



# Potential changes to the biology and challenges to the management of invasive sea lamprey *Petromyzon marinus* in the Laurentian Great Lakes due to climate change

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## Abstract

Control programs are implemented to mitigate the damage caused by invasive species worldwide. In the highly invaded Great Lakes, the climate is expected to become warmer with more extreme weather and variable precipitation, resulting in shorter iced-over periods and variable tributary flows as well as changes to pH and river hydrology and hydrogeomorphology. We review how climate change influences physiology, behavior, and demography of a damaging invasive species, sea lamprey (*Petromyzon marinus*), in the Great Lakes, and the consequences for sea lamprey control efforts. Sea lamprey control relies on surveys to monitor abundance of larval sea lamprey in Great Lakes tributaries. The abundance of parasitic, juvenile sea lampreys in the lakes is calculated by surveying wounding rates on lake trout (*Salvelinus namaycush*), and trap surveys are used to enumerate adult spawning runs. Chemical control using lampricides (i.e., lamprey pesticides) to target larval sea lamprey and barriers to prevent adult lamprey from reaching spawning grounds are the most important tools used for sea lamprey population control. We describe how climate change could affect larval survival in rivers, growth and maturation in lakes, phenology and the spawning migration as adults return to rivers, and the overall abundance and distribution of sea lamprey in the Great Lakes. Our review suggests that Great Lakes sea lamprey may benefit from climate change with longer growing seasons, more rapid growth, and greater access to spawning habitat, but uncertainties remain about the future availability and suitability of larval habitats. Consideration of the biology of invasive species and adaptation of the timing, intensity, and frequency of control efforts is critical to the management of biological invasions in a changing world, such as sea lamprey in the Great Lakes.

## KEYWORDS

biological invasions, fisheries management, integrated pest management, invasive species control, lampricide, migration, monitoring, water temperature

