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# Estimating catch curve mortality based on relative return rates of coded wire tagged lake trout in US waters of Lake Huron

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# Abstract

We estimated total mortality using catch curves based on relative return rates (RRs) of coded wire tagged lake trout in US waters of Lake Huron. RR was calculated as age specific CPUE per million of fish stocked. Annual mortality for the late 1990s through early 2000s was estimated as 38% from the 1991-1995 year-classes with an effective age range of 5-10 years, and then was estimated as 24% for the post-2000 period from the 1996-2009 year-classes. The two estimates from simple catch curve regressions based on average RR at age values were the same as from a mixed model with individual RR values from all stocking events. These two estimates were also comparable to the findings from statistical catch-at-age assessments with fundamentally different assumptions. Our approach is not constrained by the assumption that the expected recruitment is a constant over time and thus has the advantage to use multiple observations on each age from multiple cohorts. Our approach has broad applicability to aquatic ecosystems in which multiple mark-and-release events of fish stocking have been implemented.

**Key Words:** Lake Huron, lake trout strains, coded wire tags, mortality, catch curve regression

# Introduction

Catch-curve regression is a standard method for estimating total mortality of a fish population (Ricker 1975; Hilborn and Walters 1992), although more advanced stock assessments can be used to estimate mortality through time and by fish age (Maunder and Punt 2013; Methot and Wetzel 2013; Aeberhard et al. 2018). The strength of catch-curve regression is its straightforward visualization of catch-at-age data to provide statistical measures of abundance decline over time. Major assumptions are also involved in the conventional catch-curve regression, such as the age composition of fish samples is unbiased, the expected recruitment is a constant over time, and mortality is also constant over ages and time. Many reviews of catch-curve analyses are available, and the methods continue to be updated (Dunn et al. 2002; Maceina 2007; Thorson and Prager 2011; Smith et al. 2012; Millar 2015).

In the Laurentian Great Lakes, lake trout populations were reestablished by stocking hatchery-reared juveniles since the late 1960s or early 1970s, along with concurrent controls of sea lamprey abundance and fishery harvest (Eshenroder et al. 1995; Muir et al. 2012). Multiple genetic strains from remnant Great Lakes populations and adjacent inland lakes have been used in the rehabilitation program (e.g., Ebener 1998). The rate of post-stocking survival has been evaluated using relative return rate (Hansen et al. 1994; Wilberg et al. 2002; Madenjian et al. 2004; He et al. 2012; Kornis et al. 2019), and the relative return rate (RR) has also been used sometimes to indicate intensity of adult mortality (Adams et al. 2003), even though RR itself is not an estimate of either pre-recruitment mortality or adult mortality.

To illustrate the RR concept and its common applications in the Great Lakes, we provide an update of the recent Lake Huron example (He et al. 2012) in Appendix 1, with calculations as the follows:

$$RR_{a,i} = \frac{CPUE_{a,i}}{N_i} \tag{1a}$$

$$RR_{a,y} = \frac{CPUE_{a,y}}{N_{y-a}} \tag{1b}$$

where, $RR_{a,i}$ represents the relative return rate from year-class *i* at age $a$; $CPUE_{a,i}$ is the catch per unit of effort from the year-class *i* at age $a$; and $N_i$ is the number of fish stocked for the year-class *i* in million. Eqs. 1a and 1b are interchangeable for alternative presentations, with $i = y - a$ and *y* denoting the sampling year. In general, the subscript *i* could be used to denote a stocking event within a year-class, such as stocking fall fingerlings or spring yearlings for a year-class in two consecutive years, or stocking at multiple locations for a same year-class in a year. In those cases, $N_i$ is the number of fish stocked for a stocking event, and $RR_{a,i}$ is specific to the fish cohort from the stocking event.

Note that when the relative return rates for several year-classes are tracked over ages within a period of years, a corresponding catch-curve regression will allow for differences in recruitment among the year-classes, because the calculation of relative return rate is adjusted for survey effort in the capture year and for the number of fish stocked. To the best of our knowledge, however, no previous study has used the relative return rate as defined in Eq. 1 to develop a catch-curve regression allowing for multiple observations on each age from multiple cohorts.

Management agencies across the Great Lakes, including the main basin of Lake Huron, have used statistical catch-at-age (SCAA) models to assess lake trout status and trends (Sitar et al. 1999; Linton et al. 2007; Brenden et al. 2011). These SCAA assessments have integrated multiple data sources from commercial and recreational fisheries and major fishery-independent surveys, but often assume all lake trout in a lake were identical and do not account for differences in genetic strain, and their origin (hatchery reared versus wild born).

In this paper, we evaluated returns of coded wire tagged (CWT) lake trout (Jefferts et al 1963; Elrod and Schneider 1986) to the fishery-independent annual spring gillnetting surveys in US waters of Lake Huron. We tracked the relative return rate over ages and years for every stocking event, and we also calculated the total return rate across all ages-and-years from a total number of fish tagged-and-stocked. Our original goal was to estimate the variability in mortality rates across lake trout strains using catch-curve regressions based on relative return rates, assuming sufficiently high total return rates for several lake trout strains. Unfortunately, total return rates were too low to allow for robust catch-curve regressions for all but one strain of lake trout. We therefore focused on the evaluation of adult mortality for that lake trout strain but also explored reasons for the relatively low total return rates for the other strains.

We have three objectives in this paper: (*i*) to develop and apply the catch-curve regression based on relative return rates, (*ii*) to evaluate whether mortality estimates from our catch-curve regressions are comparable with the estimates from SCAA assessments, and (*iii*) to use our findings to understand status and trends of the lake trout population in two periods of years. In the main basin of Lake Huron, the abundance of adult lake trout rapidly increased during the late 1990s through the early 2000s (He 2019; He et al. 2020; Lenart et al. 2020). After 2000, Lake Huron's food web was substantially altered

(Vanderploeg et al. 2002; Barbiero et al. 2011; Madenjian et al. 2013; He et al. 2015, 2016, 2020; Rudstam et al. 2020), including the collapse of a dominant prey fish population, the alewife (Riley et al. 2008). Meanwhile, the recruitment of wild born lake trout became widespread (Riley et al. 2007; He et al. 2012; Johnson et al. 2015), but the concurrent declines in post-release survival of hatchery-reared lake trout were dramatic (Appendix 1). We hypothesized that during the rapid increases of lake trout abundance prior to the middle of 2000s, total annual mortality must have been less than the maximum limit for maintaining a population of this fish species (Healey 1978; Nieland et al. 2008), and that for the post-2000 period the total mortality must have declined to be further below such a limit, given that adult abundance did not decline rapidly after the large decline in recruitment.

