Concept Paper:

Using Genetic Information to Improve Estimates of Lake Trout Spawning Biomass in Southern Lake Michigan

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Management efforts to restore natural reproduction by Lake Trout in Lake Michigan have been occurring since the 1960s and were largely unsuccessful (Holey et al. 1995; Madenjian and DeSorcie 1999; Hansen 1999) until the early 2000s (Page et al. 2003; Hanson et al. 2013; Larson et al. 2021). Since roughly 2004, measurable levels of wild Lake Trout recruits have been captured throughout Lake Michigan by commercial, sport, and survey fisheries and abundance of these fish has increased substantially in southern Lake Michigan through 2019 (Lake Trout Working Group 2022; Ebener et al. 2020).

The expanding levels of natural reproduction by Lake Trout in Lake Michigan, while positive, does complicate management. Planting of hatchery-reared fish will have to be reduced as abundance of wild fish continues to increase (see Bronte et al. 2008), which means fishery managers will have less control over Lake Trout abundance and must now focus on protecting wild populations and understanding the stock-recruitment relationships of different reproductive stocks as in Lake Superior (Richards et al. 2004; Corridin et al. 2008). Since natural reproduction is just beginning in Lake Michigan, development of stock-recruitment relationships is also just beginning, and the available data represents only the ascending portion of the curve. In addition, recent genetic studies of wild Lake Trout recruits in lakes Michigan and Huron have found that the different strains of hatchery-reared adults did not contribute equally to the natural reproduction (DeKoning et al. 2006) and the contribution of each strain varies through time and space (Scribner et al. 2018; Fitzsimons et al. 2021; Larson et al. 2021). Thus, a unit of spawning biomass of Lake Trout is not equal throughout spatial areas of Lake Michigan or across years because the composition of biomass by strain varies according to changes in numbers and sites stocked, and this complicates understanding the stock-recruitment relationships for each reproductive stock.

In this document we briefly

1) describe the stocking information for Lake Trout strains stocked into southern Lake Michigan (Figure 1),
2) summarize the genetic data on contributions of hatchery strains of Lake Trout and subsequent wild recruits, and
3) introduce the concept of "Reproductive Power Index" using genetic data.

Our objective is to integrate the strain-specific stocking data with the genetic analysis of adults and their progeny to refine estimates of Lake Trout spawning biomass used in a stock-recruitment relationship in southern Lake Michigan. Here we summarize pre-existing information on the performance of different strains, and combine this with stocking, life-history and survival information to calculate the potential reproductive output from the mixed stock resulting from the stocking and wild recruits. Our long-term goal is to use the improved estimates of spawning biomass to predict future recruitment to the fishable population and fisheries in southern Lake Michigan.

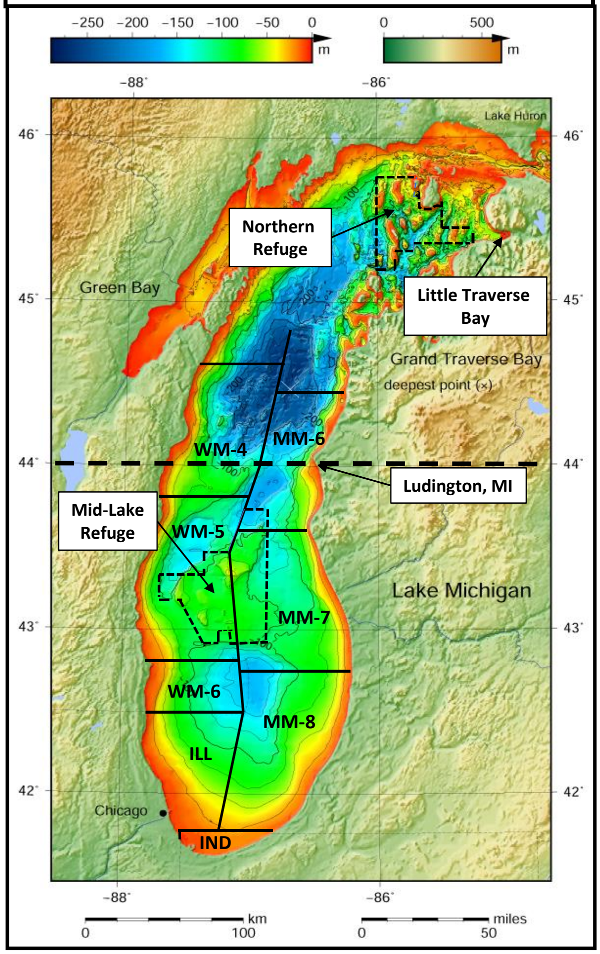
Study Area

We define southern Lake Michigan as all waters of the main basin south of a line along latitude 44°N near Ludington, MI. The study area includes statistical districts WM-4, WM-5, WM-6, MM-6, MM-7, MM-8, Ill, IND, and the Mid-Lake Refuge (Figure 1). Previous analysis of coded-wire tag recoveries showed that 90% of Lake Trout captured in our study area were previously stocked there (Ebener et al. 2020), indicating the study area represents a reproductive stock or Life History Unit.

Stocking Data

We downloaded (accessed 23 May 2023) the latest version of the Great Lakes Stocking Database from the Great Lakes Fishery Commission website (www.glfc.org/fishstocking) and queried for Lake Trout stocked into Lake Michigan from a boat since a previous stock-recruitment analysis by R.D.C. found the best relationship involved fish stocked offshore. We queried fall fingerlings and spring yearlings and excluded all other life history forms. We then queried for Lake Trout stocked in statistical districts MM-6, MM-7, MM-8, WM-4, WM-5, WM-6, Ill, and IND

Figure 1. Lake Michigan with statistical districts and locations mentioned in the text.

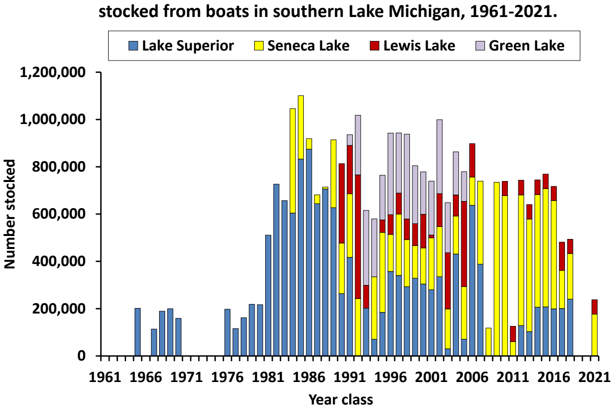


only for statistical grids >1309, which should exclude all fish stocked in northern WM-4 and MM-6. All fall fingerling stocking was converted to yearling equivalents as the number stocked multiplied by 0.40.

Numerous strains or morphotypes of Lake Trout have been stocked into Lake Michigan to increase their genetic diversity and allow them to exist in a variety of habitats (Krueger and Ihssen 1995; Bronte et al. 2008). For the 1965-2021-year classes, the annual number of Lake Trout stocked into southern Lake Michigan averaged 596,000 yearling equivalents with a low of zero and a maximum of 1.1 million (Figure 2). For simplicity we lump the seven distinct strains originating in Lake Superior as the "Lake Superior strain." Where the strain could be identified in the stocking records, the Lake Superior fish made up 47% of all stocking followed by the Seneca Lake strain at 31%, and the Lewis Lake and Green Lake strains at 11% each (Appendix A).

The allocation of strains changed substantially through time. The 1965-1983-year classes were entirely Lake Superior strain, but their contribution was slowly replaced through time first by Seneca Lake, then Lewis Lake, and finally Green Lake strains (Figure 2). The Seneca Lake strain made up 0 to 47% of the 1984-2007-year classes stocked annually into southern Lake Michigan, whereas it made up 33 to 100% of the 2008–2021-year classes. The Lewis Lake strain was stocked most years after 1989 and made up 0 to 52% of all strains stocked annually into southern Lake Michigan and it made up no more than 26% of fish stocked since the 2012-year class. The Green Lake strain was stocked for 15 consecutive years from the early 1990s to the early 2000s and made up 5 to 38% of all strains stocked annually during this time. Green Lake strain fish of the 1965- to 1975-year classes were stocked in Lake Michigan (Larson et al. 2021) but apparently not from boats in the south, or they were not identified in the stocking database.

Figure 2. Number of yearling equivalent Lake Trout strains stocked from boats in southern Lake Michigan, 1961-2021.



Genetic Data

Since 2003, five published papers used genetic analysis to determine the relative contribution of hatchery strains of stocked Lake Trout to emerging wild recruits in lakes Michigan and Huron (Page et al. 2003; DeKoning et al. 2006; Roseman et al. 2009; Scribner et al. 2018; Larson et al. 2021). Each paper described the genetic composition of wild Lake Trout and the adult brood stocks in hatcheries that would have contributed to the wild recruits. We choose not to use the data from DeKoning et al. (2006) and Roseman et al. (2009) because they did not report the "expected" contribution by each strain of hatchery fish.

