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Longitudinal analyses of catch-at-age data for reconstructing year-class strength, with an application to lake trout (*Salvelinus namaycush*) in the main basin of Lake Huron

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Abstract

We investigated using longitudinal models to reconstruct year-class strength (YCS) from catch-at-age data, with an example application to lake trout (*Salvelinus namaycush*) in the main basin of Lake Huron. The best model structure depended on the age range used for model implementation. The YCS trajectory from the full age range (3–30 years) was similar to the trajectory from a narrow age range that approximated the age of recruitment to the fishing gears (5–7 years), but YCS estimates from the full age range included additional variations due to time-dependent selectivity and mortality. When using ages younger or older than the likely ages of recruitment, YCS estimates did not represent recruitment abundances and were also biased by trends in age-specific selectivity and mortality across years. Longitudinal YCS estimates are likely more robust than single-age recruitment indices, which are often subject to interannual changes in catchability and selectivity. Our findings provide guidance for future applications of the longitudinal YCS reconstruction that in turn may inform and supplement more comprehensive research and management programs for understanding fish recruitment dynamics.

Key words: recruitment indices, age of recruitment, linear-mixed model, model selection, Laurentian Great Lakes

Introduction

The concepts of year-class strength (YCS) and recruitment are often used interchangeably to describe fish year-class abundance (Myers 2002; Maceina and Pereira 2007). We make a distinction between the two concepts based on how the indices are derived from data. A recruitment model is mostly based on indices at a given age, with each index value collected in a single year, to articulate predictive relationships with various covariates including environmental variables, stock abundance, individual growth, and abundance measures at earlier life stages (Subbey et al. 2014). The concept of YCS is more commonly used when the relative abundance is derived from repeated measures on a fish year-class across multiple ages and years (Carlander and Payne 1977).

In this paper, we focus on the reconstruction of YCS from fishery-independent surveys and fisheries monitoring and generalize the statistical descriptions as a longitudinal model (Verbeke and Molenberghs 2000). This modeling approach can be distinguished from more comprehensive fishery stock assessment models that calculate absolute abundances of fish year-classes and estimate mortality rates, such as virtual population analyses (Shepherd and Pope 2002) and statistical catch-at-age (SCAA) models (Maunder and Punt 2013; Methot and Wetzel 2013; Aeberhard et al. 2018), which require data on total removals and often rely on additional data and assumptions (Ricker 1975; Hilborn and Walters 1992; Maunder and Deriso 2003). There are also other approaches to estimating YCS based on assumptions of fish mortality, such as using residuals of catch-curve regressions (Maceina 1997; Tetzlaff et al. 2011) or individual-based approaches of population modeling (Thanassekos et al. 2016). In contrast, the YCS model that we generalize in this paper is a statistical description of indices from catch-at-age data.

Catch-at-age data are particularly suitable for tracking fish year-classes, but with only a couple of exceptions (Parsons and Pereira 2001; Honsey et al. 2020), longitudinal models have rarely been applied to catch-at-age data for estimating YCS. Many linear or generalized linear models have been used in fisheries research to separate various factors from the year effect that represents the relative abundance of a fish population (Venables and Dichmont 2004). When using age-structured data, however, a conceptual difference arises because the linear-mixed model can separate the year effect from the year-class effect, where the year effect represents annual variation in sampling efforts and catchability (rather than fish population abundance) and the year-class effect represents the relative abundance of a fish year-class based on repeated measures across multiple ages and years.

To describe survey indices for the relative abundance of a fish population, Kimura (1988) introduced a two-way analysis of variance (ANOVA):

$$\text{(1)} \qquad \log\left(N_{\mathrm{Yr,I}}\right) = \gamma_{\mathrm{Yr}} + \delta_{\mathrm{I}} + \gamma_{\mathrm{Yr,I}} + \varepsilon$$

where N is the observed value of an index, such as catch per unit effort (CPUE), γ_{Yr} is the year effect representing the relative abundance of a fish population, δ_{I} is the index effect representing survey gear or survey location, and $\gamma_{\mathrm{Yr,I}}$ is the year-by-index interaction. An average term is dropped from the right-hand side of the equation, and ε is the residual error following a standard normal distribution. When the index value ($N_{\mathrm{Yr,I}}$) is from a given young age, the year effect (γ_{Yr}) represents the indices of recruitment at the age specified.

Parsons and Pereira (2001) used a similar two-way ANOVA to analyze age-structured indices (see also Maceina and Pereira 2007). Their primary interest was in the relative abundance of a fish year-class, and the major parameters of their model captured the age (α_{Age}) and year-class (β_{Yc}) effects on the age-structured index values:

$$\text{(2)} \qquad \log\left(N_{\mathrm{Yc,Age}}\right) = \alpha_{\mathrm{Age}} + \beta_{\mathrm{Yc}} + \varepsilon$$

where the year-class effect (β_{Yc}) represents the relative abundance of a fish year-class, i.e., YCS. More recently, Honsey et al. (2020) modified eq. 2 and added a year effect (c_{Yr}) to account for interannual variation in catchability:

$$\text{(3)} \qquad \log\left(N_{\mathrm{Yc,Age,Yr}}\right) = \alpha_{\mathrm{Age}} + b_{\mathrm{Yc}} + c_{\mathrm{Yr}} + \varepsilon$$

Note that in eq. 3 and all equations of this paper, we follow McCulloch et al. (2008) in using Greek letters (e.g., α, β, γ, and δ) to represent fixed effects and Roman letters (e.g., b, c, and e) to represent random effects. In a linear-mixed model, each level of a factor estimated as a fixed effect is the expected value from an independent normal distribution. Conversely, all levels of a factor estimated as a random effect are random samples from the same normal distribution, which allows a factor to be included in a model at the cost of one degree of freedom regardless of how many levels are included within the factor.

Equation 3 has year-class and sampling year as random effects, implying that all YCS estimates are independent random draws from the distribution for the year-class effect, and likewise all levels of the year effect are independent random draws from the distribution for the year effect. This model structure not only allows for the comparisons across separate populations based on standardized estimates, N(0, 1), but also implicitly assumes that a fish population and its environment have not been undergoing any sustained major changes or trends. Meanwhile, eq. 3 has age as a fixed effect, representing the expected catch-at-age. Thus, a year-class effect can be interpreted as a deviation for a cohort, signaling the strength of that year-class. This model can be effectively applied to an age range with partial data in many years given the assumption of a constant fixed age effect. It is also assumed that the use of a particular alternative age range should not have a large impact on YCS estimates because different ages are tracking the same trends.

