Evaluation of sea lamprey-associated mortality sources on a generalized lake sturgeon population in the Great Lakes

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Abstract

Lake sturgeon populations in the Laurentian Great Lakes experience two age-specific mortality sources influenced by the sea lamprey *Petromyzon marinus* control program: lampricide (TFM) exposure-induced mortality on age-0 fish and sea lamprey predation on sub-adults (ages 7-24). We used a generic age-structured population model to show that although lampricide-induced mortality on age-0 lake sturgeon can limit attainable population abundance, sea lamprey predation on sub-adult lake sturgeon may have a greater influence. Under base conditions, adult lake sturgeon populations increased by 5.7% in the absence of TFM toxicity if there was no change in predation, whereas a 13% increase in predation removed this effect, and a doubling of sea lamprey predation led to a 32% decrease in adult lake sturgeon. Our estimates of lake sturgeon abundance were highly dependent on the values of life history and mortality parameters but the relative impacts of ceasing TFM treatment and increasing predation were robust given a status quo level of predation. The status quo predation was based on sea lamprey wounding on lake sturgeon, and improvements in this information would help better define tradeoffs between the mortality sources for specific systems. Reduction or elimination of TFM toxicity on larval lake sturgeon, while maintaining TFM toxicity on larval sea lamprey, can promote lake sturgeon restoration and minimize negative impacts on other fish community members.

Keywords: lake sturgeon, sea lamprey control, TFM toxicity, Laurentian Great Lakes

Introduction

Lake sturgeon *Acipenser fulvescens*, once abundant in the Laurentian Great Lakes, became scarce by the 1920s primarily as a consequence of intense fishing pressure intended to limit damage that fish caused to nets used to harvest more valuable species (Smith, 1968). Other factors also contributed to lake sturgeon declines, which included poor water quality, loss of spawning habitat, barriers to migration, and commercial exploitation (Auer, 1996; Harkness and Dymond, 1961; Rochard et al., 1990; Smith, 1968). More recently, researchers have implicated climate change and its related reductions in water levels and increases in water temperature and egg predation by round goby *Neogobius melanostomus* (Bruch and Binkowski, 2002; Thomas and Haas, 2002) as factors inhibiting the recovery of lake sturgeon populations. Sea lamprey *Petromyzon marinus* control efforts that have involved the application of the lampricide 3-trifluormethyl-4-nitrophenol (TFM) have also been identified as a factor contributing to age-0 lake sturgeon mortality (Boogaard et al., 2003). As a result of these stressors, lake sturgeon are listed as threatened in all of the states of the USA surrounding the Laurentian Great Lakes (Birstein et al., 1997), threatened in the Canadian province of Ontario (Great Lakes – Upper St. Lawrence River populations) under the Provincial *Endangered Species Act, 2007*, and vulnerable on the IUCN Red List (IUCN, 2011).

The lake sturgeon is a benthivore, valued for its historical role in the Great Lakes fish community, as a key element in the culture of native peoples, and for its unique prehistoric ancestry that attracts considerable public attention (Beck, 1995; Centre, 2015; Hayes and Caroffino, 2012; Peterson et al., 2007). Lake sturgeon are found throughout the Great Lakes basin (Baker, 1980; Hay-Chmielewski and Whelan, 1997; Priegel et al., 1974), including the St. Marys River (Bauman et al., 2011), the St. Clair River and Lake St. Clair (Thomas and Haas, 2002) and the Detroit River (Caswell et al., 2004; Roseman et al., 2011), and in inland waters surrounding the lakes (Bruch et al., 2006; Noakes et al., 1999; Vecsei, 2011). The larger tributaries support critical sturgeon spawning and age-0 rearing habitat, but also provide spawning areas for invasive sea lamprey. Sea lamprey are fish parasites in the Great Lakes and seek hosts in the open waters following transformation from the larval life stage (Smith and Tibbles, 1980). Sea lamprey parasitism often results in host mortality, although attack rates have been shown to vary by body length (Swink, 2003). For lake sturgeon, survival following a sea lamprey attack has also been found to vary with length, with smaller individuals generally more susceptible to mortality (Patrick et al., 2009). Larger lake sturgeon have been found with more than one sea lamprey wound indicating they can survive multiple attacks. However, ultimate fitness may be reduced for individuals following multiple sea lamprey attacks (Sepulveda et al., 2012).

One of the mandates of the binational Great Lakes Fishery Commission is to control sea lamprey in the Great Lakes and reduce their impact on historically, commercially, and ecologically important fishes such as lake trout *Salvelinus namyacush* (Gaden et al., 2008). The primary method of controlling larval sea lamprey in rivers and streams is the application of TFM or a combination of TFM and niclosamide (2', 5-dichloro-4'-nitrosalicylanilide) in three- to five-year cycles (Adair and Sullivan, 2009). Toxicity of TFM and efficacy of application varies widely and can be influenced by pH, alkalinity, season, and stream flow (Bills et al., 2000; Bills et al., 2003; Boogaard et al., 2003; O'Connor et al., 2017; Scholefield et al., 2008), but has been effective in reducing larval sea lamprey abundance and subsequent wounding caused by parasitic sea lamprey (Morse et al., 2003; Schleen et al., 1998; Smith and Tibbles, 1980). Lampricides, particularly TFM, have also been shown to increase mortality of other stream-dwelling species (Dawson et al., 2002; Lech, 1974; Maki et al., 1975), including age-0 lake sturgeon (Bills et al., 2000; Boogaard et al., 2003; Johnson et al., 1999; O'Connor et al., 2017). While toxicity of TFM to age-0 sturgeon appears to be lower than originally reported, toxicity is still estimated to be high in high alkalinity tributaries (O'Connor et al., 2017). To limit some of the negative impacts of TFM on age-0 sturgeon, the Sturgeon Treatment Protocol was developed to minimize mortality of larval lake sturgeon by applying a lower dose of TFM and delaying the time of application until after August 1st when most of the lake sturgeons exceeded 100mm in length, a size where TFM toxicity is highly reduced (Klar et al., 1999; TOP:011.10A, 2012).

Lake sturgeon survival is impacted by sea lamprey directly through parasitism on sub-adults and through TFM toxicity on age-0 fish in tributaries during lampricide treatments. When sea lamprey treatments are delayed, either later in the season (Sturgeon Treatment Protocol) or by skipping a treatment cycle to minimize the negative impact on age-0 lake sturgeon, more parasitic sea lamprey may be produced, thereby increasing parasitism of fishes in the Great

Lakes (Christie and Goddard, 2003; Ebener et al., 2003; King, 1980; Larson et al., 2003; Stewart et al., 2003). Although TFM has the potential to impact lake sturgeon abundance (Caroffino et al., 2010b), it is possible this produces only a small percentage change in total survival from egg to later life stages, given the already high natural mortality of lake sturgeon from egg to age-0. As a result, increasing the abundance of lake sturgeon is a tradeoff between mortality impacts on different age groups. In this case, it is critical to examine whether the application of TFM and its associated mortality on age-0 lake sturgeon exceeds the losses caused by sea lamprey parasitism on sub-adults and adults.

Sutton et al. (2003) and Velez-Espino and Koops (2009) used age-structured population models to examine this tradeoff and concluded that reducing sub-adult and adult lake sturgeon mortality improved long-term population viability more so than reducing mortality on younger life stages. Since these studies were completed, new information has become available on TFM toxicity to age-0 lake sturgeon and the vulnerability of older lake sturgeon to sea lamprey parasitism (O'Connor et al., 2017; Patrick et al., 2009). Consequently, we updated the analyses conducted by Sutton et al. (2003) to reexamine the effects of sea lamprey control efforts on lake sturgeon equilibrium population abundances. The objectives of this study were to (1) examine the effects of TFM-induced mortality on age-0 lake sturgeon on adult sturgeon recruitment; (2) evaluate how changes in sea lamprey predation on sub-adult lake sturgeon affects sturgeon abundance; and (3) determine which mortality sources have the greatest influence on lake sturgeon population abundance. The model results will improve our understanding of the factors impacting lake sturgeon population viability and help direct conservation efforts to areas that will provide the best chance of recovery.

