $tot$ | Total number of fish for a given set of indices (e.g. the total number of fish harvested in year "y") |
| $NY(Direct)$ | Chinook salmon direct stocked by NYSDEC |
| $NY(Pen)$ | Chinook salmon pen-stocked by NYSDEC |
| $ONT(Direct)$ | Chinook salmon direct stocked by OMNRF |
| $ONT(Pen)$ | Chinook salmon pen-stocked by OMNRF |
| $Nat$ | Naturally reproduced Chinook salmon |
| $NY(Seine)$ | NYSDEC Salmon River Chinook salmon YOY seine net survey |
| $ONT(Gill)$ | OMNRF community gillnet survey |
| $NY(Gill)$ | USGS-NYSDEC-USFWS lake trout gillnet survey (all fish) |
| $NY(CWT)$ | USGS-NYSDEC-USFWS lake trout gillnet survey (cwt fish) |
| $juv$ | USGS-NYSDEC-USFWS juvenile lake trout survival survey |
| **Parameter** | |
| $Spawn$ | Number of Chinook salmon spawners |
| $Stock$ | Proportion of Chinook salmon of stocked origin |
| $\tau_{f,s}$ | USGS-NYSDEC-USFWS alewife trawl survey catchability deviations |
| $\tau^*_{s,y,a}$ | Average age-1 alewife catchability for USGS-NYSDEC-USFWS trawl survey |
| $I$ | Survey index |
| $\beta$ | Salmon River YOY survey parameter |
| $\alpha_s$ | OMNRF community gillnet survey catchability |
| $\psi_y$ | USGS-NYSDEC-USFWS age-2 lake trout survival survey catchability |
| $\omega_{s,y}$ | Weight deviations |
| $\epsilon$ | Lake tout catchability deviations |
| $cwt$ | The proportion of lake trout with coded wire tags for a given age class in a given year |
| $\eta$ | Age-1 lake trout annual natural mortality deviations |
| $Temp$ | Predator-specific monthly ambient water temperature |
| $K_A$ | Bioenergetics function for Chinook salmon |
| $K_B$ | Bioenergetics function for Chinook salmon |
| $\sigma$ | Standard deviation |

Table S4: Objective functions related to Chinook salmon dynamics. Likelihood weighting was based on *a priori* discussions with data providers.

| Data Set | Objective Function | Eq. |
|---|---|---|
| Harvest estimates from creel surveys | $\frac{1.0}{2\sigma^2}\sum_{y}\left[\ln\left(\frac{H_{tot_{f,s=CHK,y}}}{\widehat{H}_{tot_{f,s=CHK,y}}}\right)\right]^2$ | ST4.1 |
| Age composition from creel surveys | $-100\sum_{f}\sum_{y}\sum_{a}\frac{H_{f,y,a}}{H_{tot_{f,y}}}\ln\left(\frac{\widehat{H}_{f,y,a}}{\widehat{H}_{tot_{f,y}}}\right)$ | ST4.2 |
| Age composition from surveys of spawners | $-100\sum_{f}\sum_{y}\sum_{a}\frac{Spawn_{f,y,a}}{Spawn_{tot_{f,y}}}\ln\left(\frac{\widehat{Spawn}_{f,y,a}}{\widehat{Spawn}_{tot_{f,y}}}\right)$ | ST4.3 |
| NYSDEC Salmon River of naturally reproduced par | $\frac{0.01}{2\sigma^2}\sum_{y}\left[\ln\left(\frac{I_{j=NY(Sein),y}}{\hat{I}_{j=NY(Sein),y}}\right)\right]^2$ | ST4.4 |
| OMNRF gillnet index | $\frac{1.0}{2\sigma^2}\sum_{y}\left[\ln\left(\frac{I_{j=ONT(Gill),s=CHK,y}}{\hat{I}_{j=ONT(Gill),s=CHK,y}}\right)\right]^2$ | ST4.5 |
| Proportion stocked $(a=2, a=3)$ | $-100\sum_{y}Stock_{y,a}\ln\left(\widehat{Stock}_{y,a}\right)+\left(1.0-Stock_{y,a}\right)\ln\left(1-\widehat{Stock}_{y,a}\right)$ | ST4.6 |
| Proportion stocked $(a=1, a=4)$ | $-\sum_{y}Stock_{y,a}\ln\left(\widehat{Stock}_{y,a}\right)+\left(1.0-Stock_{y,a}\right)\ln\left(1-\widehat{Stock}_{y,a}\right)$ | ST4.7 |
| Age-1 Random Walk | $\frac{0.01}{2\sigma^2}\sum_{y}\ln\left(\omega_{s=CHK,y}\right)^2$ | ST4.8 |
| Weight-at-age from creel surveys $(a=1, a=4)$ | $\frac{0.1}{2\sigma^2}\sum_{y}\sum_{m=6}^{8}\left[\ln\left(\frac{W_{s=CHK,y,m=7,a}}{\widehat{W}_{s=CHK,y,m=7,a}}\right)\right]^2$ | ST4.9 |
| Weight-at-age from creel surveys $(a=2, a=3)$ | $\frac{1.0}{2\sigma^2}\sum_{y}\sum_{m=6}^{8}\left[\ln\left(\frac{W_{s=CHK,y,m=7,a}}{\widehat{W}_{s=CHK,y,m=7,a}}\right)\right]^2$ | ST4.10 |