The assumptions and implications in eq. 3 are problematic when a fish population and its environment have been changing rapidly, as is the case for lake trout (*Salvelinus namaycush*) in the main basin of Lake Huron, one of the Laurentian Great Lakes of North America (He et al. 2015, 2016, 2020, 2022). With continued changes in juvenile selectivity and adult mortality, YCS estimates need to be separated from interannual variations in age-specific selectivity and mortality. With rapid changes in fish spatial distributions, using multiple data sources from different sampling locations not only has potential advantages, but also presents a challenge that the interannual changes in catchability and selectivity are likely different among data sources. Overall, the age, year, and year-class effects may each involve patterns and trends that cannot be interpreted as interchangeable samples from a distribution.

In this paper, we further generalize the YCS model in eqs. 2 and 3 for broad applications, particularly for reconstructing YCS of fish populations in changing environments. We have four specific objectives: (1) to integrate multiple data sources, i.e., using different surveys and fisheries in different sampling locations to estimate a common time-series of YCS for the underlying fish population, (2) to illustrate the impacts of confounding variables that must be taken into consideration when determining the most appropriate age range for estimating YCS, (3) to demonstrate the procedure of model development and to objectively incorporate year and age effects into a model structure for estimating YCS, and (4) to illustrate the overall approach by example and provide YCS estimates for lake trout in the main basin of Lake Huron.

Methods

Data sources and the age range for model implementation

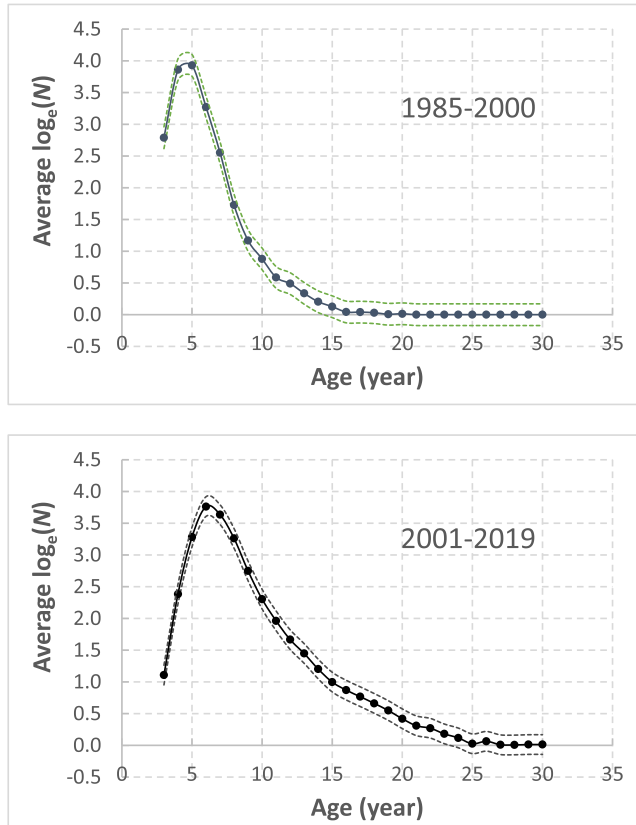
With the year effect as one of the major components of a YCS model (e.g., eq. 3), we used catch-at-age data in numbers, rather than age-structured CPUE, to estimate YCS. Our modeling approach does not require the use of fishing effort data because the year effect can be estimated and interpreted as a combination of interannual variations in sampling effort and catchability. We preferred this option because interannual variation in catchability was large for lake trout in the main basin of Lake Huron (He et al. 2020), and the data for fishing effort were not comparable between data sources and sometimes even among years within a data source. For example, the fishing pressure on lake trout based on angler-hours recorded for fishing salmon and trout has shifted as dominant species in recreational fishery catches have changed (Bence and Smith 1999; Su and Clapp 2013; Su and He 2013).

We used lake trout catch-at-age data from recreational and commercial fisheries and fishery-independent surveys in the two spatial units of the main basin of Lake Huron (Appendix A). These catch-at-age data have been used to calculate age compositions in SCAA assessments (He et al. 2015, 2020; Lenart et al. 2020). We used the six datasets to estimate a common time-series of YCS for the underlying fish population. In the main basin of Lake Huron, the lake trout population was rebuilt and supported by stocking lake trout yearlings and fingerlings (Eshenroder et al. 1995; Ebener 1998). Over 70% of stocked lake trout were from hatcheries of U.S. Fish and Wildlife Service (He et al. 2022). Lake trout migration after stocking has been detected and reported (Adlerstein et al. 2007; Kornis et al. 2020). Spawning segregated adult lake trout were often found available to fisheries outside the management unit containing their spawning location (Binder et al. 2017), although spatial units have been used for stock assessments and fisheries management (Sitar et al. 1999; He et al. 2015, 2020; Lenart et al. 2020). Since the early 2000s, the lake-wide recruitment of wild-born lake trout was driven mostly by production in the northern main basin of Lake Huron (Riley et al. 2007, 2014; He 2019), i.e., north of the extended boundary between the Ontario OH-2 and OH-3 statistical districts (i.e., extended across the international boundary as in He et al. 2022). More geographic specifics about the fishery statistical districts can be found in Smith et al. (1961).

To determine the most appropriate age range for reconstructing lake trout YCS, we analyzed the data to confirm the findings from previous studies. We calculated the averages of log-scale catch-at-age across years and the six data sources, and we plotted the average logarithm versus age for two time periods (Fig. 1). In the main basin of Lake Huron, the age that lake trout first fully recruited to the fishing gears, i.e., the age of recruitment, was not constant across years but was within a narrow age range of 5–7 years. Wilberg et al. (2002) and Johnson et al. (2004) used age-5 CPUE per unit of stocking to evaluate the relative return rate of hatchery-stocked lake trout, although the fishery catch from pre-recruitment ages was high in early years (Fig. 1). Madenjian et al. (2004) used ages 6–8 for a similar evaluation for lake trout stocked on offshore reefs in Lake Huron, including Six Fathom Bank and Yankee Reef. He et al. (2012) used age-7 CPUE per unit of stocking to repeat the lake-wide evaluation in the main basin of Lake Huron. In a more recent study of catch-curve mortality based on age-specific averages of the relative return rate of coded-wire tagged lake trout from US waters of Lake Huron, the starting age for the catch-curve regression was age 5 (He et al. 2022).

