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ARTICLE

Estimates of adult Lake Trout mortality from coded wire tags in a population with developing natural reproduction in southern Lake Michigan

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Abstract

Objective: Overfishing and Sea Lamprey *Petromyzon marinus* predation led to extirpation of Lake Trout *Salvelinus namaycush* from Lake Michigan in the 1950s. Large populations of hatchery-reared fish were developed by the 1970s, but natural reproduction was limited until the early 2000s when it began to increase in the southern main basin. Hypothesizing that the relatively low mortality of spawning-aged fish contributed to this reproductive success, we estimated the total annual mortality rate for this population.

Methods: We used catch curves to estimate the total instantaneous mortality rate Z using coded wire tags, which provided definitive ages. We made separate estimates from fish collected in three on-going surveys: a spring gill-net survey, a fall gill-net spawning survey, and a sport fishery survey.

Result: Our estimates of $Z \pm$ SE were 0.297 ± 0.019, 0.239 ± 0.009, and 0.205 ± 0.007 for the spring, spawning, and sport fishery surveys, respectively. We suggest that the mean $Z \pm$ SE of all survey estimates of 0.247 ± 0.027 would be a reasonable estimate for this population, which equates to a total annual mortality of $22 \pm 3\%$. This estimate is in the low range of rates reported for the species and is in the same range as other populations in the Great Lakes with well-established natural reproduction.

Conclusion: We concluded that these low total mortality rates contributed to the reproductive success in southern Lake Michigan through increasing spawning stock density and age structure and that previous estimates of another important population parameter, the instantaneous natural mortality rate M, were too high. Estimates of M ranged from 0.210 to 0.240 and were based on the Pauly equation, a growth- and temperature-based estimator. We suggest maximum-age-based estimators of M are more appropriate for Lake Trout. Several alternative maximum-age-based estimators produced estimates for M of 0.132–0.058, all of which are more compatible with our estimate of Z.

KEYWORDS

fisheries management, population dynamics, restoration and enhancement, tags and tagging

INTRODUCTION

Lake Trout *Salvelinus namaycush* were extirpated from Lake Michigan in the 1950s due to overfishing and predation from Sea Lamprey *Petromyzon marinus* (Wells and McClain 1973; Holey et al. 1995). In the 1960s, efforts to restore Lake Trout were initiated, including suppressing Sea Lamprey populations, stocking hatchery-reared Lake Trout, and controlling fishery harvest. The objective of the restoration programs was to reestablish populations with self-sustaining natural reproduction (Eshenroder et al. 1995). After the first 30 years of implementation, there remained little evidence of naturally produced fish (Holey et al. 1995). Reasons for this lack of progress were evaluated, including reviewing the type and quality of stocked fish, stocking practices and locations, interactions between Lake Trout and nonnative species, and effectiveness of controls of mortality (Eshenroder et al. 1999; Bronte et al. 2003). Recommendations aiming to overcome these problems included diversifying the strains and morphotypes of fish stocked, focusing stocking on reefs with the best reproductive habitat, and increasing Sea Lamprey and fishery control (Bronte et al. 2008). Many of these recommendations were implemented beginning in 1985 (e.g., Dexter et al. 2011). From the beginning of the stocking program, the U.S. Fish and Wildlife Service (USFWS), along with states that stocked Lake Trout, marked all fish with rotational fin clips to document the appearance and progress of unclipped fish that were presumed to be wild. In addition, to assess strain performance, movement, and other metrics, hatchery fish were marked and tagged with adipose fin clips and/or coded wire tags, beginning at selected locations in 1985 and then at all stocking locations beginning in 2010.

Although a few wild fish were found as early as the 1970s (e.g., Wagner 1980; Jude et al. 1981), it was not until 2010 that promising levels of sustained natural reproduction began to emerge (Hanson et al. 2013; Lake Michigan Lake Trout Working Group [LMLTWG] 2022). While it is too early to know if this reproductive success will become self-sustaining, we hypothesize that low total mortality rates for adult fish that advanced age structure and spawning stock densities contributed to reproductive success. Spawning success and fecundity are known to increase with age (O'Gorman et al. 1998; Bronte et al. 2008), and Lake Trout are relatively long lived, with reports of fish surviving to age 40 (e.g., Healey 1978; Schram and Fabrizio 1998; Campana et al. 2008; Hansen et al. 2021). Thus, low mortality of adults would be expected to increase the probability of successful natural reproduction.

Herein, we estimated mortality rates of mature, adult Lake Trout ages 9–28 in southern Lake Michigan and compared them to mortality rates reported elsewhere in the Great Lakes. We defined mature fish as those age 9 and older based on maturity schedules observed from biological surveys. Age 9 was the youngest age where nearly 100% of both males and females were mature (Ebener et al. 2020). Clearly, the initial abundance of these mature fish depends on both recruitment and mortality prior to age 9, but mortality occurring after age 9 defines the age structure and density of mature spawners. We used catch curves based on highly reliable ages from coded-wire-tagged Lake Trout to estimate mortality, and we compared estimates made from three surveys that use different gears and sampling designs.

Impact statement

Following a decades-long stocking program, promising levels of naturally produced Lake Trout are emerging. We conclude that low total mortality rates contributed to the emerging natural reproduction in southern Lake Michigan through increasing spawning stock density and age structure, and that previous estimates of the background natural mortality rate were too high. This is an important finding for encouraging Lake Trout restoration elsewhere in the Great Lakes.

METHODS

Age determination

Estimating mortality requires accurate age determination, and Lake Trout are difficult to age, especially older fish (Van Oosten and Eschmeyer 1956; Sharp and Bernard 1988; Burnham-Curtis and Bronte 1996; Schneeberger et al. 1998; Schram and Fabrizio 1998; Campana et al. 2008; Wellenkamp et al. 2015; Hansen et al. 2016). To minimize aging errors, we exclusively used ages derived from fish tagged with coded wire tags. All coded-wire-tagged fish can be referenced to a specific stocking location and year-class and, when combined with capture date, provide definitive origins and ages.

From 1985 through 2004, an average of 1.2 million Lake Trout per year were tagged, which was about 40% of the total number stocked in Lake Michigan (Bronte et al. 2012). From 2011 through 2019, all stocked fish received a coded wire tag, which averaged 3.1 million per year. Thousands of coded-wire-tagged Lake Trout survived and were recovered from agency fishery-dependent and -independent surveys, and have been used to evaluate movements and postrelease performance for different sizes at stocking, release locations, and genetic strains (e.g. Schmalz et al. 2002; Bronte et al. 2006, 2007; Adlerstein et al. 2007;

Kornis et al. 2019, 2020). In addition, He et al. (2022) used coded-wire-tagged Lake Trout to estimate total mortality rates of Lake Trout in Lake Huron.