Table S5: Objective functions related to lake trout dynamics. Likelihood weighting was based on *a priori* discussions with data providers and the weights used in earlier versions of this submodel (2011).

| **Data Set** | **Objective Function** | **Eq.** |
|---|---|---|
| USGS-NYSDEC-USFWS gillnet index (all fish) | $\frac{0.1}{2\sigma^2}\sum_{y}\left[\ln\left(\frac{I_{tot_{j=Gill(NY),s=LKT,y}}}{\hat{I}_{tot_{j=Gill(NY),s=LKT,y}}}\right)\right]^2$ | ST5.1 |
| USGS-NYSDEC-USFWS gillnet index (cwt fish) | $\frac{1.0}{2\sigma^2}\sum_{y}\left[\ln\left(\frac{I_{tot_{j=Gill(CWT),s=LKT,y}}}{\hat{I}_{tot_{j=Gill(CWT),s=LKT,y}}}\right)\right]^2$ | ST5.2 |
| USGS-NYSDEC-USFWS gillnet length composition (all fish) | $-100\sum_{y}\sum_{l}\frac{I_{j=Gill(NY),s=LKT,y,l}}{I_{tot_{j=Gill(NY),s=LKT,y}}}\ln\left(\frac{\hat{I}_{j=Gill(NY),s=LKT,y,l}}{\hat{I}_{tot_{j=Gill(NY),s=LKT,y}}}\right)$ | ST5.3 |
| USGS-NYSDEC-USFWS gillnet age composition (cwt fish) | $-100\sum_{y}\sum_{a}\frac{I_{j=Gill(CWT),s=LKT,y,a}}{I_{tot_{j=Gill(CWT),s=LKT,y}}}\ln\left(\frac{\hat{I}_{j=Gill(CWT),s=LKT,y}}{\hat{I}_{tot_{j=Gill(CWT),s=LKT,y}}}\right)$ | ST5.4 |
| USGS-NYSDEC-USFWS juvenile survival index | $\frac{0.01}{2\sigma^2}\sum_{y}\left[\ln\left(\frac{I_{tot_{j=Juv,s=LKT,y}}}{\hat{I}_{tot_{=Juv,s=LKT,y}}}\right)\right]^2$ | ST5.5 |
| OMNRF gillnet index | $\frac{0.01}{2\sigma^2}\sum_{y}\left[\ln\left(\frac{I_{tot_{j=Gill(ONT),s=LKT,y}}}{\hat{I}_{tot_{=Gill(ONT),s=LKT,y}}}\right)\right]^2$ | ST5.6 |
| OMNRF gillnet length composition | $-\sum_{y}\sum_{l}\frac{I_{j=Gill(ONT),s=LKT,y,l}}{I_{tot_{j=Gill(ONT),s=LKT,y}}}\ln\left(\frac{\hat{I}_{j=Gill(ONT),s=LKT,y,l}}{\hat{I}_{tot_{j=Gill(ONT),s=LKT,y}}}\right)$ | ST5.7 |
| NYSDEC creel survey annual harvest estimates ($f = NY$) | $\frac{1.0}{2\sigma^2}\sum_{y}\left[\ln\left(\frac{H_{tot_{f=NY,s=LKT,y}}}{\widehat{H}_{tot_{f=LKT,y}}}\right)\right]^2$ | ST5.8 |
| OMNRF creel survey annual harvest estimates ($f = ONT$) | $\frac{0.5}{2\sigma^2}\sum_{y}\left[\ln\left(\frac{H_{tot_{f=ONT,s=CHK,y}}}{\widehat{H}_{tot_{f=ONT,s=CHK,y}}}\right)\right]^2$ | ST5.9 |
| NYSDEC creel survey annual harvest length composition estimates (f = NY) | $-50\sum_{y}\sum_{l}\frac{H_{f=NY,s=LKT,y,l}}{H_{tot_{f=NY,s=LKT,y}}}\ln\left(\frac{\widehat{H}_{f=NY,s=LKT,y,l}}{\widehat{H}_{tot_{f=NY,s=LKT,y}}}\right)$ | ST5.10 |
| Fishery catchability deviations $f = NY$ | $\frac{0.5}{2\sigma^2}\sum_{y}\tau_{f=NY,s=LKT,y}^2$ | ST5.11 |
| Fishery catchability deviations $f = ONT$ | $\frac{0.05}{2\sigma^2}\sum_{y}\tau_{f=ONT,s=LKT,y}^2$ | ST5.12 |
| Weight-at-age from USGS-NYSDEC-USFWS gillnet survey | $\frac{1.0}{2\sigma^2}\sum_{y}\sum_{a=4}^{15+}\left[\ln\left(\frac{W_{s=CHK,y,m=9,a}}{\widehat{W}_{s=CHK,y,m=9,a}}\right)\right]^2$ | ST5.13 |
| Age-4 weight-at-age random Walk | $\frac{0.5}{2\sigma^2}\sum_{y}\ln\left(\omega_{s=LKT,y}\right)^2$ | ST5.14 |