In this paper, to repeatedly measure the relative abundance of lake trout year-classes, we decided to use the age range of 5–7 years for our model implementation. In that regard, we maintain a clear definition that YCS is the relative abundance of a year-class when fish first fully recruit to the fishing gears. We assume that (1) within the age range that comprises likely ages of recruitment, the deviation for each age is random and is around the expected YCS or recruitment abundance after adjustment for any potential year effect; (2) below this age range, selectivity sharply increases with increasing age, and it is impossible to separate time-dependent selectivity from YCS estimates; (3) above this age range, the abundance of a year-class is reduced from the recruitment abundance, and it is impossible to separate time-dependent mortality from YCS estimates; and (4) within the range of likely ages of recruitment, because selectivity does not differ greatly, we also expect little variation in relative vulnerability over time.

Fig. 1. Average logarithm of lake trout (*Salvelinus namaycush*) catch-at-age numbers (solid line and black dots; dot lines = 95% confidence intervals), across years and six data sources for two time periods in the main basin of Lake Huron. The six data sources include commercial and recreational fisheries and fishery-independent surveys in two management units (Appendix A).



To further support our decision and to demonstrate how confounding variables may mislead model estimates, we compared YCS time-series from many model implementations with alternative age ranges. In comparison with the age range of 5–7 years, the alternatives included (*a*) younger age ranges such as ages 3–5, 3–7, and 4–7; (*b*) older age ranges such as ages 5–8 and 5–10; (*c*) approximately balanced age ranges around those likely ages of recruitment, such as ages 3–10 and 4–8; (*d*) broad age ranges such as ages 3–15; and (*e*) the full age range of 3–30 years that has been used in the SCAA assessments (He et al. 2015, 2020).

Model development and evaluation of findings

We expected that a combination of the age, year, and year-class effects would not be the same for different age ranges. We applied two alternative strategies to find the best model structure for each age range used for model implementation. We used Akaike information criterion (AIC) (Burnham and Anderson 2002) to compare and select model structures throughout the procedures of model development.

One strategy was to first select fixed effects, adding as many as possible to ensure that systematic variations in the data were well explained, and then to evaluate random variations in the data by selecting and adding random effects to the model (Verbeke and Molenberghs 2000; West et al. 2007). For our YCS models, in addition to the index effect given by the six data sources, we only had three major factors (year-class, year, and age) to be evaluated and included in the model. We first evaluated and selected two of these three major factors as fixed effects, and then evaluated the third major factor to be included as a random effect. It is impossible to treat year-class, year, and age all as fixed effects in the model because a factor level (the expected value and its variance) cannot be estimated as coming from an independent distribution when the three fixed effects are connected by a predictive relationship: Yc = Yr − Age. For the same reason, it is also unlikely to detect interactions as fixed effects between any pair of these three major factors. There were several possible model structures with a single major factor as a fixed effect and two major factors as random effects (similar with eq. 3). Those models performed poorly in all preliminary model comparisons, and we therefore excluded them from further analyses in this paper.

Following the above strategy, our model development started with the year-class and data source index as fixed effects:

$$(4) \quad \log(N_{\mathrm{Yc,I}}) = \beta_{\mathrm{Yc}} + \delta_{\mathrm{I}} + \varepsilon$$

We then fitted and compared alternative models that added the second fixed effect of year or age either as a main effect or as an interaction with the data source index.

$$(5\text{-}1) \quad \log(N_{\mathrm{Yc,Yr,I}}) = \beta_{\mathrm{Yc}} + \gamma_{\mathrm{Yr}} + \delta_{\mathrm{I}} + \varepsilon$$

$$(5\text{-}2) \quad \log(N_{\mathrm{Yc,Yr,I}}) = \beta_{\mathrm{Yc}} + \gamma_{\mathrm{Yr,I}} + \varepsilon$$

$$(6\text{-}1) \quad \log(N_{\mathrm{Yc,Age,I}}) = \beta_{\mathrm{Yc}} + \alpha_{\mathrm{Age}} + \delta_{\mathrm{I}} + \varepsilon$$

$$(6\text{-}2) \quad \log(N_{\mathrm{Yc,Age,I}}) = \beta_{\mathrm{Yc}} + \alpha_{\mathrm{Age,I}} + \varepsilon$$

If eq. 4 was the best among the models of eqs. 4–6, then the model selection process was stopped. If any other model was the best, then the factor that was not selected as a fixed effect would be further evaluated in the model as a random effect interacting with the data source index:

$$(7a\text{-}1) \quad \log(N_{\mathrm{Yc,Yr,Age,I}}) = \beta_{\mathrm{Yc}} + \gamma_{\mathrm{Yr}} + \delta_{\mathrm{I}} + e_{\mathrm{Age,I}} + \varepsilon$$

$$(7a\text{-}2) \quad \log(N_{\mathrm{Yc,Yr,Age,I}}) = \beta_{\mathrm{Yc}} + \gamma_{\mathrm{Yr,I}} + e_{\mathrm{Age,I}} + \varepsilon$$

$$(7b\text{-}1) \quad \log(N_{\mathrm{Yc,Yr,Age,I}}) = \beta_{\mathrm{Yc}} + \alpha_{\mathrm{Age}} + \delta_{\mathrm{I}} + e_{\mathrm{Yr,I}} + \varepsilon$$

$$(7b\text{-}2) \quad \log(N_{\mathrm{Yc,Yr,Age,I}}) = \beta_{\mathrm{Yc}} + \alpha_{\mathrm{Age,I}} + e_{\mathrm{Yr,I}} + \varepsilon$$