Study area

Since 1985, hatchery-reared Lake Trout stocked in Lake Michigan have been released primarily on two historically important spawning reef complexes located in the north and south parts of the lake (Holey et al. 1995; Bronte et al. 2008; Dexter et al. 2011). Refuges where no fishing was permitted were established around most of these reefs (Figure 1). The aim of reef-refuge stocking was to develop large spawning aggregations of adult fish on the best reproductive habitat with protection from direct exploitation. This stocking strategy has been in effect for over 30 years. We limited our analysis to hatchery fish captured in central and southern waters of the lake, hereafter referred to as “southern Lake Michigan.” A recent evaluation of coded-wire-tagged Lake Trout movement in Lake Michigan demonstrated that there was minimal mixing of northern- and southern-stocked Lake Trout (Kornis et al. 2020). The reef complexes are approximately 380 km apart, and recaptures of Lake Trout are generally less than 100 km from where they were stocked (Schmalz et al. 2002; Bronte et al. 2007; Binder et al. 2017). In addition, hatchery-reared Lake Trout are released mostly as yearlings and display a tendency to return near their stocking location to spawn (Bronte et al. 2007; Binder et al. 2016). Thus, our conceptual model for the behavior of Lake Trout was that most fish dispersed from the reef where they were stocked, foraged within 100 km of the vicinity, generally returned to the vicinity of the reef to spawn, and then repeated the pattern annually. Binder et al. (2017) found similar behavior for hatchery-reared and wild Lake Trout in Lake Huron. This conceptual model leads to our assumption that the northern- and southern-stocked fish can be treated as homogeneous subpopulations for stock assessment purposes, including estimating mortality rates.

We focused our mortality estimates on the southern subpopulation because this is considered the epicenter of natural reproduction in Lake Michigan (e.g., Patterson et al. 2016; Landsman et al. 2017; LMLTWG 2022). There were both recreational and commercial fisheries outside of the southern refuge. The recreational fishery is thought to have the greatest impact on Lake Trout. Commercial fisheries, with very low fishing effort, targeted Lake Whitefish *Coregonus clupeaformis*, Bloater *Coregonus hoyi*, and Yellow Perch *Perca flavescens*, and Lake Trout were captured as nontarget bycatch. Caroffino and Lenart (2011) and Ebener et al. (2020) described these recreational and commercial fisheries in more detail. Mortality from Sea Lamprey is generally low in this area as well (Bronte et al. 2007; Kornis et al. 2019; Simpkins et al. 2021).

We defined the spatial extent of the southern subpopulation as a combination of statistical districts developed by Smith et al. (1961) and based on the movement matrix of recovered coded-wire-tagged Lake Trout presented by Kornis et al. (2020). This matrix showed that 98% of fish stocked in the southern refuge and 99% of fish stocked in Illinois (Julian's Reef) were recovered in statistical districts WM4, WM5, WM6, ILL, IND, MM6, MM7, and MM8 as defined by Smith et al. (1961) (Figure 1), and we used all coded wire tag recoveries in the region to estimate mortality. Only 5.3% of northern-stocked fish and 5.5% of southern-stocked fish were recovered in districts WM4 and MM6, but we included all recoveries in our analysis. We assumed that fish from WM4 and MM6 would have similar mortality rates regardless of origin and that including them in the analysis would cause minimal bias in our estimates.

Data sources and survey descriptions

We obtained numbers, locations, and years of Lake Trout tagged and stocked from the Great Lakes Fish Stocking Database managed by the USFWS (USFWS and Great Lakes Fishery Commission 2022). Multiple state, tribal, and federal agencies recovered fish with coded wire tags, then sent them to one of three laboratories for processing and reading: (1) the Michigan Department of Natural Resources, Charlevoix Fisheries Research Station, Charlevoix, Michigan; (2) the USFWS, Great Lakes Fish Tagging and Recovery Lab, Green Bay Fish and Wildlife Conservation Office, New Franken, Wisconsin; and (3) the U.S. Geological Survey (USGS), Great Lakes Science Center, Ann Arbor, Michigan. For recoveries, we obtained numbers collected by locations, years, ages, and survey type for coded-wire-tagged Lake Trout from these three laboratories.

We used coded-wire-tagged Lake Trout collected in three on-going surveys, and estimated total mortality rates from each survey separately. We hoped that making estimates from three surveys with different size- and age-selection characteristics would help identify the range of the potential mortality rates and provide insight into the robustness of our estimates. The three most important distinctions between the surveys with respect to estimating mortality were that they used gears with different size-selection characteristics, were deployed in different spatial configurations, and collected fish at different times of the year. The first two surveys were standardized, fishery-independent gill-net surveys, and the third was a fishery-dependent survey of catches from the recreational fishery. The gill-net surveys were cooperative federal, state, and tribal programs organized by the Lake Michigan Technical Committee that