The adult genetic samples were collected from brood stocks held at federal and provincial hatcheries in the Great Lakes basin. Page et al. (2003) evaluated the genetic structure of six strains that were maintained at two U.S. federal hatcheries and whose progeny were stocked into lakes Michigan and Huron. Scribner et al. (2018) evaluated the genetic structure of seven strains maintained at U.S. federal hatcheries and six strains from Ontario provincial hatcheries whose progeny were stocked into Lake Huron, and Larson et al. (2021) evaluated the genetic structure of eight strains from U.S. federal hatcheries whose progeny were stocked into Lake Michigan (Table 1). We considered Seneca Lake strain fish held at U.S. and Ontario hatcheries to be a single strain for this analysis although Scribner et al. (2018) treated them as separate strains. These hatchery strains accounted for nearly all yearling and fingerling Lake Trout stocked into lakes Michigan and Huron since the 1990s.

Table 1.—Hatchery strains of adult Lake Trout brood stocks evaluated for their genetic structure by Page et al. (2003), Scribner et al. (2018), and Larson et al. (2021).

Lake of Origin	Strain	Page et al. (2003)	Scribner et al. (2018)	Larson et al. (2021)
Green Lake, Wisconsin	Green Lake	X	X	X
Lake Manitou, Ontario	Lake Manitou		X	
Lewis Lake, Wyoming	Lewis Lake	X	X	X
Seneca Lake, New York	Seneca Lake	X	X	X
Lake Huron	Iroquois Bay		X	
	Big/Parry Sound		X	X
Lake Superior	Apostle Islands	X	X	X
	Isle Royale	X	X	X
	Klondike Reef			X
	Marquette	X	X	X
	Michipicoten		X	
	Slate Islands		X	
	Traverse		X	

The wild recruits evaluated for parental origin were represented by multiple year classes collected from multiple sites in both lakes. Young-of-the year wild Lake Trout were collected from Little Traverse Bay, Lake Michigan (Figure 1) and Six Fathom Bank, Lake Huron (Page et al. 2003) during 1994-2001. Wild recruits of four to ten years old were caught during agency surveys and monitoring of recreational and commercial fishery harvests from seven spatial areas in both Michigan and Ontario waters Lake Huron (Scribner et al. 2018) during 2002-2004 and 2009-2012. Finally, wild recruits >300 mm TL, probably age 2 and older, were caught during agency surveys and monitoring of recreational and commercial fishery harvests from seven spatial areas of Lake Michigan during 2009-2015 (Larson et al. 2021).

The three genetic studies used microsatellite data to estimate the observed average contribution of each hatchery strain to the genetic makeup of wild recruits, but the three studies used different statistical analyses. Page et al. (2003) used likelihood-based individual assignments and mixed-stock analysis to estimate the contribution of hatchery fish to wild recruits. Scribner et al. (2018) used a Bayesian inferential approach and deviance information criteria to compare models evaluating strain contributions at different spatial and temporal scales. Last, Larson et al. (2021) used individual assignments to estimate the contribution of hatchery strains to wild recruits, and simulations to assess the accuracy of their assignments.

Each of the studies used different methods to estimate the expected average contribution of each hatchery strain to wild recruits. Page et al. (2003) used coded-wire tag recoveries of adult Lake Trout captured during spawning surveys along with the number of each strain stocked in the vicinity of the spawning reefs to estimate the average expected contribution of each strain to wild recruits. Scribner et al. (2018) estimated the expected contributions of hatchery strains to wild recruits using both the number of each hatchery strain stocked in each spatial area and the population demographics of Lake Trout of all strains generated from statistical catch-at-age stock assessments in the same spatial area. Larson et al. (2021) integrated the number of each cohort of hatchery strains with population demographic information on age composition, fecundity, and movement patterns of adult fish captured during spawning surveys to estimate the expected contribution of hatchery strains to wild recruits. Larson et al. (2021) further stated that differences in survival or recruitment among strains and strata were not incorporated into their estimates of the expected contribution to wild recruits.

We used data from the three genetic studies to determine the average contribution of hatchery strains of adult Lake Trout to wild recruits in lakes Michigan and Huron. First, we created a database (Appendix B) of the average expected and observed values reported in tables 5 and 6 of Page et al. (2003), the mean posterior values in Michigan and Ontario waters of Lake Huron from table 3 and 4 of Scribner et al. (2018), and the estimates in table 5 of Larson et al. (2021). The observations in our database were reported by statistical districts or management area. Thus, individual data points in our analysis represent the proportional contribution of a hatchery strain to wild recruits in a spatial area and a time period (Appendix B). Next, we assigned strains based on lake of origin (Table 1).

We estimated the mean expected and observed proportional contribution of each strain to wild recruits differently for the Scribner et al. (2018) data. For the Page et al. (2003) and Larson et al. (2021) data we estimated the mean observed and expected proportional contributions to wild recruits by averaging the values for each time period for each strain reported by each study. Scribner et al. (2018) reported the expected and observed proportional contributions to wild recruits for each strain in each spatial area during each time period separately for U.S-stocked strains and Canadian-stocked strains. Thus, averaging values for each strain across all spatial areas and time periods in the database (Appendix B) for the Scribner et al. (2018) data did not produce estimates of the expected and observed contributions to wild recruits that summed to 1.0. Instead, we summed the expected and observed values for each spatial area in each time period for both U.S. and Canadian strains for the Scribner et al. (2018) data, and then calculated the mean observed ($\overline{Obp}$) and expected ($\overline{Exp}$) proportional values as:

$$\overline{Obp_s} = \frac{\left[\left(\frac{\sum_{i=1}^{n} Obp_{i,s,t=1}}{n}\right) + \left(\frac{\sum_{i=1}^{n} Obp_{i,s,t=2}}{n}\right)\right]}{2}, \quad (1)$$

$$\overline{Exp_s} = \frac{\left[\left(\frac{\sum_{i=1}^{n} Exp_{i,s,t=1}}{n}\right) + \left(\frac{\sum_{i=1}^{n} Exp_{i,s,t=2}}{n}\right)\right]}{2}, \quad (2)$$

where ***s*** represents the strain based on the lake of origin, ***i*** represents management unit, ***t*** is time period, and ***n*** is the number of management units over which the data was summed.

There were 207 observations of the genetic contribution of hatchery adults to wild recruits in 17 spatial areas of lakes Michigan and Huron during 1994-2015 covering the main basin and most large bays of both lakes (Page et al. 2003; Scribner et al. 2018; Larson et al. 2021). There were 172 observations of the proportional contribution to wild recruits in ten Lake Huron spatial areas and 35 observations in seven Lake Michigan spatial areas. The proportional contribution to wild recruits had 88 observations for the Lake Superior strain, 36 for the Seneca Lake strain, 26 for the Lake Huron strain, 23 for the Lewis Lake strain, 21 for the Green Lake strain, and 13 for the Lake Manitou strain.

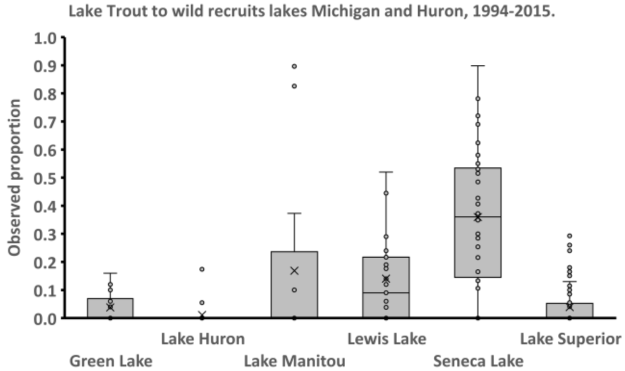
The Seneca Lake strain contributed substantially more to production of wild recruits than other strains since the 1990s (Table 2; Figure 3). The contribution to wild recruits ranged from 0 to 90% for both the Seneca Lake and

Table 2.—Observed and expected proportional contributions of adult hatchery stains of Lake Trout to wild recruits and reproductive power index (equation 3) calculated from data reported in three genetic studies conducted in lakes Michigan and Huron (Appendix B) during 1994-2015. Modeling indicates that numbers stocked were adjusted for survival (Scribner et al. 2018) or survival, growth, fecundity, and movement (Larson et al. 2021).

