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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.

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

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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, 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 100 mm 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 trade-off 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 trade-off 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 re-examine 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,

$$N_a = N_{a-1} * e^{-Z_{a-1}}, \tag{1}$$

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:

$$Z_a = M_a + Mt_a + Ms_a \tag{2}$$

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