Methods

Age-structured Model

We used an age-structured model to represent a generalized population of lake sturgeon in the Great Lakes to compare the effects of TFM-induced mortality on age-0 fish and increased sea lamprey parasitism on sub-adult lake sturgeon (Table 1). We used existing life-history data from Sutton et al. (2003) and more recent estimates for several mortality sources (Table 1). Age-0 lake sturgeon recruits were generated using a stock recruitment model that employed information about reproductive potential (Sutton et al., 2003). We estimated total abundance but only included females in reproductive calculations, assuming that a sufficient number of males exist in the population and that they experience the same level of mortality as females.

Because sources of mortality and conditional mortality rates varied by age, we divided the population into four life-stage categories: age-0, juveniles (ages 1-6), sub-adults (ages 7-24), and adults (ages 25+). The maximum age of a lake sturgeon was set to 100 years and the age of female maturity was 25 years. The model was constructed in R (R Development Core Team, 2010) and simulated 500 years to allow the population to reach equilibrium.

Numbers at age-1 and older life stages were projected using an exponential population function,

$$N_a = N_{a-1} * e^{-Z_{a-1}}, \qquad (1)$$

where age *a* was 1 to 100 years and *Z* was the instantaneous total mortality rate based on the sum of the mortality sources from natural mortality (*M)*, TFM-induced mortality (*Mt*), and sea lamprey predation (*Ms*) for each age group *a*:

$$Z_a = M_a + Mt_a + Ms_a\ . \qquad (2)$$

Age-0 recruits experience different natural morality rates during the larval life stage (Caroffino et al., 2010b), the subsequent age-0 juvenile life stage (Caroffino et al., 2010b), and the period between winter and the following summer at age one (Crossman et al., 2009). We captured the higher early mortality, by assuming an overall finite natural mortality rate for age-0 fish of 0.9998 (Caroffino et al., 2010a) and used the Sutton et al. (2003) instantaneous natural mortality rate of 0.25 for juvenile lake sturgeon that had been estimated for Gulf sturgeon *Acipenser oxyrinchus desotoi* (Pine et al., 2001). Sutton et al. (2003) assumed there was no natural mortality on sub-adult or adult lake sturgeon. However, lake sturgeon are exposed to several other sources of mortality such as boat strikes (Hayes and Caroffino, 2012), parasitism by silver lamprey *Ichthyomyzon unicuspis*, botulism poisoning (Clapp et al., 2011; Elliott et al., 2005), tribal subsistence and state-licensed sport angler harvest in some areas, and incidental capture in commercial fishing gear. Although these studies did not estimate natural mortality, we assigned a small value of natural mortality to sub-adult and adult lake sturgeon ($M_{a>6}$ = 0.01) to account for these sources of mortality.

When TFM is applied to a stream, age-0 lake sturgeon may experience an increase in mortality. Lacking specific TFM-toxicity data, Sutton et al. (2003) allowed TFM-induced mortality to vary between 0 and 100%. However, new research has estimated the mean TFM-induced mortality at 21% (O'Connor et al., 2017). Earlier research noted reduced mortality on age-0 lake sturgeon once they exceeded 100 mm (Boogaard et al., 2003), while more recent observations from the Muskegon River noted mortality impacts on lake sturgeon up to 220 mm (Justin Chiotti, USFWS, August 2017, personal communication). Given the length-at-age relationship we used, age-0 lake sturgeon reach a maximum size of 280 mm near the end of their first year of life (Figure 1); thus, we applied the mean TFM toxicity to all age-0 fish, and assumed that individuals age-1 and older were not susceptible to TFM toxicity (i.e,. $Mt_{a>0}$ = 0) (Boogaard et al., 2003).

Tributaries with larval sea lamprey are generally treated on a three- to five-year cycle (Sullivan et al., 2016). Because we did not model a specific stream, we accounted for an average treatment frequency of every four years. Rather than model pulses of TFM morality we applied a constant instantaneous TFM-induced rate, which we calculated by multiplying the conditional TFM-induced mortality rate by 0.25 before converting it to an instantaneous rate.

Given the length-at-age relationship we used, lake sturgeons exceed 40 cm in length by age 4 and become vulnerable to sea lamprey parasitism (Figure 1). Sea lamprey wounding rates (Rutter and Bence, 2003) and the probability of surviving an attack (Patrick et al., 2009) varied with lake sturgeon length. We used a relationship between average wounding rate and the probability of surviving an attack (Bence et al., 2003) to estimate an instantaneous predation mortality for ages 4 and older:

$$Ms_{a>4} = Wr * Ws_b * (1 - Ps_b)/Ps_b, \tag{3}$$

where Wr was the wounding rate (sum of A1, A2, and A3 wounds per fish; see Ebener et al. (2003) on large fish (larger than 76 cm) and was set to 0.22 (Sutton et al. 2003). The parameter Ws_b was an estimate of the relative marking rate on smaller size classes, based on relative marking rates observed on the same size classes of lake trout. This scaled the wounding rate for large fish to the smaller length bins *b* (Mark Ebener, unpublished data). Length bins were 40-57, 57.1-65, and 65.1-76 cm as in Patrick et al. (2009). The parameter Ws_b per bin was 0.236, 0.579, and 0.816, respectively. Ps_b was the probability of surviving a sea lamprey attack for length bin *b* (Patrick et al. 2009). Lake sturgeon that did not occur within one of the length bins were assumed to suffer no mortality from sea lamprey predation.

In a tank experiment, Patrick et al. (2009) assessed lake sturgeon survival following a sea lamprey attack by dividing lake sturgeon into three size classes. Their findings were somewhat inconsistent between the two smallest size classes where survival in Class I was significantly higher than survival in Class II. Patrick et al. (2009) acknowledged that these results were not expected and that small sample sizes or small host-to-lamprey weight ratios could have accounted for the higher mortality observed in Class II and higher survival in Class I. We believe a more likely relationship would be for survival to increase with size as noted by Swink (2003) for lake trout. Therefore, we created a linear relationship based on Patrick et al. (2009), such that Ps_b was 0.50, 0.74, and 0.84 per bin, respectively. Because age-0 individuals do not experience sea lamprey predation, $Ms_0 = 0$.

Patrick et al. (2009) did not include estimates of survival for lake sturgeon between 76 and 95 cm, but fish between 95 and 150 cm had 100% survival following a sea lamprey attack. Sepulveda et al. (2012) found that fish > 76 cm were able to rapidly restore red blood cells following an attack but could not conclusively determine whether these fish could survive multiple attacks. Based on these two studies, we assumed that all lake sturgeon > 76 cm did not suffer mortality following a sea lamprey attack.

Length-at-age (cm) was estimated using the von Bertalanffy growth equation:

$$L_a = L_\infty\left(1 - e^{-K(t-t_0)}\right), \tag{4}$$

where L_∞ = 228.638, K = 0.023, and t_0 = -4.713 (Harkness and Dymond, 1961). Using this relationship, lake sturgeon exceed 76 cm by age 13 while they are sub-adults.

Recruitment of age-0 fish (*R*) was generated using a Beverton-Holt stock-recruit model (Quinn and Deriso, 1999):

$$R = \frac{\alpha S}{(1+\beta S)}, \tag{5}$$

where parameters α and β were derived from values used in Sutton et al. (2003), which in turn were based on values from Pine et al. (2001). Our conventional parameterization differs from that of Sutton (2003) but represents the same function. The initial re-parameterization led to α = 1.25. This value was not plausible here because it implies that each unit of stock would produce 1.25 recruits at low population density, and stock size was measured in terms of eggs. Consequently, we set α = 1.0, as the highest feasible value, and then adjusted β to be $1.055*10^{-7}$ so that the equilibrium recruitment in the absence of TFM and sea lamprey mortality matched those of Sutton et al. (2003) for our baseline life-history parameters. Equilibrium recruitment was calculated following Quinn and Deriso (1999) (see Table 7.4). Stock size was determined as:

$$S = \sum_{a=25}^{100} pf * ps * F_a * N_a . \tag{6}$$

The proportion of the spawning population that was female in each year, *pf*, was set to 35% (Auer, 1999). The proportion of those females that spawn each year, *ps*, was 20% (Sutton et al., 2003). Fecundity for each age was based on length (Harkness and Dymond, 1961) as:

$$F_a = 3.76 * 10^{-3} * {L_a}^{3.59}. \tag{7}$$

We used the sum of lake sturgeon age 25+ at equilibrium as an indicator of population size given specific scenarios.