			Expected		Reproductive power	
Study	**Strain**	**Observed**	**stocking**	**modeling**	**stocking**	**modeling**
Page et al. (2003)	Green Lake	0.072	0.021		3.405	
	Lewis Lake	0.313	0.632	0.439	0.495	0.713
	Seneca Lake	0.479	0.142	0.311	3.371	1.542
	Lake Superior	0.146	0.103	0.251	1.421	0.584
Scribner et al. (2018)	Green Lake	0.016	0.002	0.007	8.125	2.378
	Lake Huron	0.024	0.033	0.000	0.716	
	Lake Manitou	0.183	0.149	0.035	1.227	5.276
	Lewis Lake	0.092	0.103	0.104	0.891	0.890
	Seneca Lake	0.561	0.131	0.262	4.272	2.138
	Lake Superior	0.126	0.578	0.591	0.217	
Larson et al. (2021)	Green Lake	0.076		0.227		0.333
	Lewis Lake	0.170		0.257		0.661
	Seneca Lake	0.574		0.194		2.956
	Lake Superior	0.179		0.320		0.558

Lake Manitou strains, 0 to 52% for the Lewis Lake strain, 0 to 30% for the Lake Superior strain, 0 to 17% for the Lake Huron strain, and 0 to 16% for the Green Lake strain. Only 17% of the observations for the Seneca Lake strain were zero whereas one-third exceeded 50%. In comparison, over two-thirds of the Lake Manitou strain observations were zero and only 15% exceeded 50%. Nearly three-quarters of the genetic tests were zero for the contributions to wild recruits by the Lake Superior strain (Figure 3). For the Lewis Lake strain, 30% of the observations were zero. Over half the observations for the Green Lake strain were zero although the strain made a surprising contribution to wild recruits given it was stocked in only 15 years during 1961-2021. Seneca Lake strain fish contributed 80 to 100% of genetic samples from age-0 Lake Trout collected by bottom-trawling at five locations in the main basin of Lake Huron during May through October of 2004-2006 (Roseman et al. 2009). Finally, the Seneca Lake strain made the largest contribution (49%) to the collection of Lake Trout embryos made on reef complexes in the Mid-Lake Refuge of Lake Michigan during fall 2003 (DeKoning et al. 2006), followed by the Green Lake strain (28%), Lake Superior strain (23%), and Lewis Lake strain (0%).

Figure 3. Box and whisker plot proportional contribution of hatchery adult Lake Trout to wild recruits lakes Michigan and Huron, 1994-2015.



Reproductive Power

We estimated the “reproductive power” of each strain to wild recruits as

$$RPI_s = \frac{\overline{Obp_s}}{\overline{Exp_s}} \qquad (3)$$

where RPI_s is the reproductive power index and $\overline{Obp_s}$ *and* $\overline{Exp_s}$ are as defined previously.

The RPI of the Seneca Lake strain was 1.5 to 4.3 times greater than what would have been expected based on numbers stocked or population demographics (Table 2). The Green Lake strain did contribute more to wild recruits than would have been expected (0.3 to 8.1 times) but the strain's observed proportional contribution to wild recruits was only 0.00 to 0.16 (Figure 3). The high RPI for the Green Lake strain came when the expected and observed contributions were quite low, but we could not determine if high RPI values were better for small stocking events for some unknown reason, or if these high RPI values are unreliable because they are based on small numbers. The Lake Superior strain's contribution to wild recruits was almost always less than what would be expected, while the contribution of the Lewis Lake strain was always less than what would be expected. Across all three studies, the RPI was consistently greatest for the Seneca Lake strain and lowest for the Lake Huron and Lake Superior strains (Figure 4).

Figure 4. Mean reproductive power index of Lake Trout strains to wild recruits in lakes Michigan and Huron, 1994-2015.

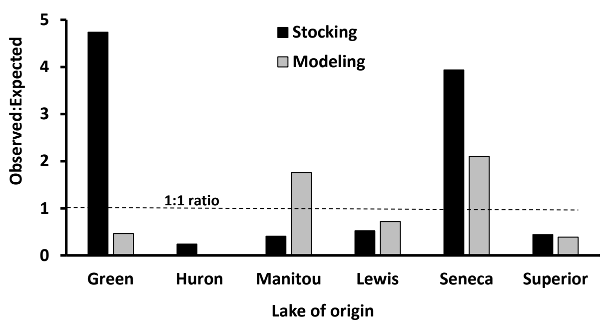
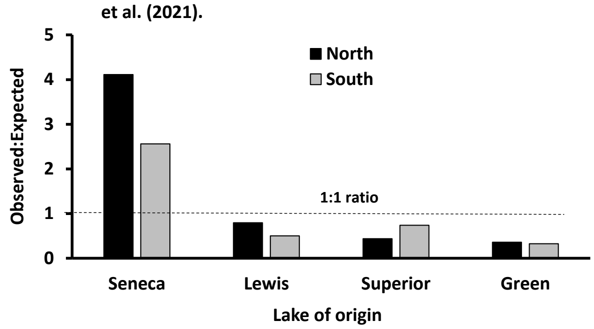


Figure 5. Mean reproductive power index of Lake Trout strains to wild recruits Lake Michigan from table 5 Larson et al. (2021).

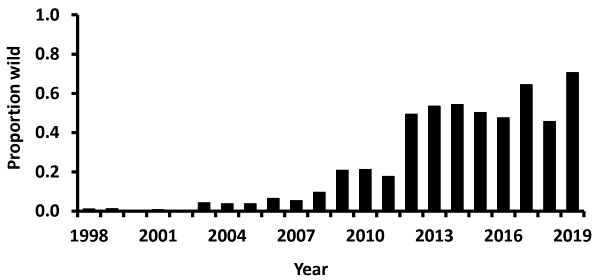


Using information from table 5 of Larson et al. (2021), we estimated that the mean RPI for the Seneca Lake strain was much greater in northern Lake Michigan (4.11) than southern Lake Michigan (2.56) and that the RPI of other strains was less than 1.0. The mean RPI in northern and southern Lake Michigan was 0.79 and 0.50 for the Lewis Lake strain, 0.44 and 0.74 for the Lake Superior strain, and 0.36 and 0.32 for the Green Lake strain, respectively (Figure 5).

Reliability of the RPI is dependent upon the underlying strain assignments and model assumptions made by each genetic study (K. Scribner, Michigan State University, personal communication). The basic assumption of the genetic models used in all three studies was that the wild recruits were first-generational (F1) descendants of hatchery fish previously stocked by Great Lakes fishery agencies (Page et al. 2003; Scribner et al. 2018; Larson et al. 2021). Their assumption is probably wrong.

Scribner et al. (2018) found that mating among strains in Lake Huron was not random because the assortative mating coefficient was very large in their first sampling period (2002-2004) and it was very near zero in their second sampling period (2009-2012), which they suggested meant that many of their wild recruits were not F1, but rather the result of mating by wild adults. Their suggestion of mating by wild adults is supported by spawning survey catches in Illinois waters of Lake Michigan (Figure 6). Wild adult Lake Trout were present on the spawning grounds prior to 2015 in Illinois waters, the last year of data collection by Larson et al. (2021). In addition, Patterson et al. (2016) reported that in 2012 unclipped (wild) Lake Trout spawners "became the dominant contributor (range = 53–55%) to the spawning populations at two spawning reefs in Illinois waters of Lake Michigan and that across all study years of 1999-2014, 20.3% of the spawner population consisted of unmarked Lake Trout."

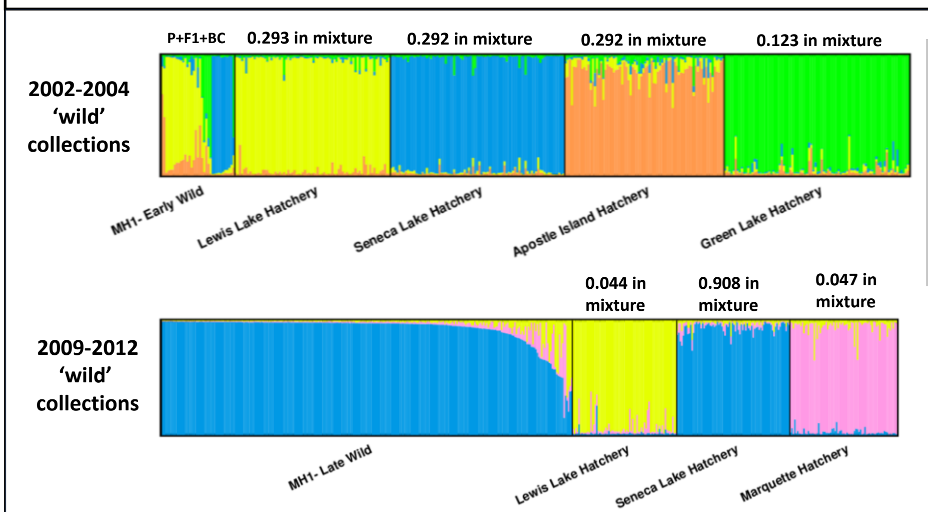
Figure 6. Proportion wild Lake Trout captured during spawning surveys in Illinois waters of 1998-2019 as reported by Patterson et al. (2016).



The superior reproductive performance of Seneca Lake strain Lake Trout has been partially attributed to their adaptive traits that facilitate increased survival in areas with high mortality due to Sea Lamprey *Petromyzon marinus* predation, but we believe they are also less vulnerable to fishing than other strains. Madenjian et al. (2011) presented evidence that the Lake Superior strain was much more vulnerable to commercial fishing than the Seneca Lake strain in the vicinity of Drummond Island Refuge of northern Lake Huron. McKee et al. (2004) reported that the Marquette strain (Lake Superior origin) survived at a significantly higher rate than Seneca Lake strain fish prior to age 3 but at similar rates after age 3 in the Mid-Lake Refuge of Lake Michigan. We argue that the apparent better survival of the Marquette strain at young ages in the McKee et al. (2004) study was actually caused by their higher catchability to survey gear than young ages of the Seneca Lake strain. For instance, Elrod et al. (1996) found that Seneca Lake fish lived shallower at ages 1 and 2 than Lake Superior strain fish in Lake Ontario, but Seneca Lake strain fish lived deeper than the Lake Superior strain after age 2. Further, Seneca Lake strain Lake Trout occupied significantly deeper and colder water than both Lake Superior and Lewis Lake strains in Lake Huron (Bergstedt et al. 2003, 2012), which would reduce the Seneca's vulnerability to fisheries.