## 1 | INTRODUCTION

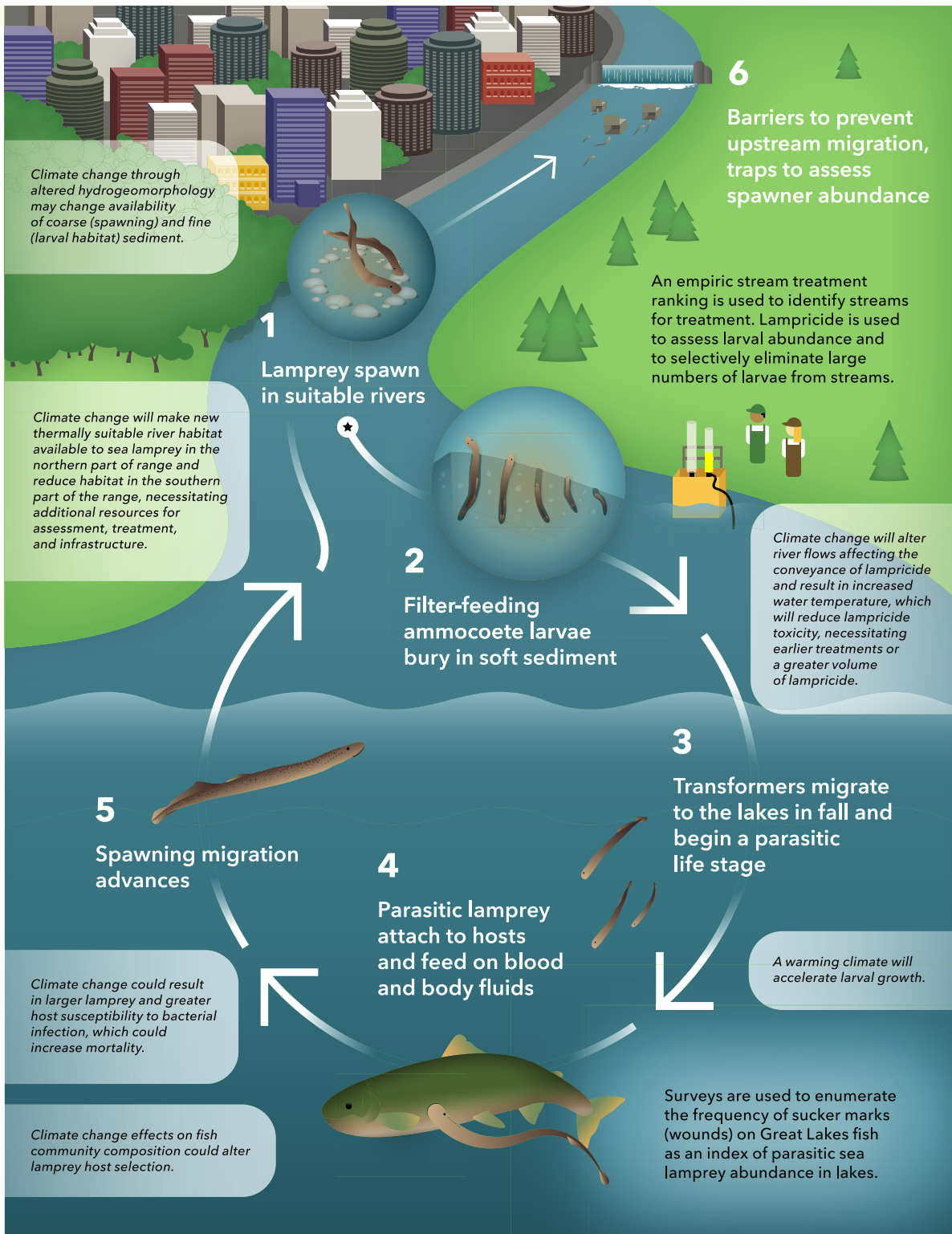
Human activities during the last century have altered climate and species distributions with realized and potential consequences for ecosystems (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Parmesan & Yohe, 2003; Walther et al., 2002) and society (McMichael, Woodruff, & Hales, 2006; Schmidhuber & Tubiello, 2007; Stern, 2008). Biological invasions are a leading cause of animal imperilment (Clavero & García-Berthou, 2005) and of substantial interest to natural resource and biodiversity management agencies. Economic damages inflicted by invasive species are globally substantial and new invasions continue to emerge as ecological opportunities arise due to a changing climate (Pimentel, Zuniga, & Morrison, 2005). In a rapidly changing world, a better understanding of the physiology and ecology of invasive species could prepare resource practitioners for the conservation and management challenges invasions pose in a changing climate. Such knowledge could also inform the development of climate change adaptation strategies for protecting aquatic ecosystems from the threats of climate change and invasive species.

The Laurentian Great Lakes of central North America are highly impacted environments; high degrees of modification due to urbanization and the highest rate of biological invasions in a freshwater ecosystem make this location of key importance to management (Escobar et al., 2018; Ricciardi, 2006). As atmospheric CO<sub>2</sub> increases, corresponding increases in atmospheric P<sub>CO<sub>2</sub></sub> may also lead to acidification of surface waters in the Great Lakes region, where declines of 0.29–0.49 pH units have been forecast to occur by 2100 (Phillips et al., 2015). Surface water's acid–base chemistry may, however, be complicated by abiotic factors such as the local geological features of the watershed's modulating alkalinity and buffer capacity (Philips et al., 2015). Water P<sub>CO<sub>2</sub></sub> would increase by 550 μatm if water P<sub>CO<sub>2</sub></sub> equilibrates with atmospheric P<sub>CO<sub>2</sub></sub> forecast to take place by the end of the century (Phillips et al., 2015). Depending on atmospheric CO<sub>2</sub>, air temperatures over the Great Lakes are expected to rise by 1–6°C by 2100 (Angel & Kunkel, 2010; Phillips et al., 2015). Warming may be more pronounced during winter and in the northern Great Lakes (Bartolai et al., 2015; Byun & Hamlet, 2018; McDermid et al., 2015; Wang, Hunag, Baetz, & Zhao, 2017). Warmer temperatures yield decreased ice coverage (Wang et al., 2017), reduced wind speeds (Desai, Austin, Bennington, & McKinley, 2009), and evaporative water loss that slows average flows. Temperature regime shifts are projected to favor warmwater and cool-water fishes throughout the Great Lakes basin at the expense of cold-water species, especially in cold-water rivers and northern watersheds (Collingsworth et al., 2017; Melles, Chu, Alofs, & Jackson, 2015). These shifts could be modulated by species-specific responses to acidification, which, based on research on marine fishes, are highly species-specific (Rummer et al., 2013). The peak daily flow in rivers and streams, however, is projected to increase with a shift toward increased flows in winter and spring and decreased flows in fall and summer (Byun, Chiu, & Hamlet, 2019). Lower flows in