Note that we compared eqs. 4–6 for each of many alternative age ranges, and the subsequent comparison with one of the alternatives in eqs. 7 was dependent on the previous selection from eqs. 5–6. We then further considered the alternative random effect as an age-by-year interaction, following the same sequence as in the previous step:

$$(8a\text{-}1) \quad \log(N_{\mathrm{Yc,Yr,Age,I}}) = \beta_{\mathrm{Yc}} + \gamma_{\mathrm{Yr}} + \delta_{\mathrm{I}} + e_{\mathrm{Age,Yr}} + \varepsilon$$

$$(8a\text{-}2) \quad \log(N_{\mathrm{Yc,Yr,Age,I}}) = \beta_{\mathrm{Yc}} + \gamma_{\mathrm{Yr,I}} + e_{\mathrm{Age,Yr}} + \varepsilon$$

$$(8b\text{-}1) \quad \log(N_{\mathrm{Yc,Yr,Age,I}}) = \beta_{\mathrm{Yc}} + \alpha_{\mathrm{Age}} + \delta_{\mathrm{I}} + e_{\mathrm{Age,Yr}} + \varepsilon$$

$$(8b\text{-}2) \quad \log(N_{\mathrm{Yc,Yr,Age,I}}) = \beta_{\mathrm{Yc}} + \alpha_{\mathrm{Age,I}} + e_{\mathrm{Age,Yr}} + \varepsilon$$

For all these models (eqs. 4–8), we included year-class as a fixed effect because our primary interest was in YCS for a year-class that influences fish catch from the year-class across multiple ages and years in every data source. In our preliminary model comparisons, even when model development was started with age or year as a fixed effect, year-class was always selected eventually as a fixed effect, rather than as an interaction with the data source index or as a random effect with or without interaction with other factors (recall the arguments and our analyses on eq. 3 in the Introduction). The potential age-by-index interaction was evaluated to represent the fact that age assignments were conducted separately by each agency lab responsible for a data source, although the lab procedures were comparable among agencies. More importantly, fish samples from each data source were often collected in different locations of the lake where fishing mortality might not be the same, and the fishing and survey selectivity were likely different among data sources. The potential year-by-index interaction was evaluated to represent interannual variations in sampling effort and catchability that were also likely different among data sources. The possible age-by-year interaction was evaluated to represent a scenario that age-specific selectivity and mortality could be different among years, or interannual variations in catchability could be age-specific because of different spatial distributions of fish age groups.

The alternative strategy for our model development was to reverse the above process of model comparison and selection by starting with the year-class and data source index as fixed effects along with the age-by-year interaction as a random effect:

$$(9) \quad \log(N_{\mathrm{Yc,Yr,Age,I}}) = \beta_{\mathrm{Yc}} + \delta_{\mathrm{I}} + e_{\mathrm{Age,Yr}} + \varepsilon$$

Here, the index effect was given by the six data sources, and the year-class effect was our primary interest. We were also interested in the age-by-year interaction as a random effect because we used an age range for multiple measures on every year-class, but those measures were from a different range of years for each year-class. Equation 9 was compared with alternative models that added the second fixed effect of year or age either as a main effect or as an interaction with the data source index (eqs. 8). If any model in eqs. 8 was better

Table 1. Model comparison and selection for different age ranges used for estimating lake trout (*Salvelinus namaycush*) year-class strength in the main basin of Lake Huron, based on the Akaike information criterion (AIC).

Model	Description	Ages 3–5	Ages 5–7	Ages 3–15	Ages 3–30
Eq. 4	Yc, Index	663.2	884.2	2708.1	5164.0
Eq. 5-1	Yc, Yr, Index	499.5	835.4	1523.8	3054.0
Eq. 6-1	Yc, Age, Index	481.2	866.2	1377.8	1015.0
Eq. 5-2	Yc, Yr × Index	**93.2**	**87.2**	**1033.7**	2902.0
Eq. 6-2	Yc, Age × Index	473.7	870.3	1281.3	**632.0**
Eq. 7a-2	Yc, Yr × Index, (Age × Index)	**0.0**	**0.0**	**0.0**	
Eq. 7b-2	Yc, Age × Index, (Yr × Index)				121
Eq. 8a-2	Yc, Yr × Index, (Age × Yr)	95.2	89.2	335.1	
Eq. 8b-2	Yc, Age × Index, (Age × Yr)				**0.0**

Note: Provided is the difference in AIC (ΔAIC) between a model and the best model, with the best model having ΔAIC = 0. Model structures include the year-class (Yc), year (Yr), age, and index (data source) effects, as well as some interactions between two factors. The lists in parentheses indicate random effects. Model equations and their development can be found in the Methods. The results from four age ranges are used to represent general findings for all age ranges examined (e.g., Figs. 2–4).

than the model of eq. 9, we further evaluated the factor that was not selected as a fixed effect as an alternative random effect interacting with the data source index (eqs. 7). In the Results section, we do not report the step-by-step comparison in this alternative strategy of model development because the final best model was the same as that selected through the first strategy of model development for a given age range.

We compared and evaluated YCS estimates across age ranges with the best model for each age range. We also evaluated uncertainty in YCS estimates with the age range of 5–7 years. In that regard, we implemented the best model for the age range of 5–7 years separately with each of the six data sources (Appendix A). We then calculated their variance-weighted means and compared the mean YCS time-series to the estimates using all data indexed and combined, with 95% confidence intervals. The variance-weighted mean YCS was calculated using the equation (Shepherd 1997)

$$(10)\qquad \overline{\mathrm{YCS}} = \frac{\sum_i \left(\mathrm{YCS}_i / s_i^2\right)}{\sum_i \left(1/s_i^2\right)}$$

where YCS_i stands for YCS estimates from the data source i, with the estimated variance s_i^2. Our model estimates were obtained using the "nlme" package in R with the maximum likelihood option (Pinheiro et al. 2022; R Core Team 2022).

Results

The best model structure for each of alternative age ranges

The best model structure (with the lowest AIC) depended on the age range used for model implementation (Table 1). When using the full age range of 3–30 years, the age-by-index interaction was selected to be the second fixed effect over other options. For other age ranges, the year-by-index interaction was selected as the second fixed effect. Thus, in addition to changes in YCS, the systematic variation within a data source was better described by interannual differences than the variations among age groups unless the full age range was used. Also, the selected random effect was the age-by-index interaction with all reduced age ranges but was the age-by-year interaction with the full age range.