## Materials and Methods

The Michigan Department of Natural Resources (MDNR) has been conducting annual fishery-independent surveys in US waters of Lake Huron since 1970 (He 2019). Within each nearshore area (Figure 1), cross-contour transects were sampled for lake trout across a depth range approximately 10-60 m, typically during late April to early June. The survey used multifilament nylon gillnets, with each net consisting of nine panels of 1.83 m tall by 30.48 m long and stretched mesh sizes ranging from 50.8 to 152.4 mm in 12.7mm 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.

The U.S. Fish and Wildlife Service reared nearly all lake trout stocked into US waters of Lake Huron, although the MDNR also stocked some lake trout in US waters, and the Ontario Ministry of Natural Resources stocked lake trout in Canadian waters. All lake trout stocked from all hatcheries (0.5-2.0 million a year) received a fin clip to denote that they were of hatchery origin (Eshenroder et al. 1995; Ebener 1998). For the 1985-2009 year-classes, 14% of fall fingerlings and 21% of spring yearlings were manually tagged with coded wire tags (CWT) and received adipose fin clip (AD). The ADCWT proportion varied among year-classes, but every tag lot unambiguously denoted stocking location, life stage, genetic strain, year-class, hatchery, and the numbers of fish tagged and released (Bronte et al. 2006). Since the 2010 year-class, all hatchery-reared lake trout received ADCWT delivered by automated tagging trailers (Bronte et al. 2012; Kornis et al. 2016).

ADCWT lake trout caught in the MDNR annual surveys were all traced back to their stocking events individually. We only used ADCWT returns to the MDNR surveys, because for the analyses of relative return rate, the returns to recreational and commercial fisheries could not be adjusted for uncertain fishing effort, and it was also hard to standardize all other fishery independent survey efforts in the lake. The MDNR survey covered the US nearshore waters from the north to the south of Lake Huron and sampled similar locations almost every year. We used ADCWT returns from the entire survey area rather than just from those sampling sites nearby to stocking locations, because the surveys were not in the spawning season and lake trout spatial migration is substantial (Adlerstein et al. 2007; Kornis et al. 2020).

Our analyses in this paper included the 1985-2009 year-classes of ADCWT lake trout. These year-classes were stocked mostly as spring yearlings (SY, about 17 months old), but fall fingerlings (FF, about 10 months old) were also used some years. There were nine genetic strains of hatchery-reared lake trout that were released in Lake Huron for these year-classes, including Jenny Lake (JL), Lewis Lake (LL), Lake Ontario (LO), Seneca Lake (SL), Marquette (MA), and Apostle Island Lake Superior (SA), Isle Royale Lake Superior (SI), Traverse Island Lake Superior (ST), and also Lake Superior fish (SM) that were likely Marquette strain. JL and LL had the same genetic origin (Ihssen et al. 1988; Bronte et al. 2007; Lantry et al. 2008). LO was likely a combination of multiple genetic strains (Elrod et al. 1996; Lantry et al. 2008). Strain composition of annual stocking varied over years, and not all genetic strains contributed to the releases each year.

For our model development and applications, we explored data availability from all stocking events with ADCWT lake trout. We summarized the total numbers released by year-class, and the total numbers of returns by year. We also summarized three statistics broken down by genetic strain, life stage (FF or SY), and stocking location, including the total numbers stocked, the total numbers of returns, and the total return rates.

From the above summaries, only LL yearlings stocked in US nearshore waters generated enough ADCWT returns, for which the analyses of relative return rates were conducted completely. The effective age range for the analyses of relative return rates and a meaningful catch-curve regression was typically 5-10 years. This was because LL lake trout did not fully recruit to the survey gear until they reached five years old, and survivors older than 10 years of age were relatively few (Figure 2). Given this effective age range of 5-10 years, we used the 1991-1995 year-classes to represent a period of the late 1990s through the early 2000s, during which lake trout adult abundance rapidly increased (He et al. 2012, 2020; Lenart et al. 2020), and the 1996-2009 year-classes to represent the post-2000 period, during which the food-web of Lake Huron was dramatically altered (Vanderploeg et al. 2002; Barbiero et al. 2011; Madenjian et al. 2013; He et al. 2015, 2016, 2020; Rudstam et al. 2020), and the recruitment of wild-born lake trout became widespread (Riley et al. 2007; He et al. 2012; Johnson et al. 2015).

For each of the two time periods we analyzed relative return rates from all stocking events of LL lake trout stocked as yearlings with ADCWT in US nearshore waters. We calculated RR for each combination of stocking event and the age of lake trout. The age of every ADCWT lake trout at capture was calculated as the difference between the capture year and the year-class for the corresponding stocking event. Age specific catch per unit of effort ($CPUE_{a,i}$) was calculated as:

$$CPUE_{a,i} = n_{a,i}/E_y \quad (2)$$

where $n_{a,i}$ is the number of returns at age $a$ from a stocking event $i$, and $E_y$ is the total survey gillnetting effort in the year ($y$) of fish capture. Accordingly, the relative return rate ($RR_{a,i}$) from Eq. 1 was calculated for a stocking event $i$, and $N_i$ is the total number of fish tagged and released for the stocking event. For all data analyzed in this paper, survey gillnetting effort varied among years in the range of 43,200-105,300 ft, the number of LL yearlings with ADCWT varied among all stocking events in the range of 25,700-64,800 fish, and the unit of RR was the number of fish caught per 100,000 ft (30480 m) of gillnet per 1,000,000 of fish tagged and released.