the fall and summer can slow channel velocities and reduce depth, while increased storm intensity or frequency can result in higher peak discharge. Increased rainfall intensities may also result in a pulse of sediments (Tucker & Slingerland, 1997), which may aggregate as eroded upland materials enter the system, followed by erosion of bed materials as the influx of sediments steadies or decreases.

Invasive species such as the spiny water flea (*Bythotrephes longimanus*), zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussels, round goby (*Neogobius melanostomus*), and carps (*Cyprinus carpio*, *Hypophthalmichthys nobilis*, *Hypophthalmichthys molitrix*, *Mylopharyngodon piceus*, and *Ctenopharyngodon idella*) are now considered problematic in the Great Lakes. The most notorious invader, however, is the sea lamprey (*Petromyzon marinus*), a jawless fish native to the Atlantic Ocean (Beamish & Potter, 1975). Sea lamprey typically spend the first 3–7 years of life burrowed in soft-sediment substrate of rivers and streams as filter-feeding larvae before undergoing a complex metamorphosis into juvenile animals that then migrate downstream to open water (Figure 1). Metamorphosis is accompanied by the formation of an oral disc and rasping tongue, which allows the juvenile sea lamprey to attach to and parasitize larger fishes by sucking on their blood (Renaud, Gill, & Potter, 2009; Youson, 1980, 2003). It is estimated that a single sea lamprey may kill 10–20 kg of fish during its parasitic phase in the Great Lakes (Farmer, Beamish, & Robinson, 1975; Swink, 2003). Following the 12–20 month parasitic phase, juvenile sea lamprey stop feeding and migrate upstream as maturing adults, spawn, and then die (Beamish & Potter, 1975). Unlike many salmonid fishes, sea lamprey do not necessarily migrate to their natal streams, but instead choose appropriate rivers based on the detection of bile salts by larval sea lampreys (Li, Twohey, Jones, & Wagner, 2007). Sex pheromones to attract females are secreted by males, which precede females onto the gravel spawning grounds (Figure 1; Johnson, Yun, Thompson, Brant, & Li, 2009). Although eradication of sea lamprey in the Great Lakes remains impractical, a program to control their populations has helped rehabilitate the fisheries in the Great Lakes and provides net benefits to the regional economy (Lupi, Hoehn, & Christie, 2003; Siefkes, 2017; Wilkie, Hubert, Boogaard, & Birceanu, 2019).

Climate change may facilitate or complicate fisheries management and sea lamprey control efforts, necessitating changes to current practices (Kitchell, Cline, Bennington, & McKinley, 2014; Kling et al., 2003). Indeed, it is not known how sea lamprey control efforts will be affected by changes to water temperature, chemistry, quantity (flow), or quality. Currently, sea lamprey control efforts are focused on chemical control methods and barriers to sea lamprey migration. Chemical control measures target sea lamprey during their residence in tributaries, when multiple generations of larval sea lamprey can be specifically targeted by applying lampicide, a chemical pesticide (i.e., piscicide), such as 3-trifluoromethyl-4-nitrophenol (TFM) and/or niclosamide (Bayluscide®) to the water (McDonald & Kolar, 2007; Wilkie et al., 2019). Barriers (e.g., dams) are used to prevent maturing (adult) sea lamprey from reaching