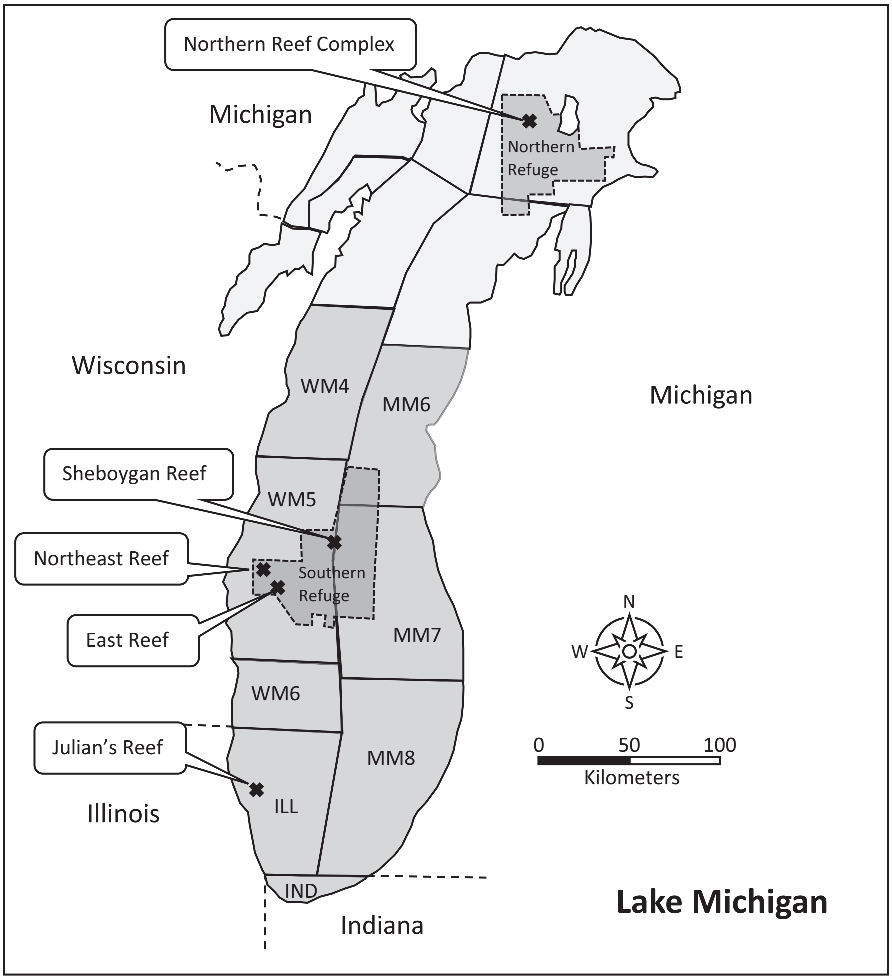

FIGURE 1 Map of Lake Michigan with locations of reefs where most coded-wire-tagged Lake Trout were stocked. The shaded statistical districts represent the total range of the southern subpopulation. These fish were stocked primarily at Julian's, East, Northeast, and Sheboygan reefs. The northern reef complex is the primary stocking site for the separate northern subpopulation. The refuges indicated in darker shading are closed to fishing.

serves the Lake Michigan Committee of the Great Lakes Fishery Commission. The sport-fishery-dependent survey was carried out by the USFWS as part of a large-scale tagging and tag and data recovery program (Bronte et al. 2012).

The first gill-net survey (hereafter, "spring survey") was a lakewide assessment, which annually sampled sites at randomized transects centered around ports and distributed throughout Lake Michigan (Schneeberger et al. 1998). The primary objective was to monitor the relative abundance, age structure, and origin of Lake Trout and to collect data on several other predator species. Sampling occurred from April to June before the water column was thermally stratified. These months were targeted because survey designers assumed that Lake Trout populations would be demersal and well mixed with respect to size and age during this time. Lake Trout with coded wire tags were measured for total length (among other metrics), and snouts were collected for tag extraction and reading. Fish were captured with bottom-set, graded-mesh multifilament nylon gill nets with eight panels of 64-, 76-, 89-, 102-, 114-, 127-, 140-, and 152-mm stretch meshes, arranged from smallest to largest. We used all coded-wire-tagged Lake Trout recoveries from the spring survey from 1998 to 2019. All handling of fish in the field was carried out in accordance with *Guidelines for the Use of Fishes in Research* by the American Fisheries Society (Use of Fishes in Research Committee 2014).

The second gill-net survey (hereafter, "spawning survey") was an assessment of Lake Trout spawning populations that targeted spawning aggregations on nine historically important reefs (LMLTWG 2022) in October and November. The primary objective was to monitor Lake Trout rehabilitation metrics, including the demographics and relative abundance of spawners, and determine their origin (hatchery-reared versus wild) (Bronte et al. 2008; Dexter et al. 2011). As in the spring survey, total lengths (among other metrics) of Lake Trout and coded wire tags were collected for aging. This survey targeted spawners, and thus nets were standardized with large mesh sizes including four panels (114-, 127-, 140-, and 152-mm stretch mesh). We used all coded wire tag recoveries from the spawning survey collected from 1998 to 2019. Finally, it should be noted also that almost all net sets for both gill-net surveys were for one night, which limited the effects of net saturation. Also, both gill-net surveys deployed some sampling effort in the refuge.

The fishery-dependent survey of recreational catches (hereafter, "sport fishery survey") was the annual field recovery effort that the USFWS began in 2012 as part of a coordinated mass-marking program (Bronte et al. 2012). This program focused on recovering biological data on hatchery fish with coded wire tags and their wild counterparts caught in the recreational fishery at over 40 locations around Lake Michigan. Sampling occurred over 7 months during April–October. Recreational fishing was more evenly distributed over space than the two gill-net surveys because thousands of boats and anglers participated and entered from hundreds of ports around the lake, although most fishing occurred within 20 km of shore and fishing was not permitted in the refuge. We used all coded wire tag recoveries from the sport fishery survey collected from 2012 to 2019.

Annual sampling effort was used to convert catches into catch per unit of effort (CPUE). For the two fishery-independent netting surveys, sampling effort was recorded as kilometer of nets set per night. Sampling effort employed by the sport fishery survey was more difficult to quantify as it depended in part on recreational fishing effort, which directly sampled the Lake Trout population, and in part on the sampling effort of the USFWS technicians who sampled the catches (Adlerstein et al. 2007). Because fishing effort of the recreational fishery was relatively constant during 2012–2019 (Ebener et al. 2020), we assumed that the annual sampling effort for the sport survey was best reflected by the number of days sampled by the USFWS technicians each year.

Mortality estimators

We estimated total instantaneous mortality rates (Z) for Lake Trout by applying catch curves to the average relative abundances by age for tagged year-classes in the study period. We arranged coded wire tag recoveries by year-class, then calculated the relative abundance by age ($n_{i,j}$) for each year-class i and age j as follows:

$$n_{i,j} = \frac{\text{CPUE}_{i,j}}{n_s}, \tag{1}$$

where $\text{CPUE}_{i,j}$ was catch per unit of effort and n_s was the initial number of tagged, yearling-equivalent fish stocked for year-class i. Most fish were stocked as yearlings, but some were stocked as fall fingerlings. Yearling equivalents included these fingerlings by assuming a 0.40 survival rate from fingerling to yearling as in Sitar et al. (1999) and Caroffino and Lenart (2011). For our analysis, we scaled the number tagged (n_s) to per billion tagged. Thus, the relative abundances by age ($n_{i,j}$) were catch per unit effort per billion tagged. This scaling allowed the smallest values of $n_{i,j}$ to be rounded off to integers across all surveys and years.

For the calculation of $\text{CPUE}_{i,j}$, it is important to notice that for a given year-class i, the fish in each age-group j were collected in different survey sampling years. Thus,

$$\text{CPUE}_{i,j} = \frac{C_{i,j}}{E_y}, \tag{2}$$

where $C_{i,j}$ is the catch of age-j fish of year-class i that were collected in sample year y, and E_y is the survey effort in year $y = i + j$. For example, age-10 fish of the 2000 year-class were collected in the 2010 sampling year y, which is $2000 + 10$ $(i + j)$.