| | | |
|---|---|---|
| Age-1 natural mortality random walk | $\frac{0.01}{2\sigma^2}\sum_y \left(\eta_{s=LKT,y}\right)^2$ | ST5.15 |

Table S6: Habitat overlap between alewife and the two predator species, Chinook salmon and lake trout, adapted from Jones et al. (1993).

| | Chinook Salmon (age-1+) | Lake Trout (age-4+) |
|---|---|---|
| Alewife (age-1) | 0.95 | 0.7 |
| Alewife (age-2+) | 0.9 | 0.7 |

Table S7: Objective functions related to alewife dynamics. Likelihood weighting was based on *a priori* discussions with data providers.

| **Data Set** | **Objective Function** | **Eq.** |
|---|---|---|
| Trawl survey abundance | $\frac{1.0}{2\sigma^2}\sum_y \left[\ln\left(\frac{T_{tot_y}}{\hat{T}_{tot_y}}\right)\right]^2$ | ST7.1 |
| Trawl survey age composition | $-100\sum_y\sum_a \frac{T_{y,b}}{T_{tot_y}}\ln\left(\frac{\hat{T}_{y,b}}{\hat{T}_{tot_y}}\right)$ | ST7.2 |
| Trawl survey catchability deviations $a = 1$ | $\frac{0.5}{2\sigma^2}\sum_y \tau^2_{s=ALE,y,a=1}$ | ST7.3 |
| Survey catchability deviations $a = 2+$ | $\frac{1.0}{2\sigma^2}\sum_y \tau^2_{s=ALE,y,a=2+}$ | ST7.4 |

Table S8: Prey energy density estimates (J/g) by month. Estimates of age 1 and adult Alewife and Rainbow Smelt (*Osmerus mordax*) energy densities are from Rand et al. 1994. Round goby (*Neogobius melanostomus;* Lee and Johnson, 2005) and Sculpin (*Cottidae sp.*; Hondorp et al. 2005) values were assumed to be time-invariant. Values were interpolated for missing months.

| **Month** | **Alewife (a=1)** | **Alewife (a=2+)** | **Rainbow Smelt** | **Sculpin** | **Round Goby** |
|---|---|---|---|---|---|
| 1 | 4912 | 6706 | 5495 | 5069 | 4600 |
| 2 | 4912 | 6415 | 5357 | 5069 | 4600 |
| 3 | 4912 | 6125 | 5218 | 5069 | 4600 |
| 4 | 4585 | 5917 | 5080 | 5069 | 4600 |
| 5 | 4258 | 5709 | 4942 | 5069 | 4600 |
| 6 | 5560 | 5083 | 4599 | 5069 | 4600 |
| 7 | 5620 | 5165 | 4814 | 5069 | 4600 |
| 8 | 5616 | 4834 | 4457 | 5069 | 4600 |
| 9 | 5612 | 4583 | 4631 | 5069 | 4600 |
| 10 | 5564 | 7059 | 4842 | 5069 | 4600 |
| 11 | 5870 | 6997 | 5771 | 5069 | 4600 |
| 12 | 5870 | 6997 | 5633 | 5069 | 4600 |