**FIGURE 1** Schematic of the sea lamprey (*Petromyzon marinus*) life cycle in the Laurentian Great Lakes and control efforts initiated by the Great Lakes Fishery Commission to mitigate damage resulting from sea lamprey on native fish populations. Filter-feeding larval sea lamprey inhabit the soft sediments of rivers and streams for 3–7 years, followed by a complex metamorphosis into parasitic, juvenile sea lamprey that migrate downstream to open water where they use their newly formed oral disc and rasping tongue to feed on the blood of large fishes (Applegate, 1950; Renaud et al., 2009). Control efforts are focused on the in-river larval stages and adults migrating upstream to spawn. Climate change could complicate sea lamprey control efforts (side panels of Figure 1) and may require shifts in strategy and the development of novel control technologies (e.g., next generation lampricides, genetic control) to keep pace [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

their spawning grounds (McLaughlin, Hallett, Pratt, O'Connor, & McDonald, 2007; Figure 1). In this synthesis, we discuss how projected changes to the abiotic and biotic environments of the Great Lakes and their tributaries resulting from climate change could undermine the efficacy of sea lamprey control, and we propose measures that could mitigate such effects. This forward-looking paper can guide resource managers and policy makers in identifying key knowledge gaps and determining climate change adaptation strategies for the Great Lakes (Figure 1). Such efforts are being undertaken broadly within the natural resource management and conservation planning spheres to prepare for a new form of resource management by identifying mechanisms of change and vulnerable species (Magurran, 2016; Pacifici et al., 2015).

## 2 | SEA LAMPREY CONTROL IN THE GREAT LAKES BASIN

### 2.1 | Larval survival

#### 2.1.1 | Will the survival, growth, or maturation of larval sea lamprey be altered?

Warming temperature and increased productivity in Great Lakes tributaries have the potential to benefit sea lamprey. Sea lamprey hatching and larval growth are temperature sensitive and sea lamprey larvae stand to benefit from warming conditions by hatching and commencing feeding earlier in the springtime than under present regimes. Eggs are fertilized in the early summer and embryos are viable only between 15 and 25°C (McCauley, 1963; Pivais, 1961; Rodríguez-Muñoz, Nicieza, & Brana, 2001). Larval sea lamprey require cool temperatures for hatching (Rodríguez-Muñoz et al., 2001), but feeding and growth are positively influenced by increased water temperature (Sutton & Bowen, 1994). Advanced hatching of sea lamprey embryos in warmer streams is likely. If larvae emerge from eggs at smaller size than they do at present, larval lamprey densities could increase in rivers due to less density dependence early in life (Applegate, 1950; Quintella, Andrade, Dias, & Almeida, 2007). However, little is known about larval lamprey predators or whether advanced hatching could increase early life mortality. Lake Ontario sea lamprey were observed to prefer temperatures from 17.8 to 21.8°C with a maximum scope for activity at 19°C (Holmes & Lin, 1994). Purvis (1980) found that larvae experiencing these temperatures (20–21°C) had faster rates of metamorphosis than those held at 14–16 or 7–11°C; however, the difference could have also been a location effect. Holmes and Youson (1998) also found high (80%) rates of metamorphosis at 21°C, declining to 58% at 25°C. Despite the apparent performance improvements in warmer waters, Reynolds and Casterlin (1978) found that lamprey exposed to a range of water temperatures in a shuttlebox preferred water of 13.8°C. Although lamprey are predominantly sedentary, they are capable of dispersal, particularly downstream, and could use this to access suitable habitat (Reynolds & Casterlin, 1978). Generally, we

predict that warming will enhance suitability for spawning and larvae in northern streams and reduce it in southern streams.