Additionally, the Seneca Lake strain has physiological traits that make it reproductively superior to other strains of Lake Trout. Krueger and Ihssen (1995) stated that Lake Trout "fat content, swimbladder gas retention, and developmental rates of eggs were different among some populations and appear to be heritable." Subsequently, Smith (2021) conducted genomic analysis of F2 wild Lake Trout recruits in Lake Huron by looking at specific chromosomes and he was able to identify regions that exhibited adaptive divergence between hatchery strains, some of which were found to underlie differences in survival, reproduction, and buoyancy regulation between strains. It appears that wild recruits in Lake Huron, and probably Lake Michigan, are becoming more Seneca-like through time (Figure 7).

Figure 7. Posterior probability densities of the proportional contribution of Seneca Lake, Lewis Lake, and Lake Superior strains (Apostle Islands and Marquette hatchery) of Lake Trout to wild recruits in northern U.S. waters of Lake Huron during 2002-2004 and 2009-2012. Figure provided by Kim Scribner, Michigan State University, that was created from data collected as part of Scribner et al. (2018) but not previously published.



Smith (2021) suggested that "differences in fitness between strains are due to behavioral and physiological factors associated with the ability to avoid and survive predation by sea lamprey." The physiological advantage of the Seneca Lake strain is further supported by results from Fitzsimons et al. (2021) who showed that Lake Trout in Seneca Lake were more tolerant than other strains of the thiamine deficiency that causes early mortality syndrome (EMS) in eggs and fry of Lake Trout. The EMS results from a diet rich in Alewife *Alosa pseudoharengus* (Fitzsimons and Brown 1998). Seneca Lake was invaded by Alewives in the late 1800s, which was much earlier than their invasion of the upper Great Lakes. Thus, the Seneca Lake strain has been exposed to Alewives for over 120 years and Fitzsimons et al. (2021) described how they could have evolved a tolerance to thiamine deficiency in that amount of time. Fitzsimons also suggested that the Seneca Lake strain's higher resistance to EMS could be more important to their observed spawning success than their presumed ability to survive Sea Lamprey predation. These recent studies show that we need to account for strain effects and wild fish abundance when estimating female Lake Trout spawning biomass.

Using Reproductive Power to Adjust Spawning Biomass

We simulated the effects of using the RPI to adjust spawning biomass of Lake Trout in southern Lake Michigan using strain-specific stocking information for the 1965- to 2021-year classes (Appendix A) and the following output from version 08-25-21 of the WIIM stock assessment (Clark et al. 2021; Ebener et al. 2020, 2021,)

- instantaneous total annual mortality rate (***Z***) by age and year,
- abundance of wild lake trout (***N_wild***) by age and year,
- survival (***S_spawn***) by age and year from the start of the year to the spawning season, and
- the proportion mature females (***Mat***) by age and year multiplied by the weight of a spawning fish (***WatSp***) by age and year.

We exported matrices of ***Z, N_wild, S_spawn***, and ***Mat*WatSP*** from the stock assessment output into EXCEL to conduct the analysis. The values of ***Mat*** were input to the data file for the WIIM stock assessment (Ebener et al. 2020), whereas ***S_spawn*** and ***Mat*WatSp*** were estimated within the stock assessment.

Abundance of each year class of each hatchery strain (*s*) at a given age (*i*) at the beginning of the year (*j*) was estimated as

$$N_{s,i+1,j+1} = N_{s,i,j} * \exp^{-Z_{i,j}} \quad (4)$$

The survival to time of spawning at a given age and year was estimated in the stock assessment as

$$S\_spawn_{i,j} = \exp(-t\_spawn * Z_{i,j}) \quad (5)$$

The weight of a spawning fish at a given age and year was estimated in the stock assessment as

$$WatSp_{i,j} = Watage_{i,j} * exp(t\_spawn * G_{i,j}) \quad (6)$$

Female spawning biomass (***SPbiomass***) at a given age and year was estimated as

$$SPbiomass_{s,i,j} = \frac{\left(N_{s,i,j} * S_{spawn_{i,j}}\right)}{2} * Mat_{i,j} * WatSp_{i,j} \quad (7)$$

where ***Watage*** is the estimated mean weight-at-age that was input to the stock assessment data file, *t_spawn* is the time of the year of spawning that was set to 0.833 (day 304 or October 31) in the stock assessment data file, and ***G*** is the instantaneous growth rate estimated within the stock assessment.

Before we used RPI to adjust spawning biomass, we estimated the composition of Lake Trout strains in the spawning biomass of southern Lake Michigan and found it changed substantially through time in relation to stocking strategies and natural reproduction (Figure 8). Spawning biomass initially peaked during 1990-1994 and the Lake Superior strain accounted for 87%. After 1994, spawning biomass declined to 1997 and the Lake Superior strain accounted for 69%. Thereafter, spawning biomass increased to a peak during 2010-2014, declined slightly thereafter, and stabilized through 2019. Strain composition of the total spawning biomass during 2010-2014 was 28% Lake Superior, 21% Seneca Lake, 14% Lewis Lake, 25% Green Lake, and 12% wild fish. By 2019, strain composition of the spawning biomass was 14% Lake Superior, 39% Seneca Strain, 8% Lewis Lake, 7% Green Lake, and 31% wild fish.

Figure 8. Lake Trout spawning biomass by strain in southern Lake Michigan, 1965-2025.

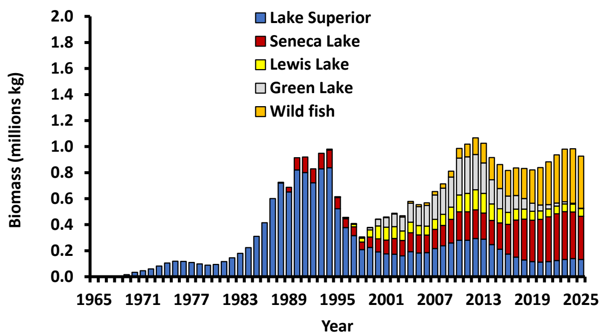
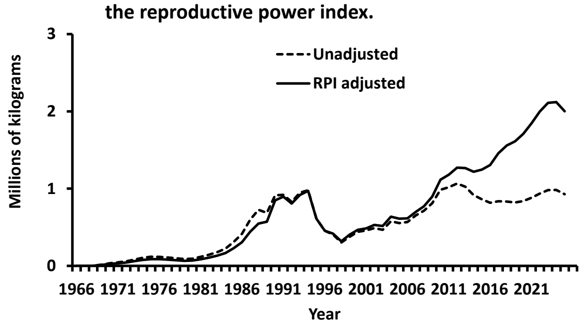


Figure 9. Predicted Lake Trout spawning biomass in southern Lake Michigan adjusted and not adjusted for the reproductive power index.



The RPI had a large effect on estimates of spawning biomass. We multiplied the average RPI for each strain times the spawning biomass for that strain in each year and summed biomass across all strains to create an Effective Spawning Biomass Index (ESBI). The strain-specific RPI for southern Lake Michigan was 2.56 for Seneca Lake, 0.74 for Lake Superior, 0.50 for Lewis Lake, 0.32 for Green Lake strains, and 2.56 for wild spawners (Figure 5). The total ESBI exceeded the unadjusted estimates of spawning biomass by 1% in 1996 to 54% by 2019, but the largest divergence occurred after 2010 (Figure 9), reflecting increases in the average RPI of fish stocked from below 1.0 to well over 1.0. The ESBI was expected to peak at 2.12 million kg in 2023, then decline thereafter. Cumulative ESBI through 2019 was 29.7 million kg. The contribution to the cumulative ESBI by each strain during 1965-2019 was 35% for Lake Superior, 41% Seneca Lake, 4% Lewis Lake, 4% Green Lake, and 16% wild fish. After 2010, the strain-specific contribution to the ESBI was 12% Lake Superior, 46% Seneca Lake, 4% Lewis Lake, 4% Green Lake, and 34% wild fish.

Analysis Issues

We made multiple assumptions that influenced the outcome of our simulations for estimating spawning biomass:

- only Lake Trout stocked from boats contributed to spawning
- the mortality, growth, and female maturity by year and age were the same for all strains during 1985–2019
- mortality rates, female maturity, and weight-at-age after 2019 were all constant at the 2019 values
- that females make up 50% of the mature population
- the RPI value for wild fish was the same as for the Seneca Lake strain

Lake Trout stocked onshore from trucks do probably contribute to wild recruits, but our analysis did not use these fish. Our estimates of ESBI would certainly be greater if we incorporated onshore stocking from trucks into our analysis, but unless the strain composition of Lake Trout stocked from trucks was substantially different than stocked from boats, the results would be similar. That is, ESBI would be greater than spawning biomass estimated by not adjusting for RPI.