Table S9: Parameter estimates from the fitted multispecies statistical catch-at-age model for Lake Ontario.

| Species | Parameter | Value |
|---:|:---|---:|
| Alewife | Initial Abundance (millions) $\left(N_{s=ALE,y=2001,m=1,b}\right)$ | |
| | *Age-2* | 2976 |
| | *Age-3* | 5958 |
| | *Age-4* | 702 |
| | *Age-5+* | 2554 |
| | Trawl Survey Catchability $\left(q_{s=ALE,y,a}\right)$ | |
| | *Age-1* | 0.64 |
| | *Age-2+* | 1.00 |
| Chinook Salmon | *Initial Abundance (millions)* $\left(N_{s=CHK,y=2001,m=1,a}\right)$ | |
| | Age-1 | 0.44 |
| | Age-2 | 0.31 |
| | Age-3 | 0.11 |
| | Age-4 | 0.01 |
| | *Weight-at-Age (kg)* $\left(W_{s=CHK,y,m=1,a}\right)$ | |
| | Age-1 (initial) | 0.53 |
| | Age-1 (average) | 0.59 |
| | Age-2 (initial) | 4.37 |
| | Age-3 (initial) | 7.38 |
| | Age-4 (initial) | (set equal to age-3) |
| | *Fishing Catchability* $(q_{s=CHK,f})$ | |
| | New York | 1.19E-07 |
| | Ontario | 1.09E-07 |
| | *Fishing Selectivity* $(S_{s=CHK,f,a})$ | |
| | Age-1 (NY) | 0.08 |
| | Age-2 (NY) | 0.49 |
| | Age-1 (Ont.) | 0.26 |
| | Age-2 (Ont.) | 0.46 |
| | *Probability of Spawning* $(\theta_a)$ | |
| | Age-1 | 0.06 |
| | Age-2 | 0.41 |
| | Age-3 | 0.92 |
| | *OMNRF Community Gillnet Survey* Catchability | 3.38E-07 |
| | *NYSDEC Salmon River Young-of-Year Survey* Catchability | 1.60E-04 |
| | $\phi_{s=CHK}$ | 2.60E-10 |
| Lake Trout | *Initial Total Abundance (Age-2+; millions)* | 2.51 |

| | | |
|---|---|---|
| | *Weight-at-age* $\left(W_{s=LKT,y,m=1,a}\right)$ | |
| | Age-4 (average) | 1.62 |
| | Age-5+ (average initial) | 3.26 |
| | *Fishing Catchability* | |
| | New York (average) $(q_{s=LKT,f,y})$ | 3.90E-08 |
| | Ontario (average) $(q_{s=LKT,f,y})$ | 1.12E-08 |
| | *Fishing Selectivity (gamma density function;* $S_{s=LKT,a,l}$*)* | |
| | $\alpha$ | 23.46 |
| | $\lambda$ | 0.77 |
| | *Length-Based Fishing Retention* $\left(\rho_{y,l}\right)$ | |
| | Pre-2007 ($l = 25$ or $l = 30$) | 0.40 |
| | Pre-2007 ($26 < l < 29$) | 0.09 |
| | Post-2007 ($25 \leq l \leq 30$) | 0.77 |
| | *USGS-NYSDEC-USFWS Survey Catchability* | |
| | Age-1 | 2.42E-07 |
| | Age-2+ | 4.08E-05 |
| | *USGS-NYSDEC-USFWS Survey Selectivity (logistic)* | |
| | $\alpha$ | 4.73 |
| | $\lambda$ | 1.10 |
| | *OMNRF Community Gillnet Survey* | |
| | Catchability | 2.62E-06 |
| | *OMNRF Community Gillnet Survey Selectivity (logistic)* | |
| | $\alpha$ | 6.11 |
| | $\lambda$ | 0.32 |
| | *USGS-NYSDEC-USFWS Juvenile Survival Catchability* | |
| | Pre-1997 | 2.53E-04 |
| | Post-1997 | 1.58E-04 |
| | $\Phi_{s=LKT}$ | 5.20E-10 |
| All | $\sigma$ | 1.36E-01 |

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