Simulated Scenarios

The parameters as described above are from the Base Model. We ran a series of scenarios where we varied either TFM-induced mortality on age-0 individuals or sea lamprey-induced mortality on sub-adults, and evaluated the results relative to those of the Base Model. Because of uncertainty in some of the life-history or mortality values, we also ran scenarios where we varied specific parameter values while holding all other values constant to examine the impact of specific values on results, again relative to the Base Model.

To compare scenarios, we used the total abundance of age-25+ lake sturgeon at equilibrium. The absolute population abundance is, in part, driven by the asymptote of the stock-recruitment function, which was based on a different sturgeon species and further likely varied among lake sturgeon populations. Therefore, we used the relative change in abundance for each scenario compared to the Base Model as a basis for evaluating both tradeoffs between TFM and sea lamprey mortality, and sensitivity of results to the values of uncertain parameters.

Mortality rates due to TFM exposure vary widely between studies and streams. In laboratory experiments, Boogaard et al. (2003) found TFM toxicity exceeded 50% mortality at the minimum lethal concentration used for effective larval sea lamprey control. O'Connor et al. (2017) tested age-0 lake sturgeon for TFM toxicity from a number of streams and found that TFM-induced mortality ranged between 0 and 0.55. To explore the effects of higher and lower TFM toxicity, we set $Mt_{a=0}$ to 0.12 which was observed in the Batchawana River, Ontario, having the lowest alkalinity (25 mg CaCO3/L) and lower TFM toxicity and set $Mt_{a=0}$ to 0.55 from the Pigeon River, Michigan, which had the highest alkalinity (203 mg CaCO3/L) and TFM toxicity examined by O’Connor et al. (2017). Streams may also be treated with a combination of TFM and niclosamide to increase effectiveness of the lampricide. This combination produced higher toxicities on age-0 lake sturgeon (O’Connor et al. 2017). Nevertheless, we did not consider higher TFM toxicity, assuming that this treatment would only be used in known lake sturgeon streams when water chemistry was such as to limit toxicity. In the scenario where TFM toxicity is lower than the Base Model, it mimics the possible positive effects of using the Sturgeon Treatment Protocol (Klar et al., 1999; TOP:011.10A, 2012). In these two scenarios, sea lamprey predation on sub-adult lake sturgeon was held constant at the value used in the Base Model.

Sea lamprey predation on the fish community in the Great Lakes increases when TFM concentrations are reduced or streams are untreated (Heinrich et al., 2003; Smith and Tibbles, 1980; Torblaa and Westman, 1980). It is difficult to predict how much sea lamprey predation would increase if fewer larval sea lamprey were killed in streams and allowed greater sea lamprey production. We simulated different sea lamprey predation rates using a multiplier on sea lamprey-induced mortality (*Ms*) such that predation rates increased by 1.1, 1.25, 1.5, 1.75, and 2.0 relative to that of the Base Model where *Ms= 1.0*. We chose this range to represent small to large increases in sea lamprey predation because the literature does not contain specific estimates of how sea lamprey predation changes when TFM is not applied to streams.

Sea lamprey wounding rates on lake sturgeon are highly variable across the Great Lakes. Examples of wounding rates on specific lake sturgeon populations include Lake Superior (0.003 to 0.03 marks/fish; Josh Scholoesser, USFWS, August 2017, personal communication), Lake Michigan (0.052 marks/fish in open waters and 0.088 marks/fish in Green Bay; Rob Elliott, USFWS, August 2017, personal communication), and Lake Huron (0.51 marks/fish in the southern part of the lake and 0.48 in the Detroit River; Justin Chiotti, USFWS, August 2017, personal communication). Some surveys regularly found no sea lamprey wounds on lake sturgeon (Corey Jerome, Little River Band of Ottawa Indians, August 2017 and Troy Zorn, Michigan Department of Natural Resources, August 2017, personal communications). Many of these surveys did not record the length of the lake sturgeon or the types of sea lamprey marks, thus making it difficult to estimate the actual wounding rate for fish < 76 cm. Nearly all of these data came from surveys that did not target juvenile lake sturgeon. Because of the wide variation in wounding rates across lakes, we chose to conduct a sensitivity analysis on a range of sea lamprey wounding rates by setting *Wr* to 0.05 and 0.10. These alternate wounding rates produced a range of actual sea lamprey predation rates based on Equation #3 (Table 2). The unusually high wounding rates in southern Lake Huron and the Detroit River, likely reflect the high sea lamprey population in that area due to withholding TFM treatment to support native fish restoration efforts and are unlikely representative of a generic lake sturgeon population that we are emulating.

The probability of surviving a sea lamprey attack (Patrick et al. 2009) was reported with uncertainty that we did not include in the Base Model. To understand the potential effect of adding uncertainty to this relationship, we ran two sensitivity analyses on Ps_b by increasing Ps_b by 20% and decreasing Ps_b by 20% on our linear adjustment to the Patrick et al. (2009) data.

In the Base Model, we used a small natural mortality rate ($M_{a>6} = 0.01$) for sub-adult and adult lake sturgeon to represent a long-lived species with minimal mortality sources. We also examined the general literature on how natural mortality relates to life history and environment, and on this basis concluded that for older lake sturgeon natural mortality could be higher; e.g., based on published approaches values in the range of 0.035 seem plausible [(Srinath, 1998): 0.035, (Pauly, 1980): 0.048, (Hewitt and Hoenig, 2005): 0.042, (Jensen, 1996): 0.066)]. Hayes and Caroffino (2012) and Schueller and Hayes (2010) set instantaneous natural mortality to 0.05 for sub-adult and adult lake sturgeon based on Baker (1980). Lake sturgeon populations have been found to be particularly sensitive to the rate of adult mortality (Schueller and Hayes, 2010; Velez-Espino and Koops, 2009), so we tested this sensitivity by setting the natural mortality rate on sub-adult and adult lake sturgeon to 0.05.

Juvenile lake sturgeon natural mortality had not been studied at the time of the Sutton et al. (2003) research. Sutton et al. (2003) used 0.25, borrowed from Gulf sturgeon (Pine et al., 2001), so we used this value in the Base Model to allow us to compare the new model to the Sutton model. More recent research has found that instantaneous natural mortality of juvenile lake sturgeon (ages 4-17) in Goulais Bay, Lake Superior was 0.14 (Pratt et al., 2014). We ran a simulation with this value for juvenile natural mortality, but otherwise the same as the Base Model to examine how this influenced results.

The length-at-age relationship used in the Base Model represented a generic lake sturgeon population used in the Sutton et al. (2003) model with average growth throughout the age ranges (Figure 1). Some lake sturgeon populations experience much quicker growth rates at earlier ages. Because several key parameters are length based, we explored the effect of higher early growth using a length-at-age relationship established for the Muskegon River, Michigan, lake sturgeon population (Harris et al., 2017).