We have attempted to overcome the lack of long-term information on strain-specific population demographics by using the RPI to adjust spawning biomass. Our matrices of growth, maturity, and mortality represent the average condition for all strains of Lake Trout in southern Lake Michigan. Development of long-term data sets that allow estimation of strain-specific population demographics would be useful, but we suspect they are a decade from completion as of 2024. The use of RPI simplifies the process of developing strain-specific information for stock assessments and accounts for differences in survival and reproduction among strains.

We assume that the sex ratio in Lake Trout populations is equal in the Great Lakes, but survey data and monitoring of fisheries data suggest otherwise. In table 2 of Madenjian and DeSorcie (1999) males outnumbered females by 1.625 times in catches on the spawning grounds from the Northern Refuge of Lake Michigan during 1991-1997. In addition, Patterson et al. (2016) reported females made up only 12-41% of annual catches of adult Lake Trout at two spawning reefs in Illinois waters of Lake Michigan during 1999-2014. Lake Trout spawning surveys on Lake Michigan reported catching 38,032 males and 15,478 females (Ebener et al. 2020) for an average sex ratio of 0.41 females per male (Figure 10a) during 1981-2019. We should expect sex ratios on the spawning grounds not to be equal even if the sex ratio in the population was equal, because of differences in maturity schedules between sexes, delayed spawning by some females, and longer stays on the spawning grounds by males than females. However, biological data compiled from spring Lakewide Assessment Plan (LWAP) catches in Lake Michigan also showed unequal sex ratios, with on average, males outnumbering females by 15% (Figure 10b) as 15,394 male Lake Trout were captured compared to 13,043 females during 1998-2019 (Ebener et al. 2020). The higher ratio of males to females in the LWAP survey may reflect a higher catchability for males than females as Madenjian et al. (2015, 2016) illustrated for multiple fish species that males have higher energy expenditure than females stemming from greater activity and a higher resting metabolic rate. We recommend that agencies investigate the assumption of equal sex ratios in Lake Trout populations of the Great Lakes as this assumption is important for projecting spawning biomass and for analyses that compare female spawning biomass among populations.

Figure 10a. Ratio female:male Lake Trout in spawning surveys Lake Michigan, 1981-2019.

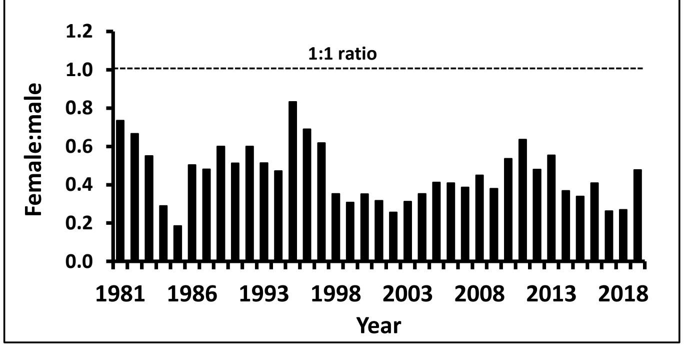
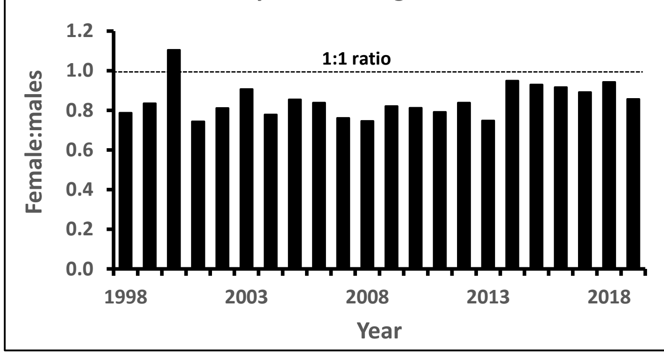


Figure 10b. Ratio female:male Lake Trout in LWAP surveys Lake Michigan, 1998-2019.



Last, because Scribner et al. (2018) and Larson et al. (2021) showed that Seneca Lake strain fish were the largest contributor to wild recruits in Lake Michigan and many of these fish appear to be the progeny of wild adults (Figure 7), it seems appropriate to use the same RPI value for both wild and Seneca Lake spawners.

Summary

We used genomic information on hatchery and wild Lake Trout to estimate a reproductive power index (RPI) of the Lake Superior, Seneca Lake, Lewis Lake, and Green Lake strains of Lake Trout that could be used to refine statistical catch-at-age estimates of spawning biomass. The RPI represents the ratio of the observed to expected genetic contribution of each strain to wild recruits. The Seneca Lake strain had the highest RPI, followed by the Lewis Lake, Green Lake, and Lake Superior strains in lakes Michigan and Huron during 1994-2015. In southern Lake Michigan, the RPI was 2.56 for the Seneca Lake strain, 0.74 for the Lake Superior strain, 0.50 for the Lewis Lake strain, and 0.32 for the Green Lake strain. To estimate annual spawning biomass for each strain in southern Lake Michigan we used year class-specific numbers stocked of each strain in combination with inputs and outputs of age- and year-specific matrices of mortality, growth, maturity, and weight-at-age from a statistical catch-at-age stock assessment in southern Lake Michigan. We created an effective spawning biomass index (ESBI) by multiplying the strain-specific estimates of spawning biomass by the RPI for each strain. Our ESBI values were lower during the 1980s and 1990s than the estimates produced by not adjusting for RPI, but after 2010 the ESBI was up to 54% greater than the unadjusted spawning biomass. Projected values of ESBI peaked in 2023 in southern Lake Michigan and declined thereafter. We recommend that the concept of the RPI be adopted by agencies on Lake Michigan and used to refine estimates of spawning biomass.

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Appendix A

Annual number of yearling equivalent Lake Trout strains of the 1961- to 2001-year classes stocked into southern Lake Michigan from boats. Data obtained from www.glfc.org/fishstocking.

	Lake Trout Strain					Cumulative
Year class	Lake Superior	Seneca Lake	Lewis Lake	Green Lake	Total	stocking
1961	0	0	0	0	0	0
1962	0	0	0	0	0	0
1963	0	0	0	0	0	0
1964	0	0	0	0	0	0
1965	201,500	0	0	0	201,500	201,500
1966	0	0	0	0	0	201,500
1967	113,840	0	0	0	113,840	315,340
1968	189,430	0	0	0	189,430	504,770
1969	200,000	0	0	0	200,000	704,770
1970	159,000	0	0	0	159,000	863,770
1971	0	0	0	0	0	863,770
1972	0	0	0	0	0	863,770
1973	0	0	0	0	0	863,770
1974	0	0	0	0	0	863,770
1975	0	0	0	0	0	863,770
1976	197,800	0	0	0	197,800	1,061,570
1977	116,000	0	0	0	116,000	1,177,570
1978	161,799	0	0	0	161,799	1,339,369
1979	218,900	0	0	0	218,900	1,558,269
1980	217,000	0	0	0	217,000	1,775,269
1981	511,100	0	0	0	511,100	2,286,369
1982	726,670	0	0	0	726,670	3,013,039
1983	657,300	0	0	0	657,300	3,670,339
1984	604,405	441,785	0	0	1,046,190	4,716,529
1985	832,727	268,271	0	0	1,100,998	5,817,527
1986	874,640	44,400	0	0	919,040	6,736,567
1987	643,900	37,548	0	0	681,448	7,418,015
1988	706,080	8,320	0	0	714,400	8,132,415
1989	627,137	286,852	0	0	913,989	9,046,405
1990	263,566	213,853	335,831	0	813,250	9,859,655
1991	417,145	268,590	204,656	45,153	935,544	10,795,199
1992	0	242,831	522,784	252,202	1,017,817	11,813,016
1993	202,000	0	96,700	316,943	615,643	12,428,659
1994	70,708	264,020	0	244,900	579,628	13,008,287
1995	184,560	338,008	52,666	189,011	764,245	13,772,532
1996	357,350	156,500	83,700	344,700	942,250	14,714,782
1997	340,500	259,600	88,600	254,400	943,100	15,657,882
1998	293,156	198,322	87,800	358,533	937,811	16,595,693
1999	328,861	138,000	92,629	245,000	804,490	17,400,183
2000	304,255	152,500	142,070	179,500	778,325	18,178,508
2001	280,074	219,220	12,000	227,894	739,188	18,917,696
2002	335,082	211,962	139,332	312,562	998,938	19,916,634
2003	30,222	168,552	237,974	211,715	648,463	20,565,097
2004	431,123	160,457	89,257	182,252	863,089	21,428,186
2005	70,948	222,190	360,223	125,650	779,011	22,207,197
2006	637,189	119,183	141,641	0	898,013	23,105,210
2007	388,114	351,041	0	0	739,155	23,844,365
2008	0	118,160	0	0	118,160	23,962,525
2009	0	734,453	0	0	734,453	24,696,978
2010	0	677,609	61,057	0	738,666	25,435,644
2011	0	60,484	65,208	0	125,692	25,561,336
2012	128,542	552,550	62,187	0	743,279	26,304,615
2013	103,226	475,467	61,711	0	640,404	26,945,019
2014	206,333	476,017	61,996	0	744,346	27,689,365
2015	207,400	500,107	61,570	0	769,077	28,458,442
2016	199,319	458,090	59,575	0	716,984	29,175,426
2017	200,797	160,933	119,740	0	481,470	29,656,896
2018	240,496	192,695	60,308	0	493,499	30,150,395
2019	0	0	0	0	0	30,150,395
2020	0	0	0	0	0	30,150,395
2021	0	177,047	60,870	0	237,917	30,388,312
Total	14,180,195	9,355,617	3,362,085	3,490,415	30,388,312	
Percentage	**47%**	**31%**	**11%**	**11%**		

Appendix B

Observed proportional contribution of hatchery strains of Lake Trout to wild recruits in lakes Michigan and Huron (Page et al. 2003; Scribner et al. 2018; Larson et al. 2021) during 1994-2015. Field **EXP-stocking** is the expected contribution based solely on numbers stocked of each strain. **EXP-Pop** is the expected contribution based on demographic data such as coded-wire tag recoveries or statistical catch-at-age analysis. Fields **OBS-L95%** and **OBS-U95%** are the lower and upper 95% confidence intervals of the contribution to wild recruits (Page et al. 2003; Larson et al. 2021) or the lower and upper highest density posterior limits to wild recruits (Scribner et al. 2018).