We calculated average relative abundance (RN_j) across age-groups for the sampling period as follows:

$$RN_j = \frac{\sum_{i=1}^{Y_j} n_{i,j}}{Y_j}, \tag{3}$$

where Y_j was the number of years that age j was sampled, which would be the same as the number of year-classes sampled for age-group j. Because we scaled the relative abundances by age ($n_{i,j}$) in equation (1) to per billion tagged, our values for RN_j were average relative abundances per billion tagged. We included zero catches ($n_{i,j} = 0$) in these averages when sampling occurred and tagged fish of the age-group were potentially present in the population at large.

We used the Chapman–Robson method (Chapman and Robson 1960) to estimate the total instantaneous mortality rate (Z) and its variance (VAR[Z]) and corrected for overdispersion of variances as recommended by Smith et al. (2012). These authors evaluated several different catch-curve estimators by applying each to simulated data with known values of Z and concluded that the Chapman–Robson approach with overdispersion correction was the best estimator and should be used more routinely. We used the same equation for the estimator as Smith et al. (2012):

$$\hat{Z} = \log_e\left(\frac{1 + \overline{T} - T_c - \frac{1}{N}}{\overline{T} - T_c}\right) - \frac{(N-1)(N-2)}{N\left[N\left(\overline{T} - T_c\right) + 1\right]\left[N + N\left(\overline{T} - T_c\right) - 1\right]}, \tag{4}$$

where $\overline{T}$ is the mean age of fish in the sample that are greater than or equal to the age of full recruitment (T_c), and N is the sample size of fish greater than or equal to age T_c. The equation for the variance is as follows:

$$\mathrm{VAR}\left(\hat{Z}\right) = \left[\frac{\left(1-e^{-\hat{Z}}\right)^2}{Ne^{-\hat{Z}}}\right] \times \overline{C}, \tag{5}$$

where $\overline{C}$, the variance inflation factor for correcting overdispersion, is the usual chi-square goodness-of-fit statistic divided by the degrees of freedom (Smith et al. 2012) and is calculated as follows:

$$\overline{C} = \frac{\sum_{j=T_C}^{T_M} \frac{\left(RN_j - \widehat{RN}_j\right)^2}{\widehat{RN}_j}}{\left(T_M - T_C - 1\right)}, \tag{6}$$

where T_M is the maximum age considered, so $T_M - T_C - 1$ (the degrees of freedom) is the number of age-classes included in the estimate minus 1, and $\widehat{RN}_{j'}$ is the predicted value of relative abundance for given age j' and is calculated as follows:

$$\widehat{RN}_{j'} = \frac{e^{-\hat{Z}\times j'}}{\sum_{j=T_C}^{T_M} e^{-\hat{Z}\times j}} \times \sum_{j=T_C}^{T_M} RN_j. \tag{7}$$

Multiplying by the second term $\sum_{j=T_C}^{T_M} RN_j$ ensures that observed and predicted relative abundances sum to the same totals.

Typically, Chapman–Robson estimates use the total number of fish sampled as N in equations (3) and (4), but in our case $N = \sum_{j=T_C}^{T_M} RN_j$, and RN_j is affected by our scaling per billion tagged. The Chapman–Robson mortality estimator includes a bias adjustment term dependent on scaling of N but, given the large number of fish sampled, this would be near zero in our case for any reasonable scaling. The variance of the Chapman–Robson mortality estimator, without an overdispersion variance inflation factor, depends substantially on the nominal sample size. However, the variance estimated using the overdispersion adjustment is completely independent of the scaling of N (i.e., if relative abundances are rescaled such that N increases, the decrease in the unadjusted variance is exactly compensated for by an increase in the variance inflation factor). Thus, our estimates are insensitive to this scaling, and more generally, the Chapman–Robson estimator with overdispersion is more widely applicable than is sometimes thought.

We included ages 9–28 in catch curves for each survey to represent the mature spawning population and to facilitate comparisons across surveys. We wanted to compare like ages for each survey, and preliminary analyses showed that fish were initially recruited to the different survey catches at different ages due to gear selectivity. We assumed that fish age 9 and older were fully vulnerable to all three surveys. We truncated at age 28 for the spawning and sport fishery surveys because this was the oldest age-group recovered in the spring survey, and auxiliary analyses using the full complement of ages in the spawning and sport fishery surveys showed that truncating made little difference in their results. Our methods also required the usual assumptions for catch-curve analysis, that recruitment was constant over time and that mortality and vulnerability to surveys were constant over time and across ages. In addition, because we relied on coded wire tags for ages, we assumed that poststocking tag loss was negligible.

RESULTS

Sampling effort (E_y) and tag recoveries for the southern subpopulation were reasonably consistent by year within each of the three survey types (Table 1). The netting effort for the spring survey ranged from 5.9 to 42.3 km of nets set per night per year from 1998 through 2019 and caught from 50 to 630 fish with readable coded wire tag ages per year. Readable here means that ages could be deciphered on the tag and were reported in the database. The netting effort for the spawning survey ranged from 2.4 to 9.4 km of nets set per night per year from 1998 through 2019 and caught from 55 to 598 fish with readable coded wire tag ages per year. The sampling effort for the sport fishery survey ranged from 133 to 355 technician days per year from 2012 through 2019 and sampled in sport catches from 82 to 1964 fish with readable coded wire tag ages per year.

Organizing the catches by age-group showed that large numbers of older fish (age 20+) were collected, and that ages used in our analysis (9–28) were fully vulnerable to all three surveys (Table 2). The spring survey collected 4960 Lake Trout with readable coded wire tags ranging from ages 2 to 28, of which 40 were age 20 or older. The spawning survey collected 8450 from ages 2 to 35, of which 224 were age 20 or older. The sport fishery survey collected 6424 from ages 2 to 34, of which 194 were age 20 or older. Ages of full vulnerability, represented as the peak ages plus one of unadjusted numbers caught, were 7, 9, and 6 for the spring, spawning, and sport fishery surveys, respectively (Table 2). Peak ages plus one were also the same for the average relative abundances by age (RN_j). Thus, fish age 9 and older were fully vulnerable to all surveys based on the peak age plus one standard.

A total of 20 Lake Trout year-classes from 1984 through 2010 were tagged with coded wire tags and could be included in the analysis. Only the 1986–1988 and 2005–2008 year-classes were not tagged during the period (Tables A.1–A.3 in the Appendix). Numbers tagged per year-class ranged from 62,800 to 1,078,400 yearling equivalents. The estimated relative abundance by year-class

TABLE 1 Sampling effort (E_y) and total number of Lake Trout sampled with readable coded wire tags per year for each survey type.