Year-class strength estimates from alternative age ranges

YCS estimates from the age range of 5–7 years increased through two decades beginning in 1978, peaked in 1997, and declined after 2000 apart from a small peak in 2010 (Figs. 2–4). When the age range was extended to include younger ages or was restricted to younger ages, YCS estimates started to decline earlier and more rapidly (Fig. 2). From the age range of 4–7 years, the decline started in 1997; from the age range of 3–7 years, the decline started in 1991; from the age range of 3–5 years, the decline started in 1980. Including younger ages was the only difference in data uses that led to the earlier and more rapid declines in YCS estimates, suggesting that those YCS estimates were likely confounded by declines in survey and fishing selectivity for young lake trout, which have been documented in previous studies (e.g., Johnson et al. 2004; He et al. 2012, 2020).

When the age range was extended to include one or more older ages, YCS estimates showed different patterns and even an opposing trend (Fig. 3*a*). From the age range of 5–8 years, YCS estimates did not show a consistent trend from the late 1990s to present. From the age range of 5–10 years, YCS estimates continued to increase after 2000. Given the well-known declines in lake trout adult mortality (He et al. 2015, 2020, 2022; Lenart et al. 2020), the different patterns and opposing trend suggested that the YCS estimates from old ages were likely confounded by declines in adult mortality.

When an extended age range was nearly balanced around the age of recruitment (e.g., 3–10 and 4–8 years), YCS estimates were almost the same as the estimates from the age range of 5–7 years, although the estimated trends for more recent year-classes still showed noticeable differences from models using different age ranges (Fig. 3*b*). The focus of our comparisons was on interannual patterns and trends, rather than the estimated magnitudes, which reflected the differ-

Fig. 2. Lake trout (*Salvelinus namaycush*) year-class strength (YCS) in the main basin of Lake Huron, estimated from the age ranges of (*a*) 4–7 years, (*b*) 3–7 years, and (*c*) 3–5 years, compared with YCS estimates from the age range of 5–7 years.

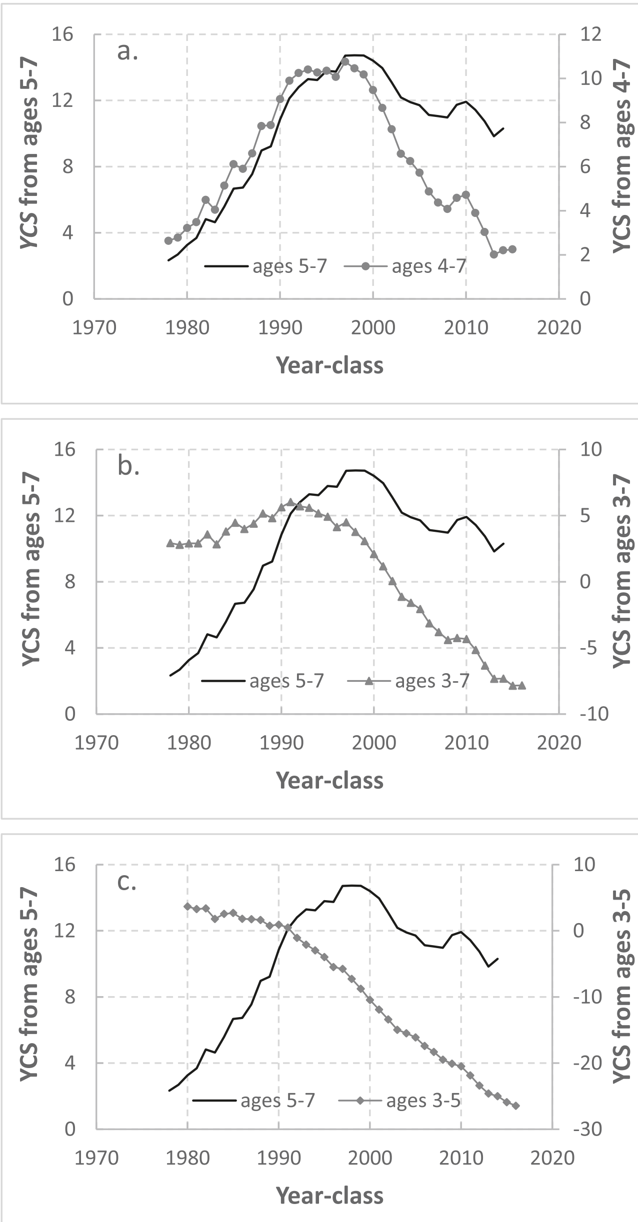
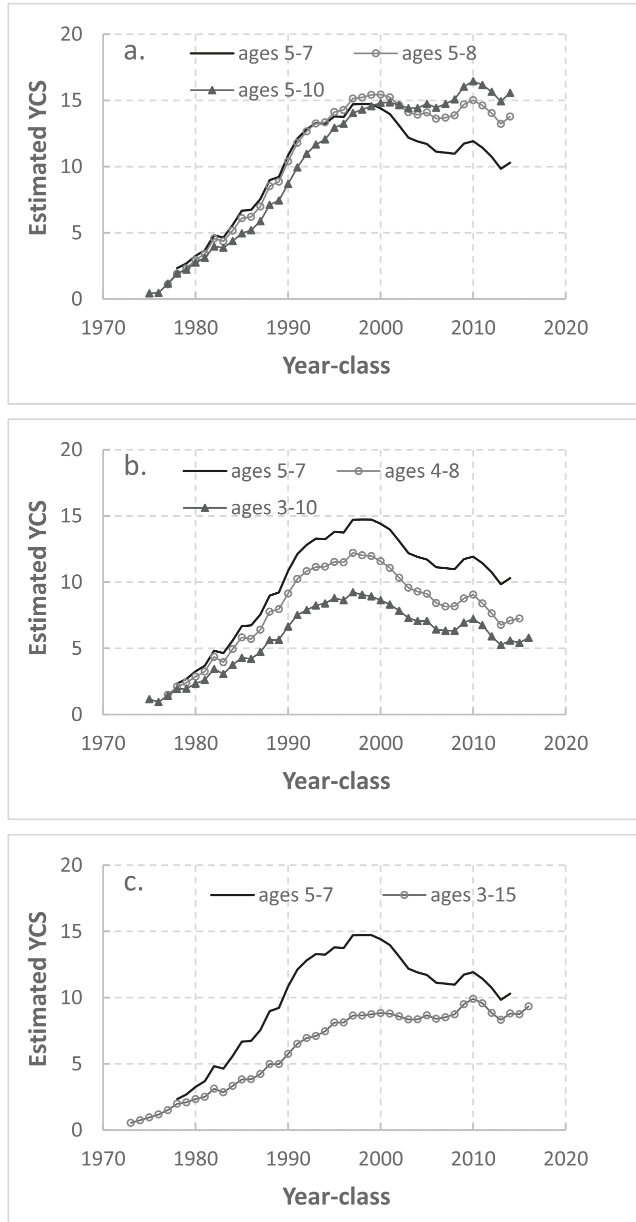