STUDY	LAKE-SITE	MGT_UNIT	STRAIN	YEARS	EXP-Stocki	EXP-P	Observ	OBS-L9	OBS-U9
Larson et al. (2021)	Michigan	ILL/IND	Green Lake	2009-2015		0.350	0.120	0.060	0.210
Larson et al. (2021)	Michigan	MM123	Green Lake	2009-2015		0.010	0.010	0.000	0.040
Larson et al. (2021)	Michigan	MM4	Green Lake	2009-2015		0.020	0.040	0.010	0.120
Larson et al. (2021)	Michigan	MM58	Green Lake	2009-2015		0.200	0.060	0.020	0.180
Larson et al. (2021)	Michigan	REFUGE	Green Lake	2009-2015		0.430	0.160	0.090	0.290
Larson et al. (2021)	Michigan	WM34	Green Lake	2009-2015		0.220	0.040	0.010	0.120
Larson et al. (2021)	Michigan	WM56	Green Lake	2009-2015		0.360	0.100	0.040	0.210
Larson et al. (2021)	Michigan	ILL/IND	Lewis Lake	2009-2015		0.270	0.060	0.030	0.130
Larson et al. (2021)	Michigan	MM123	Lewis Lake	2009-2015		0.340	0.140	0.080	0.220
Larson et al. (2021)	Michigan	MM4	Lewis Lake	2009-2015		0.510	0.520	0.350	0.720
Larson et al. (2021)	Michigan	MM58	Lewis Lake	2009-2015		0.230	0.120	0.050	0.250
Larson et al. (2021)	Michigan	REFUGE	Lewis Lake	2009-2015		0.060	0.090	0.040	0.180
Larson et al. (2021)	Michigan	WM34	Lewis Lake	2009-2015		0.220	0.190	0.100	0.320
Larson et al. (2021)	Michigan	WM56	Lewis Lake	2009-2015		0.170	0.070	0.020	0.160
Larson et al. (2021)	Michigan	ILL/IND	Seneca Lake	2009-2015		0.170	0.720	0.570	0.870
Larson et al. (2021)	Michigan	MM123	Seneca Lake	2009-2015		0.030	0.690	0.550	0.830
Larson et al. (2021)	Michigan	MM4	Seneca Lake	2009-2015		0.140	0.260	0.150	0.410
Larson et al. (2021)	Michigan	MM58	Seneca Lake	2009-2015		0.200	0.690	0.510	0.870
Larson et al. (2021)	Michigan	REFUGE	Seneca Lake	2009-2015		0.370	0.580	0.430	0.740
Larson et al. (2021)	Michigan	WM34	Seneca Lake	2009-2015		0.190	0.530	0.380	0.700
Larson et al. (2021)	Michigan	WM56	Seneca Lake	2009-2015		0.260	0.550	0.390	0.720
Larson et al. (2021)	Michigan	ILL/IND	Superior	2009-2015		0.200	0.100	0.050	0.190
Larson et al. (2021)	Michigan	MM123	Superior	2009-2015		0.620	0.160	0.090	0.260
Larson et al. (2021)	Michigan	MM4	Superior	2009-2015		0.330	0.180	0.080	0.330
Larson et al. (2021)	Michigan	MM58	Superior	2009-2015		0.360	0.130	0.050	0.280
Larson et al. (2021)	Michigan	REFUGE	Superior	2009-2015		0.140	0.170	0.090	0.310
Larson et al. (2021)	Michigan	WM34	Superior	2009-2015		0.380	0.240	0.130	0.400
Larson et al. (2021)	Michigan	WM56	Superior	2009-2015		0.210	0.270	0.150	0.046
Page et al. (2003)	Michigan-LTB	MM123	Green Lake	1994-2001	0.021		0.072		
Page et al. (2003)	Huron-SFB	MH34	Lewis Lake	1994-1995		0.267	0.039		
Page et al. (2003)	Michigan-LTB	MM123	Lewis Lake	1994-2001		0.61	0.46		
Page et al. (2003)	Michigan-LTB	MM123	Lewis Lake	1994-2001	0.632		0.445		
Page et al. (2003)	Huron-SFB	MH34	Seneca Lake	1994-1995		0.510	0.898		
Page et al. (2003)	Michigan-LTB	MM123	Seneca Lake	1994-2001		0.11	0.28		
Page et al. (2003)	Michigan-LTB	MM123	Seneca Lake	1994-2001	0.14		0.25		
Page et al. (2003)	Huron-SFB	MH34	Superior	1994-1995		0.224	0.064		
Page et al. (2003)	Michigan-LTB	MM123	Superior	1994-2001		0.278	0.260		
Page et al. (2003)	Michigan-LTB	MM123	Superior	1994-2001	0.103		0.115		
Scribner et al. (2018)	Huron	MH1	Green Lake	2002-2004	0.000	0.000	0.127	0.025	0.232
Scribner et al. (2018)	Huron	MH2	Green Lake	2002-2004	0.000	0.000	0.068	0.022	0.121
Scribner et al. (2018)	Huron	MH345	Green Lake	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Green Lake	2002-2004			0.000	0.000	0.000
Scribner et al. (2018)	Huron	GB	Green Lake	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC3	Green Lake	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Green Lake	2009-2012	0.006	0.016	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Green Lake	2009-2012	0.007	0.015	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Green Lake	2009-2012	0.007	0.010	0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Green Lake	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH23	Green Lake	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH45	Green Lake	2009-2012	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC12	Green Lake	2009-2012	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Huron	2002-2004	0.012	0.000	0.000	0.000	0.000

Appendix B continued

STUDY	LAKE-SITE	MGT_UNIT	STRAIN	YEARS	EXP-Stocki	EXP-P	Observ	OBS-L9	OBS-U9
Scribner et al. (2018)	Huron	MH2	Huron	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Huron	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Huron	2002-2004	0.002	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Huron	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Huron	2002-2004			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Huron	2002-2004			0.000	0.000	0.000
Scribner et al. (2018)	Huron	GB	Huron	2002-2004	0.113		0.055	0.015	0.096
Scribner et al. (2018)	Huron	GB	Huron	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC3	Huron	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC3	Huron	2002-2004	0.206		0.174	0.104	0.252
Scribner et al. (2018)	Huron	MH1	Huron	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Huron	2009-2012	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Huron	2009-2012	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Huron	2009-2012	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Huron	2009-2012	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Huron	2009-2012	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Huron	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Huron	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH23	Huron	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH45	Huron	2009-2012	0	0	0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH45	Huron	2009-2012	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC12	Huron	2009-2012	0		0.057	0.021	0.096
Scribner et al. (2018)	Huron	NC12	Huron	2009-2012	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Huron	2009-2012	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH23	Huron	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Lake Manitou	2002-2004	0.074	0.079	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Lake Manitou	2002-2004	0.106	0.114	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Lake Manitou	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Lake Manitou	2002-2004			0.896	0.831	0.955
Scribner et al. (2018)	Huron	GB	Lake Manitou	2002-2004	0.071		0.373	0.317	0.435
Scribner et al. (2018)	Huron	NC3	Lake Manitou	2002-2004	0.794		0.826	0.748	0.896
Scribner et al. (2018)	Huron	MH1	Lake Manitou	2009-2012	0.017	0.006	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Lake Manitou	2009-2012	0.021	0.008	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Lake Manitou	2009-2012	0.003	0.001	0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Lake Manitou	2009-2012			0.100	0.041	0.161
Scribner et al. (2018)	Huron	OH23	Lake Manitou	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH45	Lake Manitou	2009-2012	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC12	Lake Manitou	2009-2012	0.405		0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Lewis Lake	2002-2004	0.007	0.014	0.290	0.255	0.324
Scribner et al. (2018)	Huron	MH2	Lewis Lake	2002-2004	0.024	0.049	0.176	0.106	0.253
Scribner et al. (2018)	Huron	MH345	Lewis Lake	2002-2004	0.028	0.032	0.240	0.179	0.293
Scribner et al. (2018)	Huron	OH1	Lewis Lake	2002-2004			0.000	0.000	0.000
Scribner et al. (2018)	Huron	GB	Lewis Lake	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC3	Lewis Lake	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Lewis Lake	2009-2012	0.353	0.172	0.040	0.021	0.061
Scribner et al. (2018)	Huron	MH2	Lewis Lake	2009-2012	0.356	0.187	0.217	0.168	0.265
Scribner et al. (2018)	Huron	MH345	Lewis Lake	2009-2012	0.266	0.167	0.143	0.102	0.185
Scribner et al. (2018)	Huron	OH1	Lewis Lake	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH23	Lewis Lake	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH45	Lewis Lake	2009-2012	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC12	Lewis Lake	2009-2012	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Seneca Lake	2002-2004	0.202	0.154	0.291	0.255	0.324
Scribner et al. (2018)	Huron	MH1	Seneca Lake	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Seneca Lake	2002-2004	0.173	0.102	0.515	0.426	0.608
Scribner et al. (2018)	Huron	MH2	Seneca Lake	2002-2004	0.000	0.000	0.000	0.000	0.000