Lake sturgeon population models have been found to be sensitive to several life-history parameters (Schueller and Hayes, 2010). We examined the influence of life-history parameters on the equilibrium population in four scenarios by varying particular parameters while leaving all others at the values used in the Base Model. Some observers have suggested that lake sturgeon could live significantly longer than 100 years, so we ran a scenario setting maximum age to 150 years to mirror the oldest lake sturgeon caught in Wisconsin rivers. However, with loss of habitat and degraded water quality, it is equally likely that lake sturgeon life expectancy has declined, so we ran another scenario with the maximum age set to 80 years. In another scenario, we examined how a reduction in female-age-at-maturity influenced the model by reducing it from 25 to 15 years (Bruch, 1999; Hay-Chmielewski and Whelan, 1997). Loss of spawning habitat can reduce the frequency of lake sturgeon spawning (McDougall et al., 2014), which we simulated by reducing *ps* to 0.1. Conversely, lake sturgeon habitat has been improving in some areas around the Great Lakes due to restoration efforts (Bennion and Manny, 2014; Hondorp et al., 2014; Roseman et al., 2011). To simulate possible improvements in spawning related to improved habitat, we set the proportion of females spawning each year, *ps*, to 0.3. To examine the sensitivity of the model to these changes, we compared the equilibrium abundance of all scenarios to the Base Model.

Estimating increased parasitic sea lamprey when not treating a stream

Determining the impact of not treating a stream with lampricide is complex and includes the effects on multiple sea lamprey life stages and the effects across multiple streams in a lake. We used an existing stochastic operating model (MSE) that included data used for sea lamprey control efforts and a number of known uncertainties (Jones, 2009) to estimate the magnitude of increased density of larval lampreys in streams that are not treated with TFM. Typically, this model is used to determine which streams to treat with TFM given a control budget and other assumptions about a treatment regime, such as larval sea lamprey survival.

We used a newly added feature that stops TFM treatment on designated streams (Jensen, 2017). While lake sturgeon are found in a number of streams, we investigated three Lake Michigan tributaries considered to have increasing or stable lake sturgeon populations: the Big Manistee, Menominee, and Muskegon rivers (Hayes and Caroffino, 2012). We parameterized the MSE model using the sea lamprey control budget and calibration parameters used in Dawson et al. (2016) and Jensen (2017). We ran this model treating all streams, then removing each lake sturgeon stream from treatment, one at a time. Each simulation was run 300 times for 100 years, and we report the mean number of sea lamprey parasites in the lake basin created during the last 10 years over all simulations when the model reaches equilibrium. We also report the relative change in parasitic sea lamprey population size when one stream is untreated compared to treating all streams as the sea lamprey multiplier.

Results

When compared to the Base Model, reducing the TFM-induced toxicity from 0.21 to 0.12 increased adult lake sturgeon abundance by 2.5% (Table 3). If TFM was not applied, there was no TFM-induced mortality on age-0 lake sturgeon and the equilibrium abundance was 5.7% higher than the Base Model (Table 3). In contrast, when TFM toxicity was higher (Mt_0=0.55), adult lake sturgeon abundance declined by 9.3% from the Base Model (Table 3).

In model simulations where TFM was not applied, there would be an expected increase in larval sea lamprey survival which could lead to increased parasitism on large lake sturgeon and other fish species in the Great Lakes. However, the extent of this increase in sea lamprey predation on lake sturgeon is unknown. When sea lamprey predation increased by 10%, adult lake sturgeon abundance increased by 1.2% over the Base Model. Further increases in sea lamprey predation of 25, 50, 75, and 100% (doubling) caused adult lake sturgeon abundance to decline by 5.2, 15.1, and 24.0%, and 32% respectively (Table 3).

The relationship between equilibrium lake sturgeon abundance and the sea lamprey predation multiplier is approximately linear allowing us to estimate that an increase in sea lamprey predation on older lake sturgeon of 13% is the breakeven point where the effects of sea lamprey predation on sub-adult lake sturgeon have the same influence on equilibrium abundance as TFM-induced mortality, at the Base Model level, on larval lake sturgeon (Figure 2). Thus, levels of sea lamprey predation greater than 13% will exceed the effect of TFM-induced mortality on larval lake sturgeon. When TFM toxicity is lower than the Base Model, the breakeven point is 1.07 or 7% and when TFM toxicity is higher, the breakeven point is 1.35 (Figure 2).

The probability of surviving a sea lamprey attack and sea lamprey wounding rate are used to determine the mortality caused by sea lamprey predation. In scenarios where these varied from the Base Model, they have a significant impact on the equilibrium abundance estimated by the model. Increasing the probability of surviving an attack by 20% increased the equilibrium abundance by 27.3%, while decreasing the probability of survival by 20% reduced abundance by 31.8% (Table 3). Likewise, changing the wounding rate impacted the model results as compared to the Base Model. A low wounding rate (Wr=0.05) increased equilibrium abundance by 40%, while an intermediate wounding rate (Wr=0.10) increased abundance by 26.9% (Table 3).

We examined the breakeven level of sea lamprey predation across a range of wounding rates and TFM toxicity levels (Figure 3). Lower wounding rates require higher levels of sea lamprey predation to offset the impact of TMF toxicity on age-0 lake sturgeon regardless of TFM toxicity level. This suggests that when wounding rates are lower, lake sturgeon abundance may be increased by not applying TFM. Once wounding rates are higher than 0.10 marks/fish, the breakeven point is approximately flat at each TFM toxicity level (Figure 3), indicating little change in the breakeven point at higher wounding rates. Across all wounding rates, higher TFM toxicity required higher levels of sea lamprey predation to breakeven.

There are a number of mortality and life-history parameters that are unknown or not well-studied for Great Lakes lake sturgeon. Our model was sensitive to these parameters to a varying extent (Table 4). Using lower juvenile mortality ($M_{a=1\text{-}6}$ = 0.14), increased equilibrium abundance of adult lake sturgeon compared to the Base Model by 132.2% while increasing sub-adult and adult natural mortality ($M_{a>6}$=0.05) caused the equilibrium abundance to decrease by 87.8% (Table 4). Varying the natural mortality rate for juveniles and for sub-adults and adults, produced the largest changes in lake sturgeon abundance making these the most sensitive parameters in the model (Table 4).

Varying other life-history parameters also changed the equilibrium adult lake sturgeon abundance. Reducing the age of maturity from 25 to 15 years increased abundance by 20.0% (Table 4). Increasing the maximum age from 100 to 150 years increased abundance by 36.7%, whereas reducing the life expectancy to 80 years reduced abundance by 20.9 % (Table 4). Increasing the proportion of females that spawn each year from 20 to 30% only increased the population by 1.3%, while reducing the proportion of females that spawn to 10% caused abundance to decline by 3.6% (Table 4).

Using an alternate length-at-age relationship impacts several other relationships in the model including fecundity, length-based wounding rates, and the probability of surviving a sea lamprey attack. When we applied a length-at-age relationship where individuals grew faster in early ages and reached an asymptote at an earlier age and smaller size, it had a large impact on lake sturgeon abundance, increasing adult abundance by 44.8% over the Base Model. This relative change in abundance was second only to the changes caused by altering juvenile and adult natural mortality (Table 4).

Although the model projections of absolute abundance were highly dependent on the values of the life-history and mortality parameters, the estimated breakeven point was very robust. All scenarios and parameter combinations produced a very similar breakeven point, demonstrating that relatively small increases in sea lamprey predation (about 13%) on sub-adult lake sturgeon could reduce lake sturgeon abundance (Table 4). Thus, while life-history parameters are critical to understanding lake sturgeon abundance, improving our understanding of predation mortality on sub-adult lake sturgeon as well as growth may be more important in terms of evaluating how sea lamprey control impacts lake sturgeon populations.

Effect of increased survival of larval sea lamprey

The sea lamprey MSE model for Lake Michigan predicted that the parasitic sea lamprey population in the lake will increase when any one lake sturgeon stream is not treated with TFM. The amount of this increase is based, in part, on the amount of larval habitat that drives stream productivity. Untreated streams with more larval habitat have the potential to produce larger parasitic sea lamprey populations (Table 5). Subtracting the estimated number of parasitic sea lamprey when all streams are potentially treated results in a 2.1 sea lamprey multiplier when the Menominee River is not treated and a 22.6 and 32.8 sea lamprey multiplier when the Big Manistee and Muskegon rivers, respectively, are not treated (Table 5). While the sea lamprey multiplier for Menominee River is within the range of sea lamprey multipliers we used in our model, the multipliers for the Big Manistee River and the Muskegon River are more than 10 times higher than our upper sea lamprey multiplier value of 2.0, suggesting substantially higher impacts on lake sturgeon abundance and the fish community resulting from increased sea lamprey predation.