We adapted a commonly used right truncation rule (Dunn et al. 2002; Smith et al. 2012) to restrict our use of RR values in subsequent catch-curve analyses. The fish cohort from a stocking event was dropped from further analyses if ADCWT lake trout were not caught at age 5. Also, for each stocking event, only contiguous non-zero RR values were used in further analyses. We evaluated the right truncation rule with our data. When those ages with no ADCWT returns were treated as effective data points, we added a small constant to all data points prior to log transformation. We then plotted log transformation of individual RR value versus age for all stocking events within each of the two periods (Figure 3). From the data plots, a regression line would be misled by those false data points, and the regression slope (mortality estimate) would be dependent on the constant added to all data points prior to log transformation. We decided that for each fish cohort from a stocking event, the age with no ADCWT returns was an influential data point that should be excluded based on standard diagnostics of a linear regression. The right truncation rule means that we excluded all subsequent ages of the cohort from a stocking event after the first zero was encountered.

We conducted a simple catch-curve regression based on average RR for each lake trout age within a group of year-classes that were used to represent a time period. We took each fish cohort from a stocking event as a subgroup and calculated average RR for each lake trout age over those subgroups. Note that, because of the right truncation rule in using individual RR values, the number of subgroups was not always equal for every age of lake trout. The logarithm of average RR was then linearly regressed against age separately for each time period to obtain mortality estimates.

We also developed a mixed model to conduct catch-curve regression based on logarithm of individual RR values of all stocking events that were used to calculate the average RR at age values for conducting the simple catch-curve regression. We considered that individual RR values could be different among stocking events or year-classes because of their differences in early life mortality, and that variation in catchability among sampling years could also add differences to individual RR values. Those random variations, however, do not contribute to adult mortality of lake trout, and thus we interpreted the individual RR value from a stocking event ($RR_{a,i}$) as a product of the average RR at age value ($RR_{a,avg}$) and a multiplicative error ε:

$$RR_{a,i} = RR_{a,avg} \times \varepsilon \qquad \text{with } \varepsilon > 0 \qquad (3)$$

Such that to predict the logarithm of RR as a linear function of age, the multiplicative error after log transformation can be understood as random effect on the intercept, plus a residual error of prediction. Also note that a simple catch-curve regression can be conducted based on average RR at age values, and it does not need to consider random effect on individual RR values. In contrast, to conduct a catch-curve regression based on individual RR values from all stocking events, the random effect should be clarified, estimated, and separated from residual errors of predictions. Otherwise, the regression slope will be altered by random effect on the intercept and the mortality estimate will be misled. To develop the mixed model, we used Akaike information criterion (AIC; Burnham and Anderson 2002) to compare and select alternative model structures (Table 1). We first compared models with only fixed effect to decide whether the intercept, or the slope, or both the intercept and slope were different between the two time periods. Then, building the best fixed-effect model, we compared alternative mixed models step by step to evaluate random effect of stocking event, year-class, and sampling year on the intercept, with the considerations that a year-class may include several stocking events, and that fish caught at a same age from different year-classes were captured in different years.

We used 50% confidence intervals to evaluate whether mortality estimates were the same from the simple catch-curve regression and the best mixed model. We also examined whether mortality estimates were similar among other plausible mixed models ($\Delta$AIC < 4). We interpreted the negative of the regression slope as the instantaneous mortality (Z) for the lake trout population in a period of years, from which annual survival rate ($S = e^{-Z}$) and annual proportional mortality ($A = 1 - e^{-Z}$) were calculated. From the mixed models, Z was calculated as the negative sum of the coefficients for the age effect and the age-by-period interaction effect.

Rigorous comparison of catch curve mortality with SCAA mortality is problematic, because these two assessment approaches are based on fundamentally different assumptions. For Lake Huron lake trout, the current SCAA assessments estimated time-varying catchability, time-varying selectivity, and age-and-year specific mortality (He et al. 2020). Nonetheless, we evaluated general comparability between the two assessment approaches as we believed that the mortality estimates from both approaches should be adequate in reflecting the population status, and both can be used to guide fisheries management. From the SCAA assessments in northern and southern Lake Huron separately (He et al. 2020; Lenart et al. 2020), we calculated the average of age 5-10 mortalities during 1995-2005 and the average of age 5-10 mortalities after 2000. The age range of 5-10 corresponded with the age range in the catch curve regressions. Thus, the averages of mortality estimates from the SCAA assessments should be comparable with the estimates from the catch-curve regressions based on relative return rates of ADCWT lake trout.

## Results

The number of ADCWT lake trout from 1985 through 2009 year-classes varied between 118,700 and 565,300 fish and averaged at 326,841 a year (Figure 4a). Fall fingerlings were not stocked every year, hence only 745,529 ADCWT fingerlings were stocked in comparison with 7,425,487 ADCWT yearlings. The ADCWT returns increased during the late 1990s through the early 2000s, and declined thereafter (Figure 4b), which reflected changes in lake trout abundance, although the tag returns were not directly proportional to lake trout abundances.

The top three genetic strains of ADCWT lake trout stocked were 1.66 million Marquette (MA) strain, 2.36 million Lewis Lake (LL) strain, and 2.4 million Seneca Lake (SL) strain (Figure 5a). The highest total return rate was 0.75 per 1,000 stocked for LL yearlings (Figure 5b), in comparison with 0.00-0.22 per 1,000 stocked for other strains as spring yearlings or fall fingerlings.

ADCWT lake trout were not evenly released in all areas of the lake. A total of 2.95 million were released at Drummond Island refuge, 3.10 million were released at Six Fathom Bank, an offshore reef refuge, and only 1.75 million were released in the four nearshore areas of US waters (Figure 6a). Stocking location appeared to be very decisive to influence the total return rate of ADCWT lake trout based on the MDNR annual spring gillnetting surveys (Figure 6b). In our dataset, Drummond Island stocking accounted 52% for all SL lake trout with ADCWT in the lake. The offshore reef stocking accounted 48% for all SL lake trout with ADCWT in the lake. In the four nearshore areas of US waters, ADCWT lake trout released were all LL yearlings.