Fig. 3. Lake trout (*Salvelinus namaycush*) year-class strength (YCS) in the main basin of Lake Huron, estimated from the age ranges of (*a*) 5–8 and 5–10 years, (*b*) 4–8 and 3–10 years, and (*c*) 3–15 years, compared with YCS estimates from the age range of 5–7 years.



ences in catch numbers from different age ranges and should not be interpreted directly as differences in YCS. When more older ages were included in a broad age range, such as the age range of 3–15 years, YCS estimates again showed hyperstability since the late 1990s (Fig. 3*c*).

From the full age range of 3–30 years, YCS estimates did not show hyperstability, and the estimated YCS trajectory since 1990 was similar to that from the age range of 5–7 years (Fig. 4). Additional large variations in YCS estimates from the full age range likely resulted from confounding variables such as time-dependent selectivity and mortality. Using the full age range was also complicated by the fact that there were no data for older fish for early year-classes (prior to 1990) because the population was in recovery, and there were no data for older fish from recent year-classes because those year-classes have not yet reached older ages.

Uncertainty of year-class strength and using multiple data sources

Using the common age range of 5–7 years, YCS estimates differed substantially across data sources (Figs. 5*a*–5*b*). From the fisheries data, particularly the commercial data from southern Lake Huron, the early-year increases in YCS were

Fig. 4. Lake trout (*Salvelinus namaycush*) year-class strength (YCS) in the main basin of Lake Huron, estimated from the full age ranges of 3–30 years and compared with YCS estimates from the age range of 5–7 years with 95% confidence intervals.

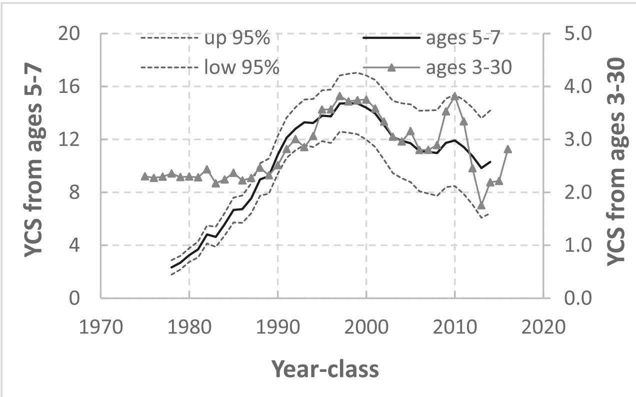
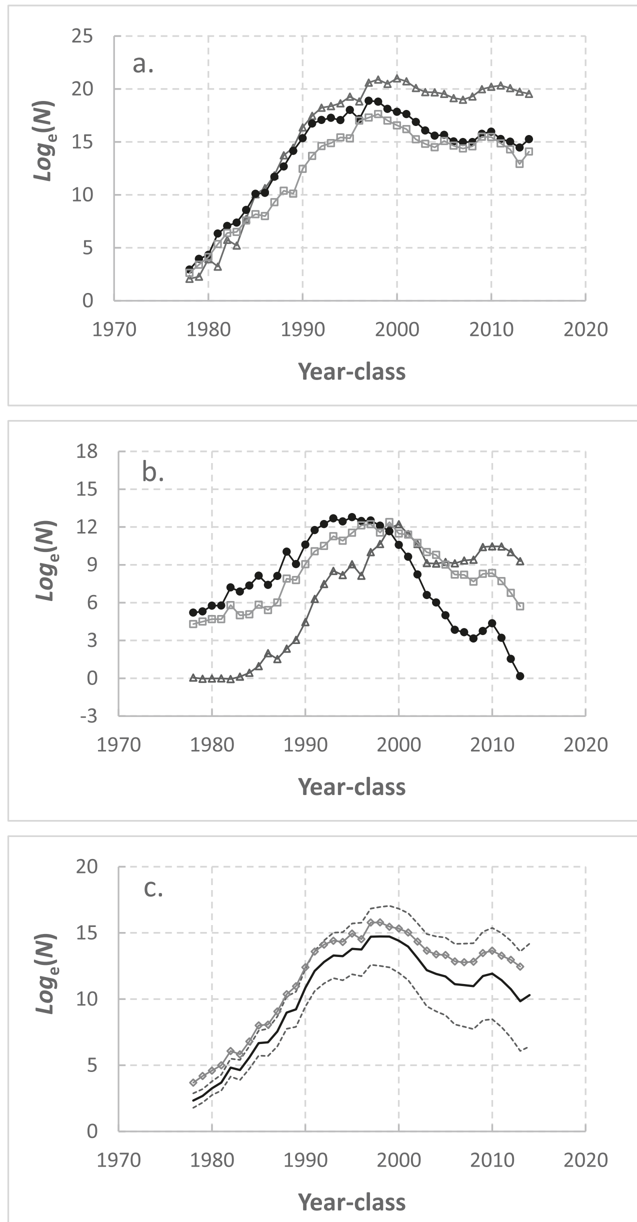


Fig. 5. Lake trout (*Salvelinus namaycush*) year-class strength (YCS) based on the age range of 5–7 years, estimated separately using commercial fishery data (open triangles and lines), recreational fishery data (open squares and lines), and fishery-independent survey data (dots and lines), from (*a*) northern Lake Huron and (*b*) southern Lake Huron. Also provided are (*c*) variance-weighted means (open diamonds and lines) from the above six YCS time-series compared with the YCS estimates based on all six data sources indexed and combined (solid line), along with 95% confidence intervals (broken lines). Herein, the northern and southern Lake Huron are separated by the extended boundary between the Ontario OH-2 and OH-3 statistical districts (i.e., extended across the international boundary as in He et al. 2022).



relatively slow, but YCS estimates for recent year-classes were relatively more stable. Variance-weighted means from the six YCS time-series were mostly within the 95% confidence intervals for the YCS estimates based on all data indexed and combined (Fig. 5*c*). The variance-weighted means appeared to be slightly higher than the estimates from the integrated data, suggesting that some relatively low estimates from a single data source were down weighted because their corresponding variances were relatively high. Based on the above findings, the uncertainty in YCS reconstruction appeared to stem from data differences, and our model provided an effective method to use multiple data sources each year.