Discussion

Reducing mortality on a species undergoing restoration efforts enhances the chance of establishing a self-sustaining population. When reduction in mortality at one life stage can lead to an increase in mortality in another, however, the outcome is less clear. In this study we evaluated the tradeoff between TFM toxicity on age-0 lake sturgeon and sea lamprey predation on sub-adult sturgeon. We found that the effects of eliminating TFM toxicity could outweigh the effects of increased predation mortality in some situations, but this required either low levels of sea lamprey mortality initially or a small increase in predation mortality when TFM treatment was eliminated, or both. For example, with our baseline TFM toxicity and sea lamprey wounding rate, removing TFM toxicity can be balanced by a 13% increase in sea lamprey predation mortality. When the sea lamprey wounding rate was reduced to 0.01, it required a four-fold increase in sea lamprey predation for the gains in age-0 lake sturgeon survival to be offset by sea lamprey predation later in life (Figure 3). In our simulations, all scenarios led to sustainable populations of lake sturgeon. This reflects, in part, our choice of stock-recruitment parameters, and in particular the α parameter of the Beverton-Holt function. If this parameter is standardized following Myers et al. (1999), it is not particularly high relative to other species of fish. This, however, reflects the life history of lake sturgeon and the slope parameter is as high as is feasible as it implies near 100% survival to the larval stage of eggs at low lake sturgeon densities. Under real-world conditions, this high value may more reflect the potential for reduced larval mortality when abundance is low, rather than 100% egg survival. Regardless, it is worth considering what the consequences would be if the recruitment productivity were so low that extinction might occur. Given that in our scenarios equilibrium recruitment was roughly constant, our results for relative equilibrium abundance translate to the approximate relative values of the Beverton-Holt stock recruitment parameter required to avoid extinction. Thus, our results for equilibrium abundance also provide a guide on the relative risk of abundance.

Natural mortality on early life stages of lake sturgeon varies. Although natural mortality declines after the egg and larval stages, overall mortality on age-0 individuals is extremely high, exceeding 99% mortality (Caroffino et al., 2010a). Year-class strength is determined by climatic and hydrological conditions during the early life stages (Nilo et al., 1997). Pollock et al. (2015) summarized research conducted over more than 80 years that demonstrated how larval lake sturgeon survival is impacted by multiple factors including predation, maternal effects, spawning time, and within-river habitat variations. Thus, age-0 lake sturgeon face enormous challenges to their survival. Even with a life-history strategy that favors high fecundity and abundant offspring (Beamesderfer and Farr, 1997; Peterson et al., 2007), few individuals survive to age-1 even without the added mortality from TFM-induced toxicity. Research focusing on reducing early life stage mortality, particularly at the egg and larval stages, could allow more individuals to survive beyond the age and size where they are most vulnerable to TFM toxicity.

Early studies of TFM-induced toxicity on age-0 lake sturgeon predicted higher levels of toxicity (Bills et al., 2000; Boogaard et al., 2003; O'Connor et al., 2017). To reduce the impact of this toxicity on age-0 lake sturgeon, lower doses of TFM were used and treatment was delayed until later in the season, but overall effectiveness of the lampricide was reduced (Hayes and Caroffino, 2012). Subsequent studies on TFM toxicity were conducted by O'Connor et al. (2017) and these researchers found that toxicity varied among and within streams and was highly affected by alkalinity. Because of this variability, we used several values of TFM-induced toxicity to elicit the impact on lake sturgeon abundance. In conditions where TFM- induced mortality was eliminated, there is no added mortality source on age-0 fish over natural mortality. Thus, our highest estimated abundance occurred when lake sturgeon are not exposed to TFM-induced mortality and there is no increase in sea lamprey predation on sub-adult lake sturgeon. While this could occur in some streams, it is not likely to be the circumstance in all lake sturgeon streams.

A more likely scenario involves a tradeoff. If TFM is applied to a stream, TFM-induced mortality affects age-0 lake sturgeon but larval sea lamprey abundance will be reduced and likely reduce sea lamprey predation on sub-adult lake sturgeon. Alternately, not applying TFM to a stream reduces age-0 lake sturgeon mortality but increases survival of larval sea lamprey leading to increased sea lamprey predation on sub-adult lake sturgeon. Our model results suggest that if TFM application was stopped in lake sturgeon streams to eliminate TFM-induced mortality on age-0 lake sturgeon, there would only be a small increase in lake sturgeon abundance and only if sea lamprey predation on sub-adults is constant and relatively low. However, it is highly unlikely that sea lamprey predation would remain low if control of larval sea lamprey was terminated in streams with known larval sea lamprey populations and habitat capable of producing substantial numbers of parasites. Further, model results showed that only a modest increase in sea lamprey predation is needed to offset the benefits of lowered mortality on age-0 lake sturgeon.

We collected data from numerous surveys around the Great Lakes and found widely varying sea lamprey wounding rates, from 0.0 – 0.5 marks/fish. Lake sturgeon length was not always included in the survey data so we had little information on wounding rates of sub-adult lake sturgeon. Instead, we allowed the wounding rate to vary from 0.01 to 0.22 marks/fish and adjusted wounding rates from information on length-based wounding rates observed in lake trout. We believe this range is representative of the actual wounding rates across most of the Great Lakes and the analysis, which included a range of TFM toxicity, provides an interesting tradeoff. At low wounding rates, sea lamprey predation on sub-adults must be high to offset the effect of TFM toxicity on age-0 lake sturgeon. This implies that lake sturgeon abundance could be increased in areas where lake sturgeon wounding rates are low and TFM is not applied. This reduction in suppression of larval lamprey would increase sea lamprey predation on all large-bodied fishes. Across the Great Lakes there are few places where wounding rates on other species such as lake trout are trivial, and not treating with TFM and allowing the escapement of large numbers of larval sea lamprey would have substantial adverse effects on the fish community, even in places where lake sturgeon might benefit.

The influence of stopping lampricide treatment of streams on the number of surviving larval sea lamprey and how they influence parasitic-phase sea lamprey abundance and predation is uncertain. Nevertheless, our simulations on changes in parasitic sea lamprey abundance resulting from excluding one of three Lake Michigan lake sturgeon producing streams from TFM treatment suggest that adult sea lamprey populations could increase substantially from 2 to over 32 times the mean abundance typically found in the lake.

The exact effect of such an increase in sea lamprey abundance on predation mortality experienced by lake sturgeon is unknown, but it is reasonable to expect a proportional increase equivalent to the rise in sea lamprey abundance. There is strong evidence that increases in sea lamprey abundance have led to increases in both attacks and mortality experienced by other prey fish such as lake trout and lake whitefish *Coregonus clupeaformis*, and to subsequent declines in their abundance (Adams et al., 2003; Harvey et al., 2008; Larson et al., 2003; Pycha, 1980). In a comprehensive evaluation on Lake Ontario, integrated sea lamprey management, which includes stream treatments with TFM, reduced the abundance of larval lampreys causing a correlative reduction in lake trout wounding rates (Larson et al., 2003). When parasitic sea lamprey feed on lake trout, Bence et al. (2003) estimated that 0.75 lake trout were killed per feeding sea lamprey in Lake Michigan. With a very large increase in sea lamprey abundance it is likely that the number of lake trout killed per sea lamprey would decrease due to compensatory responses. Nevertheless, our simulations suggest an increase of 243,012 to 3,628,481 parasitic sea lamprey could result if just one lake sturgeon stream were excluded from treatment, and clearly this would lead to a large increase in numbers of lake trout killed.