From the simple catch-curve regression, based on age-specific average relative return rate for LL yearlings stocked in US nearshore waters, the estimated instantaneous mortality rate (Z) with 95% confidence interval was 0.48 (0.38, 0.59) per year from 1991-1995 year-classes (Figure 7a), and  0.27 (0.22, 0.32) per year from 1996-2009 year-classes (Figure 7b).  These two estimates were comparable with mortality estimates from SCAA assessments (Figure 7c-d), although for the first time period the catch-curve estimate was from data of only three year-classes, so the estimate had higher uncertainty compared to the SCAA estimates, and for the second period the catch-curve estimate was similar only with SCAA estimate for northern Lake Huron.

Based on individual RR values for all stocking events, AIC comparison of alternative model structures supported different average intercepts and different slopes for the linear relationship of log RR with lake trout age for the two groups of year-classes that were used to represent two time periods (Table 1).  The AIC comparison also supported random variation of intercepts among year-classes, as all plausible models ($\Delta$AIC < 4) included a random year-class effect.  The lowest AIC model also included a random effect of sampling year suggesting that catchability might have varied among years, although the AIC for this model was only slightly lower than the model with only a random year class effect (Table 1).  From the mixed model with the lowest AIC, mortality (Z) was estimated as 0.52 for the first time period and 0.28 for the second period (Table 1).  These two estimates were each within the 50% confidence intervals for a corresponding estimate from the simple catch-curve regression: 0.48 (0.45, 0.52) from the 1991-1995 year-classes, and 0.27 (0.25, 0.28) from the 1996-2009 year-classes (Figure 5).  From the other two mixed models with almost the same AIC ($\Delta$AIC <2), mortality estimates were 0.53 and 0.54 for the first time period, and was 0.31 for the second time period, only slightly exceeded the above 50% confidence intervals. The 95% confidence intervals for the two estimates from the simple catch-curve regression were 0.48 (0.38, 0.59) for the first time period, and 0.27 (0.22, 0.32) for the second time period, which were translated to annual mortality rate of 38% (31%, 45%) for the late 1990s through the early 2000s, and 24% (20%, 27%) for the post-2000 period.

## Discussion

Based on relative return rate of ADCWT lake trout, our catch-curve regression provided further support for mortality estimates from SCAA assessments. Future investigations on our approach to catch-curve regression should further clarify the best use of data. Smith et al (2012) emphasized the variance weighted regression and downplayed the implementation of right truncation rule. In our analyses, when the right truncation rule was loosely implemented (all non-zero individual RR values within the effective age range of 5-10 years were used, and from each stocking event only a age with no ADCWT returns was dropped), the lowest AIC model only included random effect of year-class on the intercept, and also supported different residual variances for each age, so that model was variance weighted. That difference in data use and final model selection provided mortality (Z) estimates as 0.52 for the first time period, and 0.33 for the second period. The estimate for the second time period was between the SCAA estimates for northern and southern Lake Huron. When we truncated out all subsequent ages of the cohort from a stocking event after the first zero was encountered (the right truncation rule), AIC comparison did not support different residual variances for each age, and mortality estimate for the second time period was 0.28 (Table 1).

From our findings, the catch-curve regression and SCAA assessment both can be applied to address the important management concern on fish mortality, although they have fundamentally different assumptions. The estimated annual mortality of 24% in recent years seems very low in comparison with the history of lake trout population in Lake Huron, but it is consistent with our empirical observation and ecological understanding. For lake trout in the main basin of Lake Huron, non-fishing mortality includes two components: background natural mortality and sea lamprey (*Petromyzon marinus*) predation mortality (Sitar et al. 1999; He et al. 2020). The sea lamprey predation mortality has been reduced to be less than 0.05 through persistent efforts to control sea lamprey abundance (Nowicki et al. 2020). The background natural mortality has been estimated with prior information in the SCAA assessments, including the mean and SD on log scale. An informative prior, [*ln*(0.10), 0.057], is from previous studies in Lake Huron and Lake Ontario (Sitar et al. 1999; Brenden et al. 2011). Keeping all other things the same in the SCAA assessments, and using an uninformative or much less informative prior, [*ln*(0.20), 0.20], to replace the above informative prior, the natural mortality was still estimated about 0.10, as predicted by using the current maximum age over 30 (Hoenig 1983; Hewitt and Hoenig 2005). Given the non-fishing mortality of 0.15 or less, and the observation that the recent adult abundance did not rapidly decline in northern Lake Huron after the dramatic drop in overall recruitment, the estimate of annual mortality (A) of 24% is reasonable in reflecting the current stock status and fishery management (He et al. 2020). With much higher and relatively stable recruitment, previous studies have suggested that lake trout population and production is sustainable with annual mortality below 50% (Healey 1978) or about 40% (Nieland et al. 2008). From Hansen et al. (2021), lake trout annual mortality (A) varied from 0.026 to 0.792 among 248 populations in North America, with 50% of populations varying between 0.130 and 0.296, and 95% varying between 0.071 and 0.660, and the mean was lower for native (0.237, SE = 0.0097, n = 235) than for non-native (0.360, SE = 0.041, n = 13) populations.

The estimated adult mortality for Lewis Lake strain lake trout from our catch curve regression was similar with the estimated average adult mortality of all genetic strains of lake trout included in the SCAA assessments. This finding implies that, with effective control of sea lamprey abundance and reduction of sea lamprey predation mortality, a major difference in the performance of all lake trout strains in the lake should be at their early life stage, and at post-release survival for hatchery reared lake trout. In that regard, genetic diversity and habitat diversity, as well as the connection between nearshore and offshore productions should continue to be in the central concern of future management of lake trout rehabilitation and lake trout fisheries (e.g., Hecky et al. 2004; Muir et al. 2016). For example, Adams Point was the stocking area with the highest total return rate to the MDNR annual surveys, and this area also produced the highest wild recruitment in recent assessments (He 2019). This area may have benefited from a close connection to deeper water nursery habitats for juvenile lake trout, a topography similar as the situation for juvenile lake trout from the Gull Island Shoal complex in Lake Superior (Bronte et al. 1995). In future investigations, location effects should be included in paired comparisons of the performance of all lake trout strains.