Discussion

To separate YCS estimates from confounding variables embodied in catch-at-age data, it is very important to use the most appropriate age range for model implementation. We recommend using an age range that comprises likely ages that a fish year-class first fully recruits to the fishing gears. The age of recruitment typically changes through years and differs among fish species and ecosystems. We therefore also recommend using AIC comparison through the standard and objective procedures of model development to determine the best model structure for a given age range and population.

Many previous studies have estimated fish YCS using the youngest ages from available data. We caution against the use of such age ranges unless survey and fishing selectivity are constant across years. In the main basin of Lake Huron, survey and fishing selectivity for young lake trout were clearly not constant (He et al. 2012, 2020), in part due to changes in lake trout growth and body condition (He and Bence 2007; He et al. 2008, 2016), but also due to changes in spatial distributions of lake trout age and size groups (Riley and Adams 2010; He et al. 2012; He 2019). These changes in spatial distributions and age-specific catchability/availability (not just mesh-size selectivity of fishing gear) reflected a regime shift in the lake ecosystem (Riley et al. 2008; Barbiero et al. 2011; Madenjian et al. 2013; He et al. 2015, 2016, 2020; Rudstam et al. 2020) and concurrent changes in the relative contributions of wild-born and hatchery-stocked lake trout (He et al. 2012; Johnson et al. 2015).

We also caution against using age ranges that include relatively old ages. For lake trout in Lake Huron, we found that YCS estimates from a broad age range could not be disentangled from declines in adult mortality. We do not use YCS as a loose term such that increases in YCS could result from declines in adult mortality. To assess and understand population dynamics, we strictly use YCS as an interchangeable concept of recruitment. Even with a narrow older age range and constant adult mortality, YCS estimates would not represent the relative year-class abundance as fish first fully recruit to the fishery; instead, they would represent a relative abundance after major impacts of the fishery.

In general, when using a broad age range, variations in age-specific selectivity and mortality are inevitably confounded with YCS variation. Such a mix of confounding variables could be the major cause for commonly observed retrospective patterns in age-structured fishery assessments (e.g., Mohn 1999), as a potential solution with SCAA models would require comprehensive diagnostics of the model structures for many key variables such as recruitment, mortality, catchability, and selectivity (Stewart and Martell 2014; Hurtado-Ferro et al. 2015; Szuwalski et al. 2018).

Using longitudinal mixed-effects models, we exploited two aspects of the information in catch-at-age data. With the full age range, the best selected model structure represented our understanding of three major processes of a fish population, including interannual changes in recruitment, over-age reduction of a year-class in each data source, and interannual changes in age-specific selectivity and mortality. With reduced age ranges, the best selected model structure reflected another reality of the catch-at-age data: the variations among year-classes and among years were systematic, while the variations among ages were random. This combination of systematic and random variations was true even with a broad age range such as 3–15 years, likely because the year effect and age effect were different among data sources as indicated by the year-by-index and age-by-index interactions. With the age range of 5–7 years, the three repeated random measures from each of the six data sources (Appendix A) excluded the confounding information from pre-recruitment ages and from older ages after fishing mortality with full vulnerability to the fishery. These repeated random measures appeared to be sufficient to reliably reflect the strength of a year-class, in comparison with using the full age range for a more complete understanding of all major processes influencing the catch-at-age data, while using the full age range did not allow for a clear separation of confounding variables.

Our reconstruction of YCS for lake trout in the main basin of Lake Huron was consistent with previous findings that adult abundance rapidly increased during the late 1990s through the early 2000s, but then started to decline, particularly in southern Lake Huron (He et al. 2020; Lenart et al. 2020). Previous studies attributed the population recovery to successful controls of fishing mortality and sea lamprey (*Petromyzon marinus*)-induced mortality (Johnson et al. 2004, 2015; He et al. 2012). Those previous studies, however, also maintained the observations that the recent, more effective control of sea lamprey abundance did not happen until the end of the 1990s (Adams et al. 2003), and the rigorous control of fishing mortality was not implemented regularly until the early 2000s (United States v. Michigan 2000). Our YCS reconstruction suggests that the increases in lake trout YCS preceded the subsequent declines in mortality, implying a cause–effect relationship between these two patterns. Fishery removals were limited by fishing effort capacity (He et al. 2020), and sea lamprey attacks were limited by sea lamprey abundance and the upper rate at which they could feed (Nowicki et al. 2021). Thus, lake trout deaths likely did not increase in proportion to lake trout abundance, and the increases in recruitment combined with lower per capita mortality can lead to substantial increases in adult lake trout abundance during the 1990s through the early 2000s.

Longitudinal estimates of YCS are survey and monitoring indices that do not require any assumptions on natural mortality, catchability, or selectivity to be explicitly parameterized in the model. Explicit parameterization for every major process can be implemented in models such as SCAA for comprehensive descriptions of a complex fishery system, but such parameterizations may also build up uncertainties due to gaps in data and the limitation of our understanding. With longitudinal models, the year and age effects are used to represent time-dependent catchability, selectivity, and mortality, and adequate model structures can effectively separate those confounding variables from YCS estimates.

We do not consider the longitudinal reconstruction of YCS to be a replacement for SCAA assessments. The estimated recruitment patterns should be similar when using the same data for both models as we have seen in our additional analyses for lake trout in the main basin of Lake Huron, but the longitudinal estimates are relative abundances, and the SCAA estimates are absolute abundances. More investigations and developments are needed to use longitudinal YCS estimates as recruitment indices, such as rescaling the relative year-class abundance to the absolute abundance of recruitment at a given age. For example, while the YCS estimates contain valuable information that might benefit SCAA assessments if added as a data source, further statistical evaluations of how to appropriately add them are needed, such as accounting for correlations among the indices due to shared parameters and assuring their independence from other data already used in an assessment.