The connection between sea lamprey abundance and mortality on a particular species is complicated because of feedbacks between any changes in the fish community through the sea lamprey functional response (Bence et al., 2003). For example, assuming a type-2 multi-species functional response, as is widely used for sea lamprey, if an increase in sea lamprey abundance led to a decrease in a preferred species abundance (such as lake trout) then one would expect the predation rate on alternative prey (which would include lake sturgeon) to increase more than in proportion to the increased sea lamprey abundance just because some attacks that would have occurred on the preferred prey now occur on the alternate. The extent of this effect would be greater if the prey selectivity for an alternative prey increased when a preferred prey declined (Bence et al., 2003). One would expect a given percentage increase in sea lamprey to lead to less than that percentage increase in mortality only if indirect effects (e.g., release from competition) led to some alternative prey to increase sufficiently to draw away attacks from lake sturgeon. Regardless of uncertainty regarding how a specific fish species, like lake sturgeon, would be impacted, the aggregate fish production across the community used by additional sea lamprey resulting from not treating lake sturgeon producing streams would be substantial, as we showed in our simulations for Lake Michigan, consistent with the overall well-established adverse effects of sea lamprey on Great Lakes fish communities (Bence et al., 2003; Larson et al., 2003; Stewart et al., 2003; Swink, 2003). Even under circumstances where withholding TFM treatment may enhance lake sturgeon abundance, there will always be a need to carefully consider the impact of increasing sea lamprey predation on the lakewide fish community.

In addition to TFM, a number of control methods are used to limit larval sea lamprey populations including trapping or blocking spawning phase sea lamprey in streams (Adair and Sullivan, 2009). Models by Velez-Espino et al. (2008) showed that employing other larval sea lamprey control methods could reduce the application of TFM by 20% without an impact on lamprey abundance. Future research and new control techniques could alter or eliminate the use of TFM in the integrated management program. One promising program could be used to target the highest producing sea lamprey streams that also have high alkalinity, a combination of factors that leads to the worst set of outcomes. In two such streams, fisheries managers have attempted to remove the majority of age-0 lake sturgeon prior to TFM application, returning the lake sturgeon to the river after TFM toxicity has dissipated, lessening any toxic effects on the age-0 lake sturgeon (LRBOI, 2017). While this method appears promising, the economics of the procedure need to be evaluated and further study is needed to understand the tradeoffs of reduced age-0 survival due to removal versus TFM toxicity. Certainly, reducing mortality on all lake sturgeon life stages provides the best chance of rehabilitating the species. This said, TFM application has long been part of the integrated sea lamprey management plan and the success of this program is clear [e.g., Sullivan et al. (2016)]; therefore, eliminating TFM treatment on large parts of any lake's streams would profoundly affect ongoing sea lamprey control efforts given current capabilities for alternative control.

Lake sturgeon populations have been shown to be genetically diverse (Welsh et al., 2008) and possess varying life-history characteristics [e.g., age of maturity in Baker (1980) and

Billard and Lecointre (2000)]. However, not all life-history parameters have been studied or updated to reflect current lake sturgeon populations. We employed data from several studies and used means for parameters when life-history values varied over a range to produce a generic Great Lakes lake sturgeon population model and we reported relative change in abundance to reflect trends rather than absolute change in abundance.

Our model predicted widely differing lake sturgeon abundances when life-history parameters were changed. Although absolute abundance was not the focus of this study, these results suggest that obtaining accurate information about key life-history parameters, such as female age-at-maturity, maximum age, or adult natural mortality, is critical to the development of realistic lake sturgeon population models. All of these parameters influence sub-adult and adult lake sturgeon population dynamics and have a greater impact on abundance in a long-lived species population model than additional mortality (e.g., TFM-induced mortality) on age-0 fish with high natural mortality. Additionally, it will be critical to track changes in life-history characteristics as restoration continues. Recent improvements in water quality, increased quantity of habitat, and stocking programs successfully increased or re-established lake sturgeon populations and could eventually alter life-history characteristics such as life expectancy and fecundity (Peterson et al., 2007).

Future monitoring efforts should be directed towards improving estimates of sea lamprey length-based wounding rates on lake sturgeon. We found two types of critical information missing from a number of surveys -- lake sturgeon length and sea lamprey wound type. Additionally, lake sturgeon are also parasitized by silver lamprey that produce small wounds but these were not always clearly separated from the total number of wounds per fish. Length is an important factor to create length-based wounding rates and a clear understanding of the actual wound type is needed to separate old and new wounds. New surveys should be developed to target juveniles and sub-adults to acquire the best estimates of wounding rates on these size fish.

The lake sturgeon is a charismatic species, is culturally important to Great Lakes tribal communities, and has been the focus of considerable restoration efforts. For these reasons, the loss of any lake sturgeon is a serious concern. Sea lamprey predation poses a threat to sub-adult lake sturgeon, while lampricide treatment of streams to reduce larval sea lamprey poses a threat to age-0 lake sturgeon. We created a population model to examine the tradeoff of these two sources of mortality on lake sturgeon equilibrium abundance. These results also provide insight on population viability given that the scenarios that led to higher abundance are also scenarios that could avoid extinction at relatively low levels of lake sturgeon recruitment productivity. Although further research is needed to quantify several lake sturgeon life-history variables and obtain better length-based sea lamprey wounding rates, our simulations of a generic lake sturgeon population show that for a highly fecund and long-lived species, minimizing sub-adult mortality sources improves adult recruitment under average conditions. Under conditions of low sea lamprey wounding rates, not applying TFM may be the better option to improve lake sturgeon abundance but only at the expense of higher sea lamprey predation rates on all large-bodied fish. Researching ways to eliminate TFM toxicity on larval lake sturgeon should be the focus of both lake sturgeon restoration and sea lamprey control.

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Table 1 – Description of symbols, their initial values, and their sources that were used in the age-structured lake sturgeon model.

Description	Symbol	Initial Value	Source
Numbers-at-age	N_a		
Ages (years)	a	Juveniles : 1-6 Sub-adults : 7-24 Adults: 25-100	Sutton et al. (2003)
Total instantaneous mortality	Z_a		
Natural mortality	M_a	M_0=0.9998	Caroffino et al. (2010a)
		M_{1-6} =0.25	Sutton et al. (2003)
		M_{7+}=0.01	Assumed for this paper
TFM-induced toxicity	Mt_a	Mt_0=0.21 Mt_{1+}=0	O'Connor et al. (2017)
Sea lamprey predation mortality	Ms_a		
Beverton-Holt stock-recruitment parameters	R		Derived from Sutton et al. (2003)and Pine et al. (2001)
	α	1.0	
	β	$1.055*10^{-7}$	
Stock size	S		
von Bertalanffy growth parameters for length-at-age L_a (cm)	L_∞	228.638	Harkness and Dymond (1961) as used in Sutton et al. (2003)
	K	0.023	
	t_0	-4.713	
Fecundity-at-age	F_a	$3.76*10-8*L_a^{3.59}$	Harkness and Dymond (1961) in Sutton et al. (2003)
Proportion mature females	pf	0.35	Auer (1999) in Sutton et al. (2003)
Proportion of females spawning each year	ps	0.20	Priegel and Wirth (1977); Auer (1999) in Sutton et al. (2003)
Lake sturgeon length bins	b	40 – 57 cm 57.1 - 65 cm 65.1 - 76 cm	Bin sizes used in Patrick et al. (2009)
Sea lamprey overall wounding rate	Wr	0.22	Sutton et al. 2003
Scaling factor to convert *Wr* to length (*b*) based wounding rate	Ws_b	$Ws_{40\text{-}57\ cm}$ =0.263 $Ws_{57.1\text{-}65\ cm}$=0.579 $Ws_{65.1\text{-}76\ cm}$=0.816	Ebener (unpublished data)
Probability of surviving sea lamprey attack for length bin *b*	Ps_b	$Ps_{40\text{-}57\ cm}$ =0.50 $Ps_{57.1\text{-}65\ cm}$=0.74 $Ps_{65.1\text{-}76\ cm}$=0.84	Linear model based on Patrick et al. (2009)

Table 2: Calculated sea lamprey predation rates (Ms_b, Equation #3) for the Base Model and scenarios where either the overall wounding rate (Wr) or the probability of surviving a sea lamprey attack (Ps_b) varied from the Base Model. Lake sturgeon that do not fall within the length bins (b) were assumed to suffer no mortality from sea lamprey predation.