Appendix B continued

STUDY	LAKE-SITE	MGT_UNIT	STRAIN	YEARS	EXP-Stocki	EXP-P	Observ	OBS-L9	OBS-U9
Scribner et al. (2018)	Huron	MH345	Seneca Lake	2002-2004	0.153	0.080	0.296	0.256	0.341
Scribner et al. (2018)	Huron	MH345	Seneca Lake	2002-2004	0.000	0.000	0.165	0.081	0.253
Scribner et al. (2018)	Huron	OH1	Seneca Lake	2002-2004			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Seneca Lake	2002-2004			0.000	0.000	0.000
Scribner et al. (2018)	Huron	GB	Seneca Lake	2002-2004	0		0.216	0.152	0.259
Scribner et al. (2018)	Huron	GB	Seneca Lake	2002-2004	0		0.300	0.239	0.360
Scribner et al. (2018)	Huron	NC3	Seneca Lake	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC3	Seneca Lake	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Seneca Lake	2009-2012	0.252	0.481	0.781	0.720	0.842
Scribner et al. (2018)	Huron	MH1	Seneca Lake	2009-2012	0.000	0.000	0.133	0.078	0.192
Scribner et al. (2018)	Huron	MH2	Seneca Lake	2009-2012	0.222	0.422	0.530	0.460	0.603
Scribner et al. (2018)	Huron	MH2	Seneca Lake	2009-2012	0.000	0.000	0.106	0.046	0.165
Scribner et al. (2018)	Huron	MH345	Seneca Lake	2009-2012	0.209	0.335	0.624	0.542	0.701
Scribner et al. (2018)	Huron	MH345	Seneca Lake	2009-2012	0.000	0.000	0.138	0.068	0.210
Scribner et al. (2018)	Huron	OH1	Seneca Lake	2009-2012			0.433	0.396	0.467
Scribner et al. (2018)	Huron	OH1	Seneca Lake	2009-2012			0.406	0.372	0.440
Scribner et al. (2018)	Huron	OH23	Seneca Lake	2009-2012			0.349	0.251	0.438
Scribner et al. (2018)	Huron	OH23	Seneca Lake	2009-2012			0.485	0.388	0.593
Scribner et al. (2018)	Huron	OH45	Seneca Lake	2009-2012	0		0.372	0.329	0.417
Scribner et al. (2018)	Huron	OH45	Seneca Lake	2009-2012	0		0.383	0.336	0.426
Scribner et al. (2018)	Huron	NC12	Seneca Lake	2009-2012	0		0.427	0.364	0.484
Scribner et al. (2018)	Huron	NC12	Seneca Lake	2009-2012	0.102		0.536	0.459	0.583
Scribner et al. (2018)	Huron	MH1	Superior	2002-2004	0.000	0.000	0.293	0.257	0.326
Scribner et al. (2018)	Huron	MH1	Superior	2002-2004	0.705	0.752	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Superior	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Superior	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Superior	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Superior	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Superior	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Superior	2002-2004	0.681	0.735	0.240	0.159	0.326
Scribner et al. (2018)	Huron	MH2	Superior	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Superior	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Superior	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Superior	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Superior	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Superior	2002-2004	0.802	0.876	0.300	0.259	0.345
Scribner et al. (2018)	Huron	MH345	Superior	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Superior	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Superior	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Superior	2002-2004	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Superior	2002-2004			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Superior	2002-2004			0.104	0.045	0.169
Scribner et al. (2018)	Huron	OH1	Superior	2002-2004			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Superior	2002-2004			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Superior	2002-2004			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Superior	2002-2004			0.000	0.000	0.000
Scribner et al. (2018)	Huron	GB	Superior	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	GB	Superior	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	GB	Superior	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	GB	Superior	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	GB	Superior	2002-2004	0.465		0.055	0.023	0.090
Scribner et al. (2018)	Huron	GB	Superior	2002-2004	0.351		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC3	Superior	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC3	Superior	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC3	Superior	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC3	Superior	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC3	Superior	2002-2004	0		0.000	0.000	0.000

Appendix B continued

STUDY	LAKE-SITE	MGT_UNIT	STRAIN	YEARS	EXP-Stocki	EXP-P(	Observ	OBS-L9!	OBS-U9!
Scribner et al. (2018)	Huron	NC3	Superior	2002-2004	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Superior	2009-2012	0.080	0.121	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Superior	2009-2012	0.103	0.163	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Superior	2009-2012	0.035	0.040	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Superior	2009-2012	0.014	0.039	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Superior	2009-2012	0.272	0.161	0.046	0.024	0.068
Scribner et al. (2018)	Huron	MH1	Superior	2009-2012	0.002	0.004	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Superior	2009-2012	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH1	Superior	2009-2012	0.005	0.001	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Superior	2009-2012	0.011	0.023	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Superior	2009-2012	0.223	0.118	0.085	0.047	0.126
Scribner et al. (2018)	Huron	MH2	Superior	2009-2012	0.006	0.012	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH2	Superior	2009-2012	0.000	0.000	0.061	0.025	0.097
Scribner et al. (2018)	Huron	MH2	Superior	2009-2012	0.050	0.052	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Superior	2009-2012	0.006	0.009	0.055	0.024	0.090
Scribner et al. (2018)	Huron	MH345	Superior	2009-2012	0.244	0.155	0.041	0.014	0.069
Scribner et al. (2018)	Huron	MH345	Superior	2009-2012	0.017	0.024	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Superior	2009-2012	0.000	0.000	0.000	0.000	0.000
Scribner et al. (2018)	Huron	MH345	Superior	2009-2012	0.213	0.258	0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Superior	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Superior	2009-2012			0.061	0.015	0.115
Scribner et al. (2018)	Huron	OH1	Superior	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Superior	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Superior	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH1	Superior	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH23	Superior	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH23	Superior	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH23	Superior	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH23	Superior	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH23	Superior	2009-2012			0.165	0.081	0.252
Scribner et al. (2018)	Huron	OH23	Superior	2009-2012			0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH45	Superior	2009-2012	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH45	Superior	2009-2012	0		0.094	0.037	0.156
Scribner et al. (2018)	Huron	OH45	Superior	2009-2012	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH45	Superior	2009-2012	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	OH45	Superior	2009-2012	0		0.151	0.078	0.229
Scribner et al. (2018)	Huron	OH45	Superior	2009-2012	1		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC12	Superior	2009-2012	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC12	Superior	2009-2012	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC12	Superior	2009-2012	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC12	Superior	2009-2012	0		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC12	Superior	2009-2012	0.493		0.000	0.000	0.000
Scribner et al. (2018)	Huron	NC12	Superior	2009-2012	0		0.000	0.000	0.000

Appendix C

Instantaneous total mortality matrix of Lake Trout estimated with the 08-25-21 version of the WIIM stock assessment and used to project abundance, within year survival, and spawning biomass in southern Lake Michigan. Age-1 mortality rates for 1980, 1981, and 1984 were positive in the stock assessment output because abundance at age 2 was greater than at age 1, so we used the average mortality during 1973-1983 in 1980 and 1981 and the adjacent value of 1983 for 1984.