	Spring survey		Spawning survey		Sport fishery survey	
Sample year	Effort (km of nets per night)	Number sampled	Effort (km of nets per night)	Number sampled	Effort (number of days sampled)	Number sampled
1998	5.9	82	7.8	522		
1999	7.8	113	5.6	598		
2000	19.0	266	6.3	579		
2001	19.0	156	8.2	421		
2002	34.7	262	6.1	522		
2003	29.1	147	6.8	473		
2004	34.4	245	8.0	443		
2005	36.0	360	5.3	178		
2006	37.7	287	7.3	458		
2007	38.6	257	9.4	521		
2008	36.7	236	6.3	423		
2009	26.8	240	5.4	550		
2010	38.3	169	8.5	566		
2011	27.8	112	4.9	173		
2012	33.7	131	5.5	301	133	82
2013	26.3	73	5.3	55	314	128
2014	25.4	50	6.6	268	333	248
2015	22.9	163	6.3	313	355	934
2016	38.5	462	5.8	477	334	1964
2017	42.3	462	3.9	182	222	915
2018	25.3	57	2.4	116	271	1488
2019	40.7	630	5.1	311	170	665
Average	29.4	225	6.2	384	267	803

and age ($n_{i,j}$), numbers of year-classes sampled by age (Y_j), and average relative abundance by age (RN_j) for all year-classes and surveys used in the analysis are presented in Tables A.1–A.3.

Estimates of total instantaneous mortality rate $Z \pm$SE for Lake Trout age 9 and older were 0.297 ± 0.019, 0.239 ± 0.009, and 0.205 ± 0.007 for the spring, spawning, and sport fishery surveys, respectively (Figure 2). These estimates equal total annual mortality rates of $26 \pm 2\%$, $21 \pm 1\%$, and $18 \pm 1\%$, respectively.

DISCUSSION

We think that the relatively large number of age-groups in the catch curves (20) and the high accuracy of coded wire tag ages reduced biases in our analysis and made the methods more robust. We propose that the mean $\pm$SE of the three survey estimates would be a reasonable estimate of $Z \pm$SE for southern Lake Michigan Lake Trout and argue that this is supported by the relative consistency of the individual estimates from surveys with different size- and age-selectivity characteristics. Treating each survey estimate as an independent observation is sensible in this case and gives 0.247 ± 0.027, which equals $22 \pm 3\%$ total annual mortality. This estimate is in the lower part of the range of mortality estimates reported for the species (Hansen et al. 2021).

Potential violations of assumptions

Our main assumptions for the catch curve analysis were that recruitment was constant over time, mortality and vulnerability to surveys were constant over time and across ages, and tag loss after stocking was negligible. We also assumed that the designs of each survey provided samples that were representative of the age structure of Lake Trout ages 9–28. We know that all these assumptions were likely violated to some degree, so we consider the potential consequences here. Moderate variability in these factors across years and ages were

TABLE 2 Total number by age of Lake Trout sampled with readable tags by each survey type from 1998 to 2019.

Age	Spring survey	Spawning survey	Sport fishery survey
2	22	4	18
3	168	34	105
4	430	254	781
5	1081	533	1973
6	1215	782	1511
7	813	977	586
8	432	1193	348
9	249	1056	127
10	147	767	56
11	87	560	78
12	72	518	78
13	51	419	111
14	60	345	89
15	33	239	108
16	19	187	75
17	11	152	45
18	18	98	45
19	9	83	36
20	11	67	48
21	3	44	42
22	9	34	28
23	10	35	24
24	2	28	28
25	5	16	24
26	1	8	17
27	1	4	14
28	1	5	9
29	0	3	5
30	0	3	6
31	0	1	1
32	0	0	5
33	0	0	2
34	0	0	1
35	0	1	0
Total	4960	8450	6424

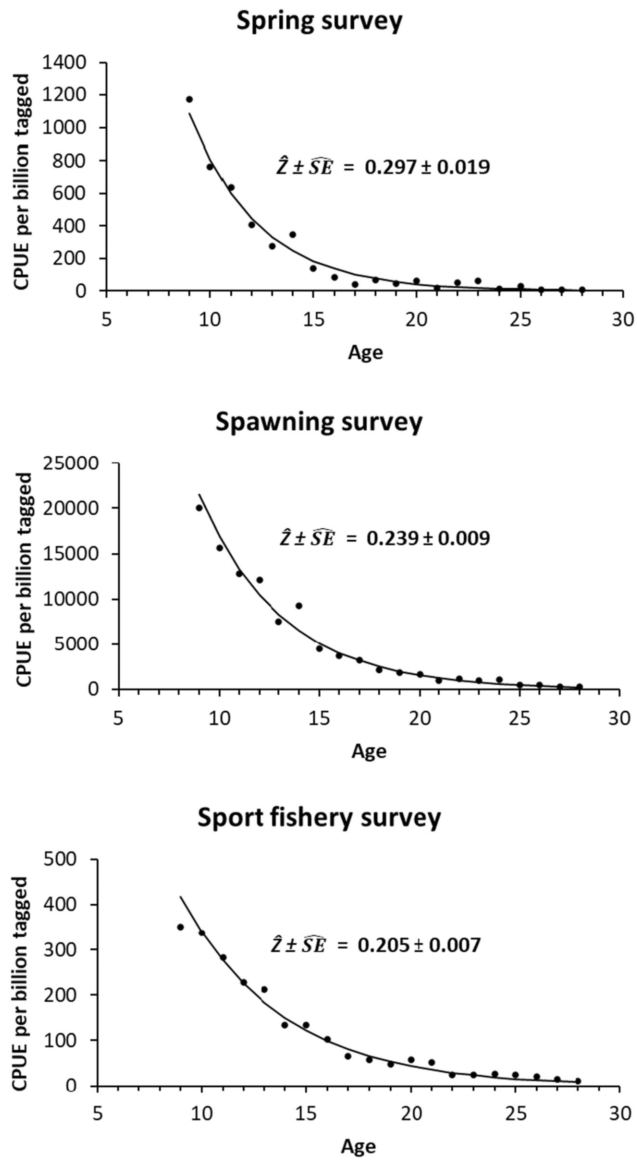

FIGURE 2 Chapman–Robson estimates of $Z \pm$SE from each survey along with plots of observed values (RN_j) from Tables A.1–A.3 as markers versus predicted values $\left(\widehat{RN}_j\right)$ from equation (7) as lines.

expected and would not introduce significant biases in the estimates. However, trends over years or ages could introduce biases, so we focused on identifying trends and considering their potential effects. We did not attempt to quantify the suspected biases but only judged if they would be expected to cause overestimates or underestimates of mortality in our catch curves. Overall, our assessment was that violations in assumptions were probably modest in scale given the consistency of estimates from the three different survey types. If biases did occur, there were more indications that our methods resulted in a small overestimate of total mortality rather than an underestimate.