Description of model parameters	***Wr***	***b (cm)***	***Ws_b***	***Ps_b***	***Ms_b***
Lower wounding rate	0.05	40-57	0.263	0.50	0.003
		57.1-65	0.579	0.74	0.002
		65.1-76	0.816	0.84	0.002
Intermediate Wounding rate	0.10	40-57	0.263	0.50	0.013
		57.1-65	0.579	0.74	0.010
		65.1-76	0.816	0.84	0.008
Base Model	0.22	40-57	0.263	0.50	0.058
		57.1-65	0.579	0.74	0.045
		65.1-76	0.816	0.84	0.034
Lower probability of surviving a sea lamprey attack	0.22	40-57	0.263	0.40	0.087
		57.1-65	0.579	0.59	0.089
		65.1-76	0.816	0.67	0.088
Higher probability of surviving a sea lamprey attack	0.22	40-57	0.263	0.60	0.039
		57.1-65	0.579	0.88	0.017
		65.1-76	0.816	1.00	0.000

Table 3: Relative change in equilibrium population size of adult lake sturgeon (age 25+) compared to the Base Model for scenarios where TFM toxicity (Mt_0) and overall sea lamprey wounding rate (Wr) varied by scenario.

Parameters that varied from Base Model	**TFM toxicity Mt_0**	**Wr**	**Relative change from *Base Model***
No TFM and sea lamprey multiplier 1.00	0	0.22	5.7%
No TFM and sea lamprey multiplier 1.10	0	0.22	1.2%
No TFM and sea lamprey multiplier 1.25	0	0.22	-5.2%
No TFM and sea lamprey multiplier 1.50	0	0.22	-15.1%
No TFM and sea lamprey multiplier 1.75	0	0.22	-24.0%
No TFM and sea lamprey multiplier 2.00	0	0.22	-32.0%
Base Model	***0.21***	***0.22***	***0.0%***
Low TFM Toxicity	0.12	0.22	2.5%
High TFM Toxicity	0.55	0.22	-9.3%
20% lower probability of surviving attack	0.21	0.22	-31.8%
20% higher probability of surviving attack	0.21	0.22	27.3%
Lower wounding rate	0.21	0.05	40.0%
Intermediate wounding rate	0.21	0.10	26.9%

Table 4: Relative change in equilibrium population size of adult lake sturgeon (age 25+) compared to the Base Model where each analysis varied one life-history parameter and all other values were held constant at the Base Model value. The breakeven point indicated the level of sea lamprey predation on sub-adult lake sturgeon that results in the same equilibrium abundance as TFM-induced mortality on larval lake sturgeon.

Parameters that varied from Base Model	**Relative change from *Base Model***	**Breakeven level of sea lamprey predation**
Maximum lake sturgeon age 80 years	-20.9%	1.13
Maximum lake sturgeon age 150 years	36.7%	1.13
Female maturity occurs at age 15	20.0%	1.13
Proportion of females spawning each year is 10%	-3.6%	1.13
Proportion of females spawning each year is 30%	1.3%	1.13
Juvenile natural mortality is 14%	132.2%	1.13
Adult natural mortality is 5%	-87.8%	1.13
Alternate growth curve from Muskegon River lake sturgeon population	44.8%	1.36

Table 5: Estimated mean number of sea lamprey parasites, from the MSE model (Jones, 2009), produced annually in Lake Michigan. Results are shown when all streams are potentially treatable and ranked for treatment, and when one stream, known to contain lake sturgeon (either the Menominne River, Big Manistee River, or Muskegon River) is not available for treatment. The sea lamprey multiplier is the relative change in the parasitic population when all streams are treated versus one stream left untreated. Larval habitat is shown as a measure of stream productivity and to highlight the reason for the large differences in estimated parasitic population size for among streams.

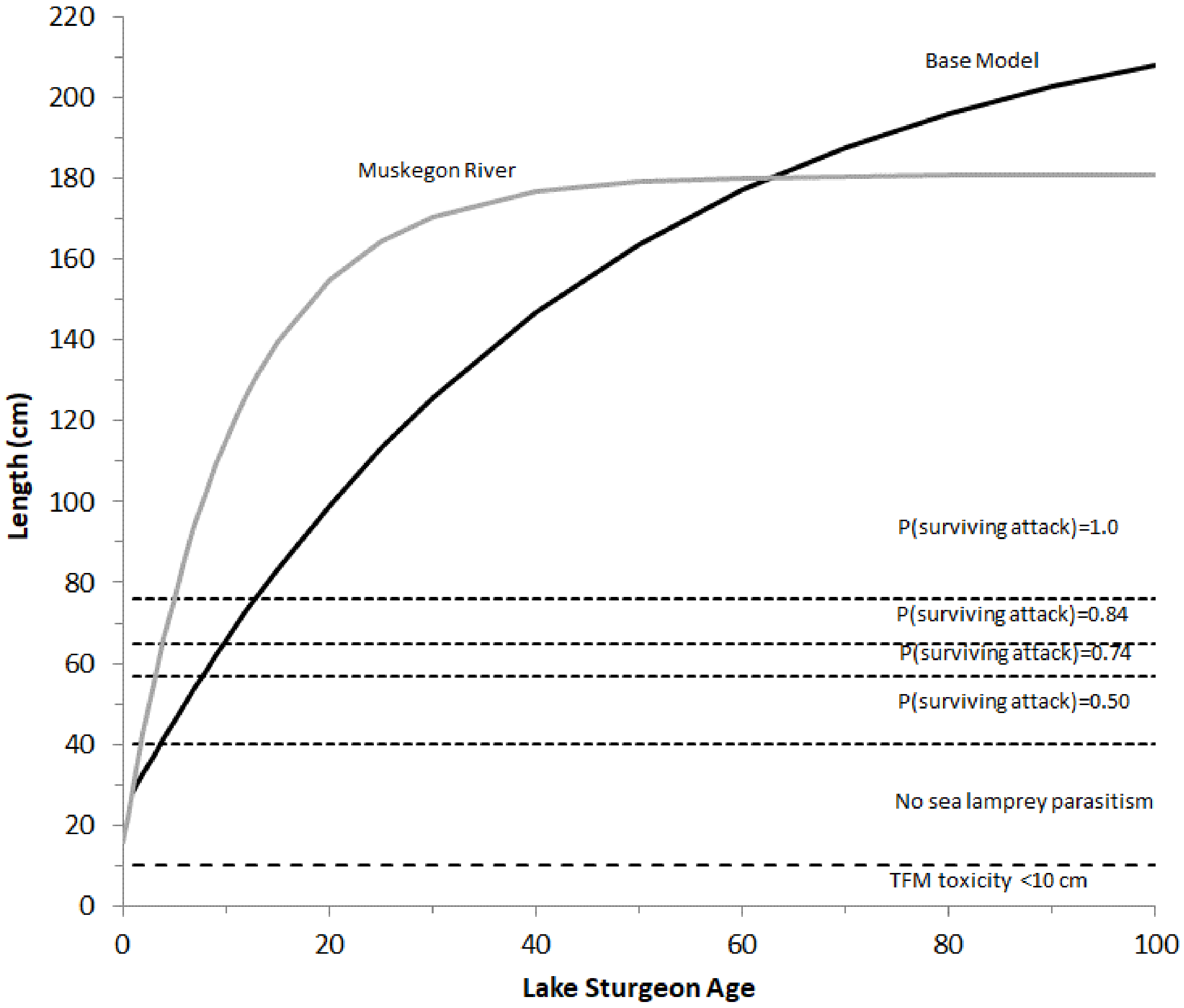
Streams available for TFM treatment	**Larval habitat (m^2)**	**Estimated mean number of parasites in lake**	**Sea lamprey multiplier**
All streams	17,304,589	110,739	
All streams EXCEPT Menominee River	249,780	353,750	2.1
All streams EXCEPT Big Manistee River	1,600,132	2,616,471	22.6
All streams EXCEPT Muskegon River	2,667,427	3,739,220	32.8

List of Figures

Figure 1 – Length-at-age of lake sturgeon used in the Base Model (black line) and the Muskegon River, Michigan (gray line). Dashed lines demarcate lengths at which mortality sources and the probability of survival from a sea lamprey attack change with text explaining what applies in a given length range.