	Age																			
Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20+
1965																				
1966	0.4116																			
1967	1.1591	0.5276																		
1968	1.0518	0.5276	0.2100																	
1969	1.0836	0.5276	0.2100	0.2100																
1970	0.6078	0.5276	0.2100	0.2100	0.2100															
1971	0.5166	0.5276	0.2100	0.2100	0.2100	0.2100														
1972	0.6487	0.5276	0.2100	0.2100	0.2100	0.2100	0.2100													
1973	0.3383	0.5276	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100												
1974	0.3594	0.5276	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100											
1975	0.3902	0.5276	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100										
1976	0.3381	0.5276	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100									
1977	0.1980	0.5276	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100								
1978	0.1372	0.5276	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100							
1979	0.1775	0.5276	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100						
1980	0.2754	0.5276	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100					
1981	0.2754	0.5276	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100				
1982	0.1816	0.5276	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100			
1983	0.3580	0.5276	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100		
1984	0.3580	0.5276	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	0.2100	
1985	0.4597	0.4333	0.0956	0.1216	0.1693	0.1776	0.1761	0.1716	0.1718	0.1702	0.1736	0.1884	0.1758	0.1806	0.1740	0.1708	0.1708	0.1708	0.1708	0.1708
1986	0.5543	0.4343	0.1021	0.1365	0.2052	0.2241	0.2296	0.2299	0.2330	0.2333	0.2388	0.2549	0.2421	0.2479	0.2412	0.2379	0.2379	0.2379	0.2379	0.2379
1987	0.5092	0.4333	0.0964	0.1249	0.1758	0.1864	0.1840	0.1796	0.1798	0.1772	0.1816	0.1952	0.1829	0.1876	0.1811	0.1779	0.1779	0.1779	0.1779	0.1779
1988	0.4448	0.4343	0.1016	0.1383	0.2061	0.2229	0.2276	0.2252	0.2264	0.2248	0.2292	0.2448	0.2324	0.2371	0.2306	0.2275	0.2275	0.2275	0.2275	0.2275
1989	0.6017	0.4441	0.1842	0.2504	0.3333	0.3673	0.3771	0.3849	0.3904	0.3924	0.3944	0.4068	0.3976	0.4026	0.3972	0.3945	0.3945	0.3945	0.3945	0.3945
1990	0.8801	0.4353	0.1030	0.1579	0.2175	0.2358	0.2451	0.2464	0.2535	0.2548	0.2603	0.2774	0.2656	0.2714	0.2647	0.2615	0.2615	0.2615	0.2615	0.2615
1991	0.5896	0.4361	0.1077	0.1508	0.2763	0.3127	0.3238	0.3294	0.3340	0.3384	0.3432	0.3562	0.3484	0.3528	0.3480	0.3457	0.3457	0.3457	0.3457	0.3457
1992	0.5056	0.4352	0.1115	0.1825	0.2853	0.3658	0.3838	0.3934	0.4058	0.4106	0.4187	0.4347	0.4259	0.4321	0.4264	0.4236	0.4236	0.4236	0.4236	0.4236
1993	0.8754	0.4335	0.1053	0.1498	0.2451	0.2639	0.2644	0.2565	0.2561	0.2523	0.2565	0.2747	0.2579	0.2641	0.2555	0.2513	0.2513	0.2513	0.2513	0.2513
1994	0.6167	0.4336	0.1070	0.1557	0.2565	0.2786	0.2742	0.2684	0.2667	0.2635	0.2680	0.2880	0.2693	0.2763	0.2667	0.2621	0.2621	0.2621	0.2621	0.2621
1995	1.0991	0.4331	0.0900	0.1237	0.2387	0.2733	0.2720	0.2675	0.2674	0.2652	0.2667	0.2751	0.2668	0.2697	0.2657	0.2638	0.2638	0.2638	0.2638	0.2638
1996	0.7950	0.4360	0.1195	0.1833	0.3129	0.3899	0.4284	0.4468	0.4557	0.4704	0.4789	0.4935	0.4901	0.4960	0.4920	0.4900	0.4900	0.4900	0.4900	0.4900
1997	1.1691	0.4382	0.1135	0.1904	0.3163	0.3710	0.3910	0.3980	0.4045	0.4046	0.4126	0.4266	0.4178	0.4236	0.4183	0.4157	0.4157	0.4157	0.4157	0.4157
1998	1.0966	0.4399	0.1267	0.2099	0.4089	0.4792	0.4934	0.4968	0.5034	0.5050	0.5122	0.5317	0.5178	0.5254	0.5188	0.5160	0.5168	0.5174	0.5189	0.5189
1999	0.8863	0.4355	0.1081	0.1557	0.2639	0.2921	0.2918	0.2865	0.2868	0.2842	0.2883	0.3054	0.2901	0.2962	0.2888	0.2853	0.2856	0.2857	0.2861	0.2861
2000	0.8895	0.4373	0.0986	0.1406	0.2526	0.2981	0.3094	0.3149	0.3196	0.3222	0.3251	0.3297	0.3281	0.3302	0.3295	0.3294	0.3299	0.3302	0.3310	0.3310
2001	0.8717	0.4370	0.0943	0.1317	0.2341	0.2796	0.2932	0.3012	0.3069	0.3107	0.3135	0.3157	0.3170	0.3183	0.3190	0.3196	0.3202	0.3205	0.3215	0.3215
2002	0.6044	0.4380	0.0976	0.1333	0.2161	0.2542	0.2672	0.2748	0.2804	0.2841	0.2869	0.2894	0.2903	0.2916	0.2922	0.2927	0.2932	0.2936	0.2945	0.2945
2003	0.7223	0.4438	0.1187	0.1708	0.2493	0.2930	0.3154	0.3296	0.3398	0.3465	0.3514	0.3551	0.3574	0.3596	0.3609	0.3620	0.3629	0.3636	0.3652	0.3652
2004	0.4639	0.4383	0.0988	0.1305	0.1822	0.2114	0.2267	0.2365	0.2436	0.2484	0.2519	0.2546	0.2562	0.2578	0.2587	0.2595	0.2601	0.2606	0.2618	0.2618
2005	0.9566	0.4437	0.1168	0.1614	0.2217	0.2553	0.2727	0.2837	0.2915	0.2966	0.3004	0.3035	0.3050	0.3068	0.3077	0.3084	0.3091	0.3096	0.3108	0.3108
2006	0.9502	0.4428	0.1141	0.1577	0.2152	0.2492	0.2681	0.2803	0.2890	0.2947	0.2989	0.3021	0.3040	0.3059	0.3070	0.3080	0.3087	0.3093	0.3107	0.3107
2007	1.3625	0.4382	0.0979	0.1266	0.1735	0.1990	0.2115	0.2194	0.2252	0.2290	0.2318	0.2341	0.2352	0.2365	0.2372	0.2378	0.2383	0.2387	0.2396	0.2396
2008	1.8733	0.4394	0.1009	0.1317	0.1871	0.2140	0.2245	0.2308	0.2353	0.2383	0.2405	0.2423	0.2431	0.2441	0.2446	0.2450	0.2454	0.2457	0.2464	0.2464
2009	1.4143	0.4393	0.0993	0.1259	0.1739	0.1961	0.2040	0.2086	0.2118	0.2139	0.2155	0.2170	0.2174	0.2182	0.2184	0.2187	0.2190	0.2192	0.2197	0.2197
2010	1.4214	0.4394	0.1005	0.1290	0.1798	0.2035	0.2124	0.2175	0.2212	0.2235	0.2254	0.2272	0.2276	0.2285	0.2288	0.2291	0.2294	0.2296	0.2302	0.2302
2011	0.9614	0.4390	0.0989	0.1264	0.1802	0.2040	0.2118	0.2161	0.2192	0.2211	0.2227	0.2244	0.2245	0.2254	0.2255	0.2258	0.2260	0.2262	0.2267	0.2267
2012	0.9479	0.4371	0.0926	0.1163	0.1706	0.1941	0.2010	0.2048	0.2076	0.2093	0.2107	0.2121	0.2123	0.2131	0.2132	0.2134	0.2137	0.2139	0.2143	0.2143
2013	1.0789	0.4374	0.0937	0.1187	0.1757	0.2003	0.2075	0.2114	0.2142	0.2160	0.2174	0.2188	0.2191	0.2198	0.2200	0.2202	0.2205	0.2206	0.2211	0.2211
2014	1.2555	0.4365	0.0908	0.1183	0.1946	0.2270	0.2354	0.2399	0.2432	0.2453	0.2468	0.2480	0.2487	0.2494	0.2498	0.2502	0.2505	0.2507	0.2512	0.2512
2015	1.3191	0.4339	0.0818	0.1034	0.1864	0.2183	0.2230	0.2250	0.2264	0.2273	0.2279	0.2285	0.2288	0.2291	0.2292	0.2294	0.2295	0.2296	0.2298	0.2298
2016	0.9827	0.4338	0.0818	0.1064	0.2048	0.2418	0.2463	0.2479	0.2490	0.2497	0.2503	0.2511	0.2510	0.2514	0.2514	0.2515	0.2516	0.2516	0.2518	0.2518
2017	0.9826	0.4335	0.0804	0.0998	0.1775	0.2066	0.2101	0.2113	0.2122	0.2127	0.2132	0.2139	0.2137	0.2141	0.2140	0.2140	0.2141	0.2142	0.2143	0.2143
2018	0.9827	0.4341	0.0824	0.1047	0.1891	0.2215	0.2261	0.2280	0.2292	0.2301	0.2307	0.2313	0.2315	0.2318	0.2319	0.2321	0.2322	0.2323	0.2325	0.2325
2019	0.9827	0.4341	0.0826	0.1063	0.1971	0.2317	0.2364	0.2382	0.2395	0.2403	0.2409	0.2416	0.2417	0.2421	0.2421	0.2422	0.2423	0.2424	0.2426	0.2426