Constant recruitment

Trends in recruitment over time may have caused modest biases in our estimates. We adjusted for variation in numbers tagged in equation (1), but this would not account for changes in annual mortality from age 1 to age 9.

Age 9 was the starting age in our catch curves, so trends in relative abundances at age 9 across year-classes could represent trends in recruitment to the survey. We did not estimate mortality from age 1 to age 9, but there was a moderate increasing trend in relative abundances of age-9 fish in the spring and spawning survey data, which might have been from decreasing mortality from age 1 to age 9 over time. The relative abundance of age-9 fish increased from 495 for the 1998 year-class to 3631 for the 2004 year-class in the spring survey (Table A.1) and from 10,525 for the 1998 year-class to 35,781 for the 2004 year-class in the spawning survey (Table A.2). Data from the sport fishery was not available prior to the 2003 year-class and thus could not be examined. In general, this type of increasing recruitment to the survey gears would cause younger fish to be overrepresented in a catch curve and would cause an overestimate of the total mortality rate.

Constant mortality

Trends in mortality over time may have caused modest biases in our estimates. Evidence indicated a moderate trend over sampling years but no consequential trend across age-groups. Mortality from fishing and Sea Lamprey were the major sources of Lake Trout mortality during the period. Stock assessment models applied to Lake Trout in the region have shown that mortality from these sources generally decreased over time during our study but were relatively constant across ages 9 to 28 (Caroffino and Lenart 2011; Ebener et al. 2020). In general, a decreasing trend in mortality would cause younger fish to be overrepresented in a catch curve and would cause an overestimate of mortality.

Constant vulnerability

Trends in survey selectivity and differences in behavior across ages may have caused modest biases in our estimates. Survey selectivity is a combination of selectivity caused by the physical characteristics and mode of capture of the gears, the behaviors of different size- or age-groups of fish, and the size preferences for harvest of fishers. We tried to minimize the effects of gear selectivity by applying the catch curves to ages we thought were fully vulnerable. Nonetheless, it is unlikely that these potential biases were fully mitigated. Size selectivity of gill nets has been well studied and it is known to affect vulnerability by age. For example, size and age selectivity of Lake Trout was estimated by Hansen et al. (1997) in gill nets with panels using mesh sizes that were a subset of the mesh sizes used in the spring and spawning survey nets in our study. They found a dome-shaped selectivity curve across ages 7–11, which were assumed to be fully vulnerable. They determined that catch curves applied to these ages and based on single mesh sizes from 102- to 152-mm stretch measure would overestimate mortality by about 20% for Lake Superior Lake Trout. In contrast to the gill-net surveys, we suspect that vulnerability might have increased with age in the sport fishery survey. Anglers are known to sort out smaller fish from their catches in favor of larger ones. Hence all sport-caught coded-wire-tagged Lake Trout were what was landed as opposed to what was caught, which means that the sport survey selectivity was affected by the behavior of the fishers and the true vulnerability to the sport fishing gear was unknown. Also, about 56% of the sport fishery data were collected from fishing tournaments, which could have exacerbated this bias since tournament fishers would be more motivated to seek and retain larger fish.

We think it is unlikely that major trends in vulnerability to sampling gears occurred over time during our study period. For example, changes in growth rates over time would be one of the most important factors causing changes in vulnerability by age over time. But growth of Lake Trout expressed as length or weight at age did not exhibit any temporal trends in Lake Michigan during 1986–2019 (Ebener et al. 2020), leading us to believe that age-specific vulnerability to the survey gears remained constant over time.

Tag loss

Coded wire tag loss was low for the adult fish in our study and likely had little effect on our estimates. Most tag loss for coded wire tags occurs at young ages shortly after tagging and not at older ages, where it would have a bigger effect on catch-curve analyses. Initial tag loss observed in the hatcheries among four closely studied tag lots of different genetic strains was between 0.0% and 5.5% and stabilized at 2.8–5.7% 100–150 days afer tagging (Kornis et al. 2016). More broadly, initial tag loss exceeded 5.5% in 14.2% of tag lots tagged by automated methods ($n = 197$, 2010 and later year-classes) and exceeded 5.5% in 28.1% of tag lots tagged using manual methods ($n = 1080$, 2009 and earlier year-classes; Kornis et al. 2016). Overall, tag loss was 6.5% in adipose-fin-clipped Lake Trout returning to the sport fishery from 2012 to 2021, accounting for fish from the 1984–2017 year-classes (Matthew S. Kornis, unpublished data). If significant tag loss had occurred between ages 9 and 28, it would have caused mortality to be overestimated in our catch curves. However, given that tag lots stabilize within 1 year postrelease, this scenario is very unlikely.

Survey designs

Lake Trout are known to exhibit spatial and temporal differences in behavior that are related to size, age, and maturity. As a result, differences in survey designs have the potential to affect catch data and interpretation. However, estimates of mortality were strikingly similar from each survey for Lake Trout ages 9–28 in southern Lake Michigan. Thus, we conclude that bias attributable to differences in survey design was minimal with respect to estimating the mortality rate of fish in this age range.

Total mortality rate of adults and reproductive success

Success of natural reproduction is generally negatively correlated with total mortality rate of adult fish in the Great Lakes and elsewhere. Our estimate of 22 ± 3% total annual mortality was in the same range as estimates in other populations in the Great Lakes, where natural reproduction is well established and likely contributed to the recent reproductive success observed in southern Lake Michigan. For example, in reproducing populations in western Lake Huron and southern Lake Superior, the total mortality rates were respectively 24% during 2001–2006 (He et al. 2022) and 24–28% during 1985–2018 (Caroffino and Seider 2020). In contrast, natural reproduction was limited in populations in northern Lake Michigan, where total mortality was higher at 35–54% (Caroffino and Seider 2020; LMLTWG 2022). All these reproducing populations have total mortality rates that are well below the 40% management benchmark suggested for restoring Lake Trout populations by Bronte et al. (2008) and the total mortality in the one population with little reproduction is above the benchmark. Thus, the benchmark performed well for these cases. However, there are Lake Trout populations in the Great Lakes with low total mortality but little natural reproduction. For example, Brenden et al. (2011) estimated that total annual mortality was only 26% in Lake Ontario, and yet no significant natural reproduction has been observed there. This indicates that other factors can inhibit reproduction even when mortality of adults is low. Nonetheless, these comparisons support the idea that maintaining a low rate of total annual mortality of adult fish is important for restoring Lake Trout populations in the Great Lakes.