Our long-term data set did not allow us to directly compare subpopulation parameters among lake trout strains stocked into Lake Huron, due to the unbalanced temporal and spatial nature of the stocking program. Genetic studies have shown that wild-born lake trout in the main basin of Lake Huron were produced mostly by Seneca Lake strain (Scribner et al. 2018), and a similar observation was also reported in Lake Michigan (Larson et al. 2021). In Lake Huron, those observations can be explained by the stocking history that Seneca Lake strain was the dominant strain stocked in the Drummond Island and offshore reef areas but was not stocked in US nearshore waters, where the long-term MDNR survey has been conducted. It is also the case that the Lewis Lake strain was never stocked in the Drummond Island area where most of the first pulse of wild recruitment occurred. Future investigations of subpopulation parameters of major genetic strains of lake trout, including adult mortality and early-life survival to a critical life stage, could contrast results from different approaches to fish spatial distribution and movement. For example: 1) using lake wide return of ADCWT lake trout released in only one area of the lake, 2) using region specific return of ADCWT lake trout released lake wide, and 3) using the return of ADCWT lake trout to a stocking-and-spawning site based on fall (spawning season) surveys.

Comparisons of lake trout strains could be substantially influenced by other major factors such as stocking year, stocking location, and life stage at stocking. Many paired-stocking experiments have already been conducted to compare survival of fall fingerlings versus spring yearlings. Pycha and King (1967) found that the fall fingerling to spring yearling survival rate was 15-26% in Lake Superior. Kornis and Bronte (unpublished data) found that this survival rate was 33% in Lake Michigan. Elrod et al (1988) found that the survival rate was 40% in Lake Ontario. Current lake trout stock assessments in the Great Lakes all assumed 40% equivalence of fingerling stocking to yearling stocking (Sitar et al. 1999; Linton et al. 2007; Brenden et al. 2011). From the data used in this paper, we compared total return rate between ADCWT lake trout stocked as fall fingerlings and as spring yearlings, with all lake trout strains and all over-year stocking events combined. We found that the total return rate was 0.13 per 1,000 fall fingerlings stocked, and 0.30 per 1,000 spring yearlings stocked, which suggested that the fingerling-to-yearling survival rate was 43%. Unfortunately, the data did not allow us to sort out potential effects of all other major factors, such as stocking year, stocking location, and genetic strain of lake trout.

In future applications, our new catch-curve regression could be further refined by incorporating survey selectivity (Hansen et al 1997), following the approach of Thorson and Prager (2011). This potential refinement will demand some complex computations because the age-specific selectivity from the current SCAA assessments for lake trout in the main basin of Lake Huron has been estimated as time-varying over years (He et al. 2020). See also the review and recommendation of Smith et al (2012) for standard catch curve analyses.

We anticipate that our approach to catch-curve regression based on relative return rates will be broadly applied in future investigations. Propagated fish have long become an integral part of fisheries almost everywhere (Nickum et al. 2005). Lake trout management in the Laurentian Great Lakes is just one example of the programs practiced throughout the world that fish culture and stocking programs have played a central role for recoveries of depleted fish populations. We believe that major issues on genetic integrity and diversity with fish culture and stocking programs, and fishery harvest of mixed fish stocks in general, can be better investigated with standard assessments of population and subpopulation parameters including reliable estimates of adult mortality and survival to a critical early-life stage. Our application in this paper has the advantage that the age and year-class of every ADCWT fish is known, with little error. To apply such methods in cases where fish released from hatcheries are identified only by rotational fin clips as opposed to ADCWT, it is important that aging structures (e.g. maxilla or otolith section) be collected along with fin clip data so as to narrow down the true age of individual fish (Wellenkamp et al. 2015). Our results suggest that the estimate of average population mortality was not compromised by year-to-year variations in catchability, selectivity and mortality. This is likely because of careful and justified choice of time blocks and most importantly, our application of catch curves to cohorts of essentially known recruitment thereby avoiding the unrealistic assumption of expected recruitment to be a constant, which is critical for the use of conventional catch-curve analyses. Overall, our approach to catch-curve regression based on relative return rates has broad applicability to aquatic ecosystems in which multiple mark-and-release events of fish stocking have been implemented as integral parts of management programs.

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## Table Caption

**Table 1.** The development of a mixed model using R nlme package with the maximum likelihood method (Pinheiro et al. 2020), where gls() is a function of generalized least square, lme() is a function of linear mixed model, lnRR is log transformed relative return rate, Age is fish age, PD is coded as 0 or 1 for a group of year-classes representing a period of years, YR stands for sampling year, EV stands for stocking event, YC stands for year-class, and the extent .fc indicates the variable was treated as a factor. Model presents standard R syntax for models, which are interpreted in the Description column.

**Table 1.**

| Step | Model | Description | ΔAIC |
|---|---|---|---|
| 1 | gls(lnRR ~ Age) | the same slope (mortality) for two periods | 61.0 |
| 2 | gls(lnRR ~ Age + PD : Age) | only the slope (mortality) differs between two periods | 54.7 |
| 3 | gls(lnRR ~ Age + PD) | only the intercept differs between two periods | 50.4 |
| 4 | gls(lnRR ~ Age * PD) | both intercept and slope (mortality) are different between two periods. | 43.9 |
| 5 | lme(lnRR ~ Age * PD, random=list(YR.fc=~1) ) | random effect of sampling year on intercept, and both intercept and slope (mortality) differ between two periods | 30.8 |
| 6 | lme(lnRR ~ Age * PD, random=list(EV.fc=~1) ) | random effect of stocking event on intercept, and both intercept and slope (mortality) differ between two periods | 19.6 |
| 7 | lme(lnRR ~ Age * PD, random=list(YC.fc=~1) ) | random effect of year-class on intercept, and both intercept and slope (mortality) differ between two periods | 0.74 |
| 8 | lme(lnRR ~ Age * PD, random=list(YR.fc=~1, EV.fc=~1) ) | random effect of sampling year and stocking event on intercept, and both intercept and slope (mortality) differ between two periods | 32.8 |
| 9 | lme(lnRR ~ Age * PD, random=list(YC.fc=~1, EV.fc=~1) ) | random effect of year-class and stocking event on intercept, and both intercept and slope (mortality) differ between two periods | 1.37 |
| 10 | lme(lnRR ~ Age * PD, random=list(YC.fc=~1, YR.fc=~1) ) | random effect of year-class and sampling year on intercept, and both intercept and slope (mortality) differ between two periods | 0.0 |
| 11 | lme(lnRR ~ Age * PD, random=list(YC.fc=~1, YR.fc=~1), weights=varIdent(form=~1\|Age) ) | random effect of year-class and sampling year on intercept, both intercept and slope (mortality) differ between two periods, and residual variance differ among age groups | 6.7 |