Figure 2 – Breakeven point where the effect of sea lamprey predation on adult lake sturgeon on age 25+ equilibrium lake sturgeon population size matches the effect of TFM-induced toxicity on age-0 lake sturgeon on age 25+ equilibrium population size. The No TFM Applied line represents only the impact of sea lamprey predation on equilibrium population size across varying levels of the sea lamprey predation multiplier. The points represent the breakeven level of sea lamprey predation for varying degrees of TFM toxicity – Base Model Mt_o= 0.21 (open square), low TFM toxicity Mt_o = 0.12 (closed circle), and high TFM toxicity Mt_o = 0.55 (closed triangle).

Figure 3 – The effect of changing sea lamprey wounding rate, Wr, on the breakeven point for the sea lamprey predation multiplier, where the effects of sea lamprey predation on adult lake sturgeon and TFM-induced toxicity on age-0 lake sturgeon have equal effects of age 25+ lake sturgeon equilibrium abundance. Each line represents results for varying TFM toxicity levels: Base Model Mt_o= 0.21 (solid), low TFM toxicity Mt_o = 0.12 (dashes), and high TFM toxicity Mt_o = 0.55 (dots).



Length (cm)
Lake Sturgeon Age
0
20
40
60
80
100
120
140
160
180
200
220
0
20
40
60
80
100
Base Model
Muskegon River
P(surviving attack)=1.0
P(surviving attack)=0.84
P(surviving attack)=0.74
P(surviving attack)=0.50
No sea lamprey parasitism
TFM toxicity <10 cm

FIGURE 1

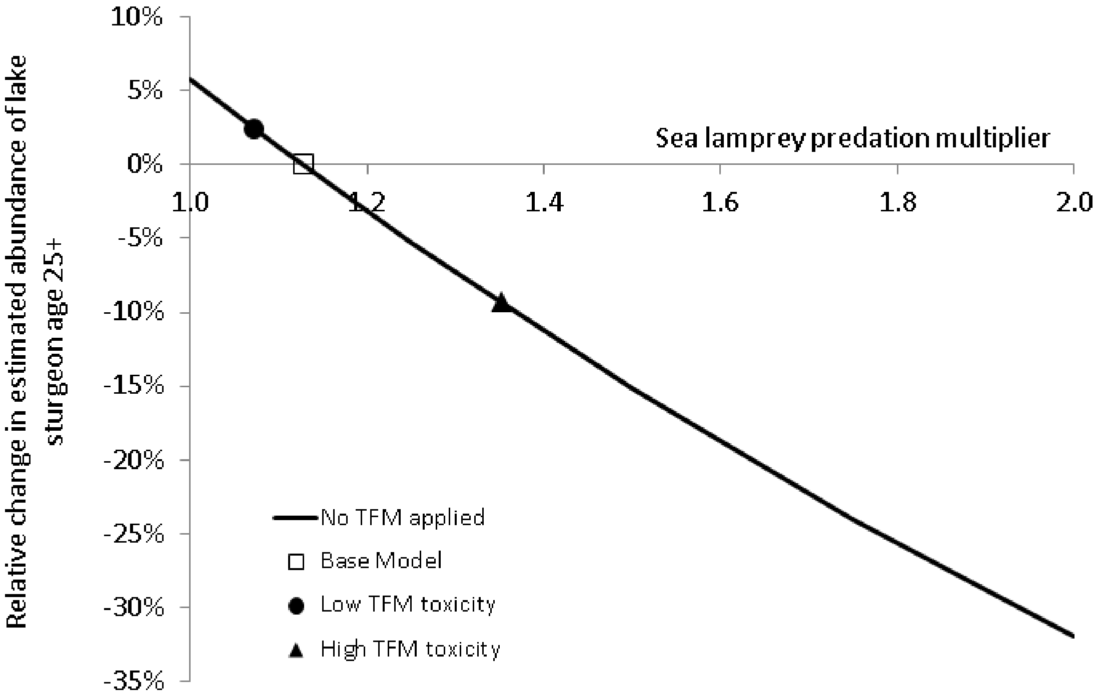

10%
5%
0%
-5%
-10%
-15%
-20%
-25%
-30%
-35%
Relative change in estimated abundance of lake sturgeon age 25+
Sea lamprey predation multiplier
1.0
1.2
1.4
1.6
1.8
2.0
No TFM applied
Base Model
Low TFM toxicity
High TFM toxicity

FIGURE 2

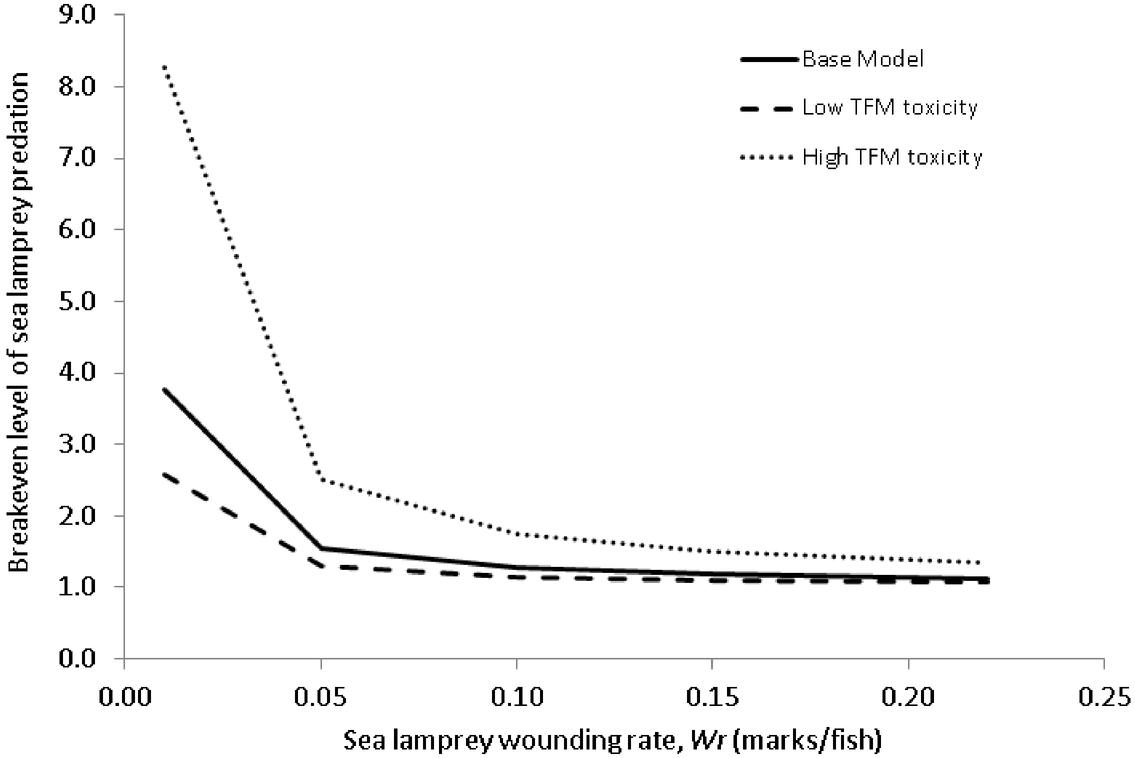

9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Breakeven level of sea lamprey predation
0.00
0.05
0.10
0.15
0.20
0.25
Sea lamprey wounding rate, Wr (marks/fish)
Base Model
Low TFM toxicity
High TFM toxicity

FIGURE 3