Total mortality rate of adults and natural mortality rate

Our results also suggest that previous estimates of the instantaneous natural mortality rate M, for Lake Trout in Lake Michigan are probably too high. While M is an important input parameter for stock assessment models, estimating M is always challenging. Numerous methods have been developed for this purpose, including estimators based on growth and temperature (e.g., Pauly 1980) or maximum age (e.g., Hoenig 1983) and assessments that estimate Z in lightly exploited stocks (e.g., Kenchington 2014; Maceina and Sammons 2016). The latter rely on the idea that M in the absence of fishing should equal Z. Stock assessment analysts have been estimating M with the Pauly estimator for Lake Trout in Lake Michigan. These estimates have ranged from 0.210 to 0.240 (Caroffino and Lenart 2011; Caroffino and Seider 2020), and these estimates appear incompatible with our estimate of 0.247 ± 0.027 for $Z \pm \mathrm{SE}$.

Even though exploitation is relatively low in our study area, when the estimated exploitation is combined with the other known mortality factor in the area, Sea Lamprey predation, it seems unlikely that M could be even as high as 0.200. Lake Trout stock assessment models currently express total mortality as $Z = M_B + M_L + F$, where M_B is the background natural mortality rate, M_L is the Sea Lamprey-induced natural mortality rate, and F is the fishing mortality rate (Caroffino and Lenart 2011; Truesdell and Bence 2016; Ebener et al. 2020). The term M_B is applied to fish ages 2 and older and is considered equivalent to the M estimated by the Pauly and other estimators. Both M_L and M_B are inputs to the models and are estimated prior to model runs by independent methods, whereas F is estimated within the models. The term M_L is estimated based on Sea Lamprey wounding rates on fish caught in biological surveys (King and Edsall 1979; Rutter and Bence 2003). For stocks in Lake Michigan, estimates of M_L have averaged 0.093 for fish age 9 and older from 1998 to 2019 (Ebener et al. 2020). The term M_B has been estimated using the Pauly estimator (Pauly 1980) as mentioned earlier. The sum of M_L and M_B for these estimates would be 0.303 to 0.333, which is higher than the estimates of Z from any of the surveys we used. We suggest that M_B is the most uncertain and likely incorrect of the component estimates, at least for age-9-and-older fish, and that the applicability of the Pauly estimator to Lake Trout is questionable.

Several reviews of natural mortality estimation techniques have suggested that other estimators perform better than the Pauly estimator for species with life history characteristics like those of Lake Trout. Kenchington (2014) evaluated 29 estimators for 13 species and Maceina and Sammons (2016) evaluated 9 estimators for 5 species using well-founded natural mortality estimates from unexploited stocks. Both studies included the Pauly estimator and agreed that maximum age estimators (e.g., Hoenig 1983; Quinn and Deriso 1999; Kenchington 2014)

TABLE 3 Estimates of instantaneous natural mortality rates (M_B) for Lake Trout from a variety of maximum-age-based and growth-based estimators. Maximum ages used for estimators were as follows: 35 from Lake Michigan (this study), 42 from Lake Superior (Schram and Fabrizio 1998), 50 from Canadian Arctic lakes (Campana et al. 2008), and 62 from Kaminuriak Lake (Healey 1978). Growth and temperature parameters for growth-based estimators were for southern Lake Michigan (Ebener et al. 2020).

	Maximum age for estimate			
Estimator reference	**35**	**42**	**50**	**62**
Estimates of M_B based on maximum age				
Quinn and Deriso (1999)	0.132	0.110	0.092	0.074
Hoenig (1983)	0.119	0.099	0.083	0.067
Kenchington (2014)	0.125	0.099	0.101	0.058
Estimates of M_B based on growth				
Pauly (1980)	0.271			
Lorenzen (1996)	0.241			
Jensen (1996)	0.334			

performed well for species with rapid early growth and great longevity, such as Lake Trout, and that growth estimators (e.g., Pauly 1980; Jensen 1996 and Lorenzen 1996) did not perform well for species with these characteristics. We applied several maximum-age-based and growth-based estimators to Lake Trout for comparison (Table 3). Estimates of M_B from maximum-age-based estimators (0.132–0.058) were compatible with those of Z in our present study (0.297–0.205), whereas the range of estimates of M_B from growth-based estimators (0.241–0.334) was higher. Thus, we recommend using maximum-age-based estimators as a standard protocol in the future to derive M_B for Lake Trout. Given our estimate of Z and the evidence that the maximum age of Lake Trout in the Great Lakes is at least 42 (Schram and Fabrizio 1998), it seems likely that M_B for age-9-and-older Lake Trout in Lake Michigan is about 0.100 (Table 3).

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data used in this study were collected by the fisheries management agencies responsible for Lake Michigan and shared through their participation and collaboration through the Great Lakes Fishery Commission, Lake Michigan Committee. A data release for the data generated from the USGS-funded portion of this study is available at https://doi.org/10.5066/F75M63X0.

ETHICS STATEMENT

All handling of fish was carried out in accordance with the *Guidelines for the Use of Fishes in Research* by the American Fisheries Society (Use of Fishes in Research Committee 2014).

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APPENDIX

TABLE A.1 Number of Lake Trout initially tagged by year-class (i) and relative abundance ($n_{i,j}$) at age (j) for those captured in the spring survey. The number of year-classes sampled by age for the period is presented as Y_j. The average relative abundance by age (RN_j) was used in catch curves to estimate the total mortality rate. Shaded cells were year-class–age combinations in years not sampled or not tagged. Years sampled (y) were 1998–2019, and the $n_{i,j}$ for a given sampling year (y) follow a diagonal across year-classes. For example, the $n_{i,j}$ for fish collected in 2010 are underlined.