Summary of Model 10

| | Estimate | Standard Error | DF |
|---|---|---|---|
| Intercept | 9.0912 | 0.6197 | 82 |
| Age | -0.5230 | 0.0631 | 30 |
| PD | -2.5626 | 0.8681 | 7 |
| Age:PD | 0.2395 | 0.1030 | 30 |

## Figure captions

**Figure 1.** Statistical districts for fisheries management in Lake Huron, from Smith et al. (1961) and Ebener (1998). The boundary between statistical districts of OH-2 and OH-3, stretching across international boundary to Thunder Bay North Point, is suggested to be the boundary between MH-2 and MH-3 (He 2019; Lenart et al. 2020). Black dots approximately represent 14 sampling transects, but one of them is in the Drummond Island refuge so the dot was not shown.

**Figure 2.** The total number of ADCWT return at age for Lewis Lake strain of lake trout stocked as yearlings. (**a**) From the 1991-1995 year-classes. (**b**) From the 1996-2009 year-classes.

**Figure 3.** Log transformed relative return rates [$log_e(RR + 1)$] within the effective age range of 5-10 years for all individual stocking events (dots), for Lewis Lake strain of lake trout stocked as yearlings with ADCWT. Broken lines show the regressions influenced by violating the right truncation rule and including false data points (squares) that no ADCWT return was recorded at an age for a stocking event. (**a**) From the 1991-1995 year-classes. (**b**) From the 1996-2009 year-classes.

## Figure captions (continued)

**Figure 4.** **a)** The numbers of ADCWT spring yearling (YR) and fall fingerling (FF) lake trout released for a year-class, and **b)** the numbers of returns of ADCWT fish in a year.

**Figure 5.** **a)** The numbers of ADCWT yearling (YR) and fall fingerling (FF) of nine Lake Trout strains released, and **b)** the total return rate of ADCWT fish for each of the nine lake trout strains.

**Figure 6.** **a)** The numbers of ADCWT lake trout released in seven locations (and nearby areas) of Lake Huron, including Ontario waters of the main basin (Ontario), Drummond Island (DI), offshore reefs including Six Fathom Bank and Yankee Reef (Offshore), the east of the Thumb (Thumb), from Au Sable Point to South Point of Thunder Bay (Au Sable Pt.), from North Point of Thunder Bay to Presque Isle (Presque Is.), from Adams Point to Hammond Bay (Adams Pt.). **b)** The total return rate from ADCWT lake trout stocked in each of these seven locations.

**Figure 7.** Catch-curve mortality (CCM) based on relative return rate of Lewis Lake strain lake trout stocked as yearlings in US nearshore areas of Lake Huron, compared with averages of age 5-10 mortalities estimated from SCAA assessments for lake trout population in northern Lake Huron (NLH) and southern Lake Huron (SLH). (**a**) The catch-curve regression for 1991-1995 year-classes. (**b**) The catch-curve regression for 1996-2009 year-classes. (**c**) Comparisons of three mortality estimates for the late 1990s through the early 2000s. The Boxes were 50% confidence

intervals and the bars were 95% confidence intervals, and they were the same for the next panel. (**d**) Comparisons of three mortality estimates for the post-2000 period.