Longitudinal models have major advantages over single-age recruitment indices based on annual survey CPUE. First, YCS is reconstructed from repeated measures across multiple ages and years, while single-age recruitment indices could be biased by various unknown factors and events in annual surveys (Rosenberg et al. 1992; Shepherd 1997). Second, an adequate YCS model can remove year effects from YCS time-series, while the single-age recruitment indices from annual CPUE could be biased by long-term trends in catchability and selectivity because of changes in fish abundance and distribution (Rose and Kulka 1999; Harley et al. 2001; Wilberg and Bence 2006). Third, for reconstructing YCS, the repeated measures across multiple ages can be designed to recognize and represent the reality that the age of recruitment is not constant across years, but the single-age recruitment indices from annual CPUE cannot effectively account for this variation. Finally, a longitudinal model can be used with multiple data sources, including routine fishery-independent surveys and fisheries monitoring, and does not necessarily require fishing effort data. The uncertainty of YCS reconstruction can be substantially reduced by improving the design and consistency of fish sample collection from fishery-independent surveys and fisheries monitoring. In contrast, single-age recruitment indices from annual CPUE typically require additional targeted efforts to be maintained with specialized methods and fishing gears.

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Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare there are no competing interests.

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Appendix A

Annual samples for lake trout (*Salvelinus namaycush*) age frequency have been collected from the two management units in the main basin of Lake Huron (Table A1). Commercial samples were collected by the Chippewa Ottawa Resource Authority and Ontario Ministry of Natural Resources and Forestry (see He et al. 2015, 2020), and the commercial fisheries were distributed only in Canadian waters and the 1836 treaty ceded areas of US waters, mostly using large mesh (stretched length 114 mm) gillnets and trap nets (Brown et al. 1999; United States v. Michigan 2000). Recreational samples were collected by the Michigan Department of Natural Resources (MDNR) creel survey program, and US Fish and Wildlife Service headhunter program (coded wire tag (CWT) return collection), when charter boats and anglers return to major ports along the US shoreline (Bence and Smith 1999; Su and Clapp 2013; Su and He 2013; Kornis et al. 2020). Fishery-independent samples were collected from the annual spring gillnetting surveys conducted by the MDNR. The MDNR surveys covered every nearshore area of US Waters. Cross-contour transects (approximately 10–60 m) were sampled for lake trout, typically during late April to early June, using multifilament nylon gillnets. A net consists of nine panels that are 1.83 m tall and 30.48 m long, with stretched mesh sizes ranging from 50.8 to 152.4 mm in 12.7 mm increments. The mesh sizes were in consecutive order of panels and were not randomized. The nets were set on the lake bottom and lifted after one night.

Age assignments to lake trout samples were conducted within each management agency. Prior to 2000, most of age assignments were based on a 6-year rotation of fin-clips, with the reference of lake trout size, and scales were used for the age assignments to wild-born juvenile lake trout occasionally captured. This procedure eventually became unreliable due to increased numbers of older lake trout (Wellenkamp et al. 2015). When lake trout body length approached their asymptotic size, they often overlapped among year-classes with the same fin-clips. The abundance of wild-born adult lake trout also increased since the mid-2000s (Riley et al. 2007; He et al. 2012; Johnson et al. 2015). During 2001–2010, several otolith methods and a new maxilla method were explored and compared for age assignments. Wellenkamp et al. (2015) and Murphy et al. (2018) have reported consistency of age assignments between maxilla and otolith sections. Since 2011, maxilla or otolith sections were used to estimate ages of all wild lake trout, and the combination of a fin-clip with a maxilla or otolith section was used to narrow down the true age for a hatchery-stocked lake trout that did not carry a CWT to indicate a year-class (Yc). A total 14% of fall fingerlings and 21% of spring yearlings for the 1985–2009 year-classes from hatcheries were manually tagged with CWTs, and all lake trout stocked after 2010 were tagged with CWT using automated tagging trailers (Bronte et al. 2012). For those lake trout captured with a CWT return, the lake trout age in the capture year (Yr) was calculated as Age = Yr − Yc.

Table A1 appears on the following page.

Table A1. Annual sample sizes for lake trout (*Salvelinus namaycush*) age frequency from the commercial fishery (CF), recreational fishery (RF), and fishery-independent surveys (SV) in the two spatial units for lake trout stock assessment and fisheries management in the main basin of Lake Huron (He et al. 2020; Lenart et al. 2020).

	Northern Lake Huron			Southern Lake Huron		
Year	CF	RF	SV	CF	RF	SV
1985	118	191	811	—	396	1185
1986	464	286	505	—	516	901
1987	399	201	446	—	495	696
1988	266	152	387	—	230	815
1989	355	24	490	571	16	590
1990	350	3	194	10	54	555
1991	303	13	58	11	275	411
1992	257	91	112	—	203	633
1993	876	26	112	—	89	527
1994	501	67	170	378	100	700
1995	848	201	505	1551	197	538
1996	357	349	482	210	169	595
1997	291	347	246	1442	202	441
1998	556	182	455	866	240	678
1999	350	183	476	1630	218	842
2000	407	159	393	788	253	924
2001	351	173	419	505	123	690
2002	556	124	402	439	137	614
2003	495	79	300	58	343	762
2004	444	228	378	179	150	476
2005	265	199	371	91	199	304
2006	427	241	251	41	184	200
2007	286	341	302	61	166	320
2008	317	323	188	38	114	235
2009	468	347	112	120	170	279
2010	548	388	363	209	153	166
2011	479	299	262	281	73	306
2012	470	481	185	34	262	108
2013	404	472	302	176	298	173
2014	304	399	332	438	200	267
2015	789	449	369	371	129	298
2016	343	406	386	84	202	126
2017	287	476	264	63	171	274
2018	524	396	367	216	223	250
2019	602	321	221	—	—	—

Note: Dashes indicate the absence of data. The two spatial units are defined and separated by the boundary between the Ontario OH-2 and OH-3 statistical districts extended across the international boundary as in He et al. (2022).