Year-class (i)	Number tagged	Relative abundance ($n_{i,j}$) by age (j)																			
		9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1984	775,000						441	0	0	0	111	0	37	0	0	67	0	0	34	0	0
1985	575,100					0	223	0	183	0	0	0	0	0	45	47	0	0	0	0	0
1986–1988																					
1989	699,500	977	183	225	75	165	98	0	40	0	111	39	53	0	0	42	0	0	0	0	0
1990	747,100	515	633	70	0	46	78	74	36	35	0	200	0	0	80	0	0	117	0	0	0
1991	765,400	1099	550	301	314	114	254	382	34	142	244	0	94	39	50	0	0	68	0	52	32
1992	495,000	425	639	0	411	112	590	157	220	75	0	0	120	77	79	264	105	0	0	0	
1993	316,900	636	0	458	88	84	82	0	0	0	0	0	0	0	138	0	0	0	0		
1994	536,900	575	379	259	445	434	305	139	97	0	111	71	0	0	145	44	0	46			
1995	362,900	640	459	439	143	75	308	0	99	0	0	108	241	72	0	0	0				
1996	367,500	680	1012	211	371	304	71	196	81	103	0	119	0	0	0	134					
1997	358,500	370	361	76	104	219	201	497	106	110	243	0	132	0	0						
1998	365,700	495	671	510	500	295	406	312	0	0	142	0	108	0							
1999	350,000	1557	639	597	411	170	217	0	249	74	67	113	0								
2000	364,200	1331	717	593	326	731	108	240	0	65	0	0									
2001	363,900	1579	1087	979	627	108	480	0	65	0	0										
2002	366,000	1769	2110	935	215	358	355	65	108	67											
2003	367,200	3722	2279	1071	1664	354	129	0	67												
2004	62,800	3631	1252	3473	827	1128	1891	391													
2005–2008																					
2009	92,000	0	0																		
2010	1,078,400	1070																			
Y_j		18	17	16	16	17	18	18	17	16	15	14	13	12	11	10	9	8	7	6	5
RN_j		1171	763	637	407	276	346	136	81	42	69	46	60	16	49	60	12	29	5	9	6

TABLE A.2 Number of Lake Trout initially tagged by year-class (i) and relative abundance (ni,j) at age (j) for those captured in the spawning survey. The number of year-classes sampled by age for the period is presented as Yj. The average relative abundance by age (RNj) was used in catch curves to estimate the total mortality rate. Shaded cells were year-class–age combinations in years not sampled or not tagged. Years sampled (y) were 1998–2019, and the ni,j for a given sampling year (y) follow a diagonal across year-classes. For example, the ni,j for fish collected in 2010 are underlined.

Year-class (i)	Number tagged	Relative abundance ($n_{i,j}$) by age (j): 9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1984	775,000						14,057	7834	1428	1564	1274	2086	2092	0	1059	0	1628	722	151	265	235
1985	575,100					5348	2173	2748	1054	0	767	0	0	0	558	823	0	408	0	0	0
1986–1988																					
1989	699,500	16,489	19,909	12,201	6413	7293	5462	3565	1623	3521	459	1353	1332	2179	586	1824	0	434	451	0	0
1990	747,100	33,219	22,002	9087	14,978	11,409	7844	2532	4579	2147	1478	3493	942	823	976	752	609	211	231	0	549
1991	765,400	41,095	19,641	26,230	24,193	15,477	5933	7152	3632	3503	5358	3065	1072	4286	490	2578	824	1354	679	536	765
1992	495,000	18,613	30,250	13,062	13,098	5351	6911	3456	9559	13,180	4027	1657	5523	0	1840	1912	2791	525	1657	788	
1993	316,900	31,153	9737	9442	1791	864	1012	1991	4117	1480	647	1725	0	0	1493	0	0	0	0		
1994	536,900	12,591	9754	5991	7901	7766	2350	7291	5242	3819	4074	0	3110	1175	965	0	3055	363			
1995	362,900	12,369	7299	6788	9722	11,735	11,814	4524	2825	6529	1549	4183	1738	2380	716	1130	538				
1996	367,500	10,297	5958	11,055	6009	11,667	6382	3906	4960	1020	2478	3004	1880	0	4464	1062					
1997	358,500	11,833	13,122	4840	12,999	4907	4004	2034	523	2540	3519	1927	725	0	0						
1998	365,700	10,525	9920	17,331	3848	5046	7975	1537	2905	1725	2361	0	1121	534							
1999	350,000	22,083	28,761	14,744	9374	10,936	535	6939	6759	6415	742	2343	1672								
2000	364,200	38,384	18,675	6756	7506	514	5417	7794	4268	1426	3378	1071									
2001	363,900	17,079	12,959	12,521	3089	6256	3900	5695	1427	1127	536										
2002	366,000	11,765	23,405	2559	13,270	8618	8494	1419	6723	1066											
2003	367,200	26,311	8165	17,363	13,316	11,290	1415	7819	1063												
2004	62,800	35,781	26,573	35,141	46,729	4134	71,797	3105													
2005–2008																					
2009	92,000	0	0																		
2010	1,078,400	10,856																			
Y_j		18	17	16	16	17	18	18	17	16	15	14	13	12	11	10	9	8	7	6	5
RN_j		20,025	15,655	12,819	12,140	7565	9304	4519	3687	3191	2176	1851	1631	948	1195	1008	1050	502	453	265	310

TABLE A.3 Number of Lake Trout initially tagged by year-class (i) and relative abundances (ni,j) at age (j) for those captured in the sport fishery survey. The number of year-classes sampled by age for the period is presented as Yj. The average relative abundance by age (RNj) was used in catch curves to estimate the total mortality rate. Shaded cells were year-class–age combinations in years not sampled or not tagged. Years sampled (y) were 1998–2019, and the ni,j for a given sampling year (y) follow a diagonal across year-classes. For example, ni,j for fish collected in 2012 are underlined.

Year-class (i)	Number tagged	Relative abundance ($n_{i,j}$) by age (j)																			
		9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1984	775,000																				<u>0</u>
1985	575,100																			<u>13</u>	6
1986–1988																					
1989	699,500															<u>21</u>	14	13	0	13	45
1990	747,100														<u>0</u>	9	8	4	16	18	0
1991	765,400													<u>69</u>	21	12	26	43	29	34	8
1992	495,000												<u>46</u>	6	6	11	30	73	60	0	
1993	316,900											<u>0</u>	0	0	9	0	0	0	0		
1994	536,900										<u>42</u>	18	39	31	72	76	55	11			
1995	362,900									<u>83</u>	44	25	85	83	50	41	49				
1996	367,500								<u>82</u>	17	25	31	81	98	40	32					
1997	358,500							<u>63</u>	18	42	39	33	88	51	0						
1998	365,700						<u>82</u>	44	33	39	65	123	71	80							
1999	350,000					<u>107</u>	36	146	105	68	116	84	50								
2000	364,200				<u>248</u>	79	124	124	107	148	101	65									
2001	363,900			<u>124</u>	140	149	124	156	198	30	32										
2002	366,000		<u>185</u>	226	164	208	254	283	141	96											
2003	367,200	<u>369</u>	243	286	161	375	209	251	144												
2004	62,800	456	860	493	429	358	117	0													
2005–2008																					
2009	92,000	40	64																		
2010	1,078,400	540																			
Y_j		4	4	4	5	6	7	8	8	8	8	8	8	8	8	8	7	6	5	5	5
RN_j		351	338	282	228	213	135	133	103	66	58	47	58	52	25	25	26	24	21	16	12