**Figure 1.**

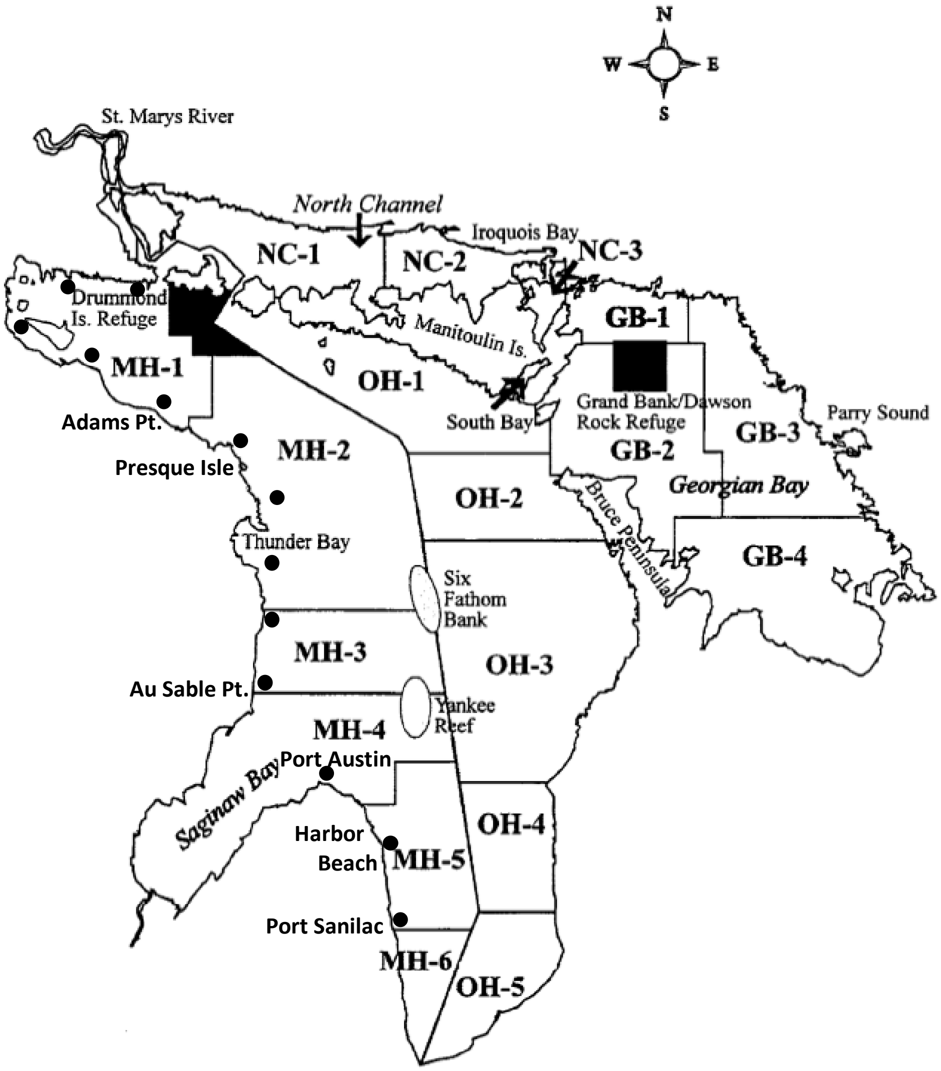

N
W
E
S
St. Marys River
North Channel
Iroquois Bay
NC-1
NC-2
NC-3
Drummond Is. Refuge
Manitoulin Is.
GB-1
MH-1
OH-1
Adams Pt.
South Bay
Grand Bank/Dawson Rock Refuge
Parry Sound
GB-3
MH-2
GB-2
Presque Isle
Georgian Bay
OH-2
Bruce Peninsula
Thunder Bay
GB-4
Six Fathom Bank
MH-3
OH-3
Au Sable Pt.
Yankee Reef
MH-4
Saginaw Bay
Port Austin
OH-4
Harbor Beach
MH-5
Port Sanilac
MH-6
OH-5

**Figure 2.**

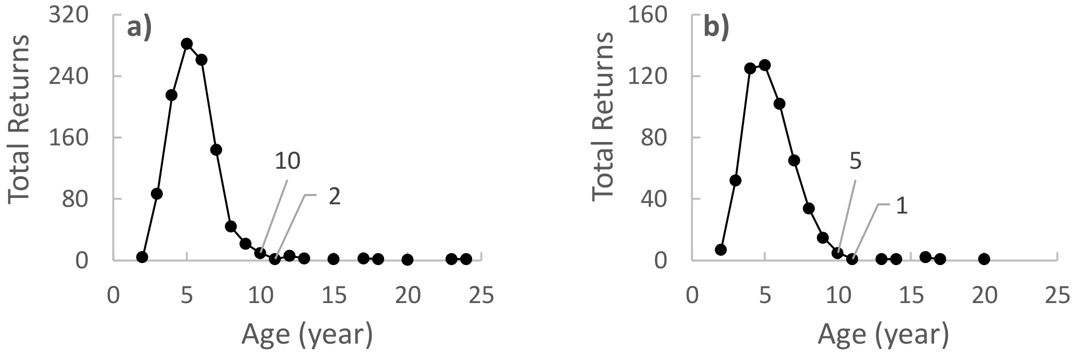


**Figure 3.**

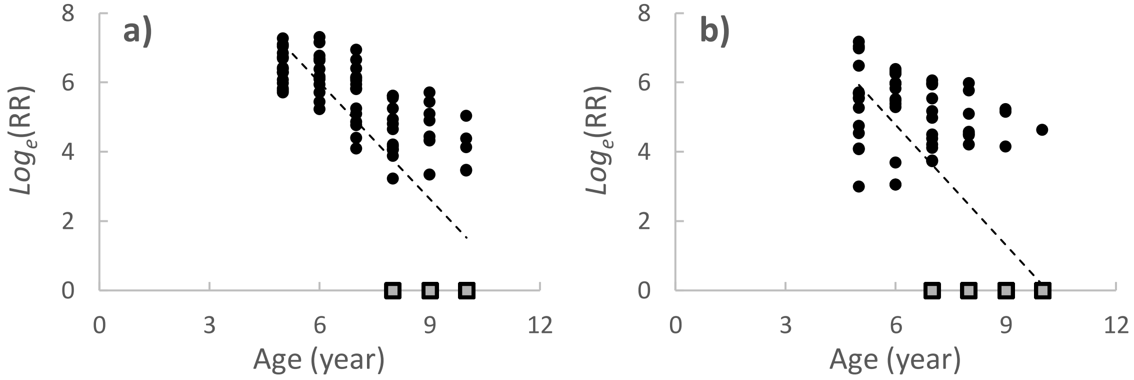


**Figure 4.**

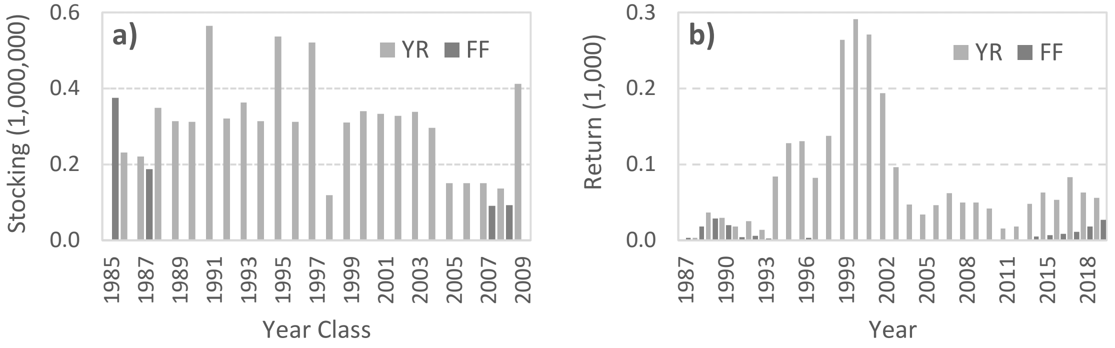


**Figure 5.**

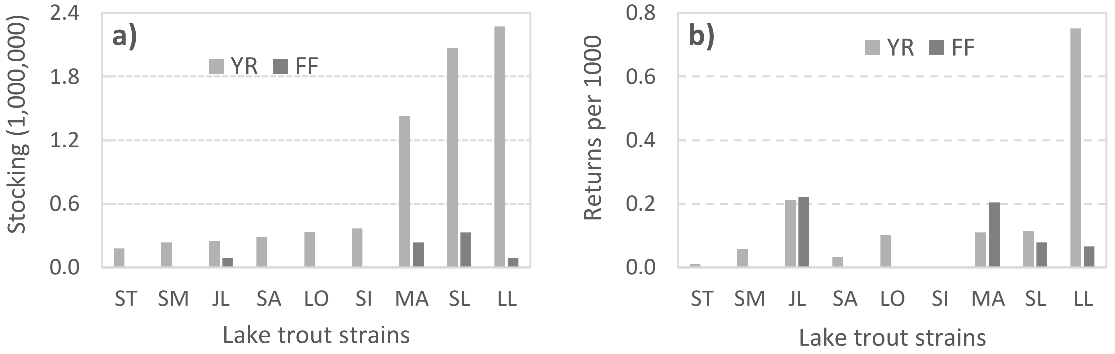


**Figure 6.**

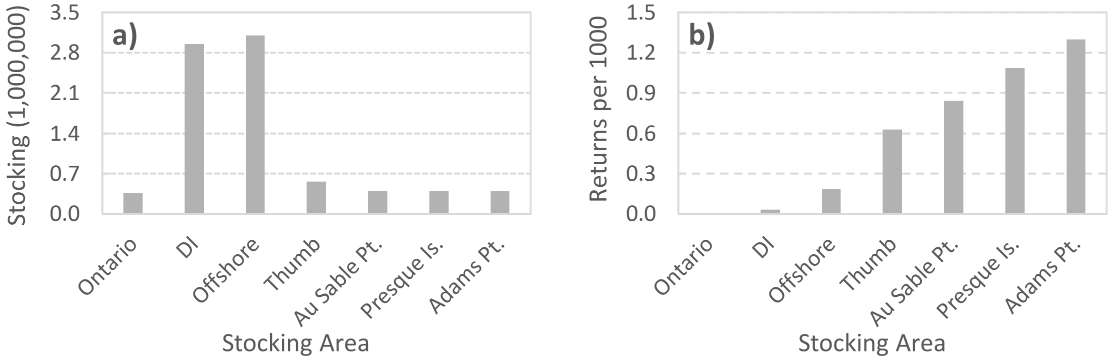
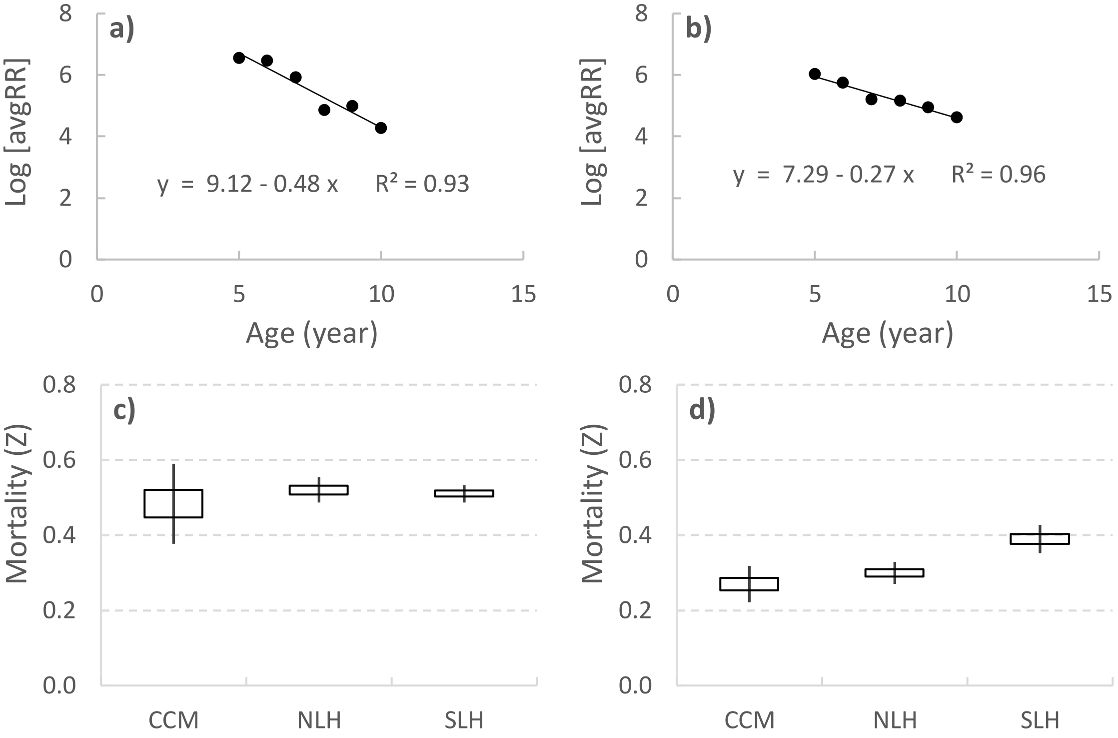


**Figure 7.**


a)
Log [avgRR]
8
6
4
2
0
y = 9.12 - 0.48 x R² = 0.93
0
5
10
15
Age (year)
b)
Log [avgRR]
8
6
4
2
0
y = 7.29 - 0.27 x R² = 0.96
0
5
10
15
Age (year)
c)
Mortality (Z)
0.8
0.6
0.4
0.2
0.0
CCM
NLH
SLH
d)
Mortality (Z)
0.8
0.6
0.4
0.2
0.0
CCM
NLH
SLH

**Appendix 1** Age-7 lake trout per 1,000 ft (304.8 m) of gill nets per 1,000,000 of yearling equivalent stocked in the main basin of Lake Huron, based on MDNR annual spring gillnetting surveys, and updated from the analysis in He et al. (2012). See also the first analysis on age-5 CPUE per recruit (Wilberg et al. 2002).