Hypoxia associated with peak temperatures in shallow, slow-moving, or southern streams may have little effect on sea lamprey larvae because some species of lampreys are tolerant of low oxygen conditions (Potter, Hill, & Gentleman, 1970). In exercise trials, sea lamprey larvae recovered energetic substrates rapidly following anaerobic swimming, which Wilkie, Bradshaw, Joanis, Claude, and Swindell (2001) suggested could be an adaptation to cope with unpredictable oxygen availability associated with burrowing into substrate, although further research is needed to establish this. Taken together with the thermal niche of lamprey, southern streams or those with less groundwater input, shading, or other cooling mechanisms could have reduced sea lamprey production under a warming climate. One river surveyed by Dawson and Jones (2009) sustained temperatures beyond 20.8°C (the optimum suggested by Holmes & Lin, 1994) and had very low sea lamprey recruitment; continued monitoring of lamprey larvae and water temperatures is necessary to make better inferences about the relationship between lamprey larvae and climate change.

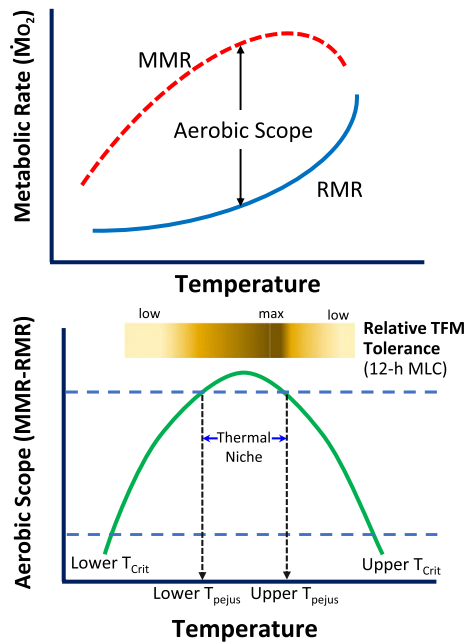
Sea lamprey larvae distributions also may be impacted by alterations in sediment input and flood timing. Sea lamprey larvae prefer soft, burrowable substrates of fine sands (<0.5 mm dia.) with organic detritus (Applegate, 1950; Hardisty & Potter, 1971; Potter, 1980), sediments that are more readily mobilized by elevated flows and deposited at low flows. Changes to the abundance of sandy sediments throughout a river system are the result of the net influx of sediments into the system and erosion. Depending on the source of upland sediment input, aggregation of sandy material could increase larval habitat whereas input of fine silts and clay could reduce habitat suitability. Shifts in water flow regimes may negatively affect larval sea lamprey if detritus, their main food, is not conveyed as efficiently by extreme variation in water flows (Sutton & Bowen, 1994). Sea lamprey larvae are, however, tolerant to anaerobic exercise that could be induced by high flows but also spend most of the time burrowed, allowing them to avoid such conditions (Wilkie et al., 2001). Patterns of stream productivity may shift with longer growing seasons, increasing aquatic vegetation growth, bacterial activity, and perhaps producing more detritus. Indeed, Holmes (1990) used stream water conductivity as a proximate indicator of productivity and suggested that it may also have a positive influence on larval development.

#### 2.1.2 | How will lampricide effectiveness change?

Sea lamprey control relies on TFM, a chemical pesticide targeting sea lamprey that is applied to rivers and streams from the early spring through mid-autumn (Box 1). TFM selectively targets sea lamprey because they have a lesser capacity to detoxify the compound compared to most non-target vertebrates and invertebrates (Applegate, Howell, Moffett, & Smith, 1961; Boogaard, Bills, & Johnson, 2003; McDonald & Kolar, 2007; Wilkie et al., 2019). Granular formulations of niclosamide (2',5-dichloro-4'-nitrosalicylanilide; trade name: Bayluscide™) are also used to target larval sea lamprey in lentic habitats and large, fast

**BOX 1 Potential effects of climate change on the toxicity of TFM to sea lamprey and non-target fishes.**

Predicted relationship between temperature-induced changes in aerobic scope on the tolerance of ectothermic larval sea lamprey and non-target fishes to TFM.



Anticipated increases to water temperatures due to climate change may result in increased routine metabolic rate (RMR, solid blue line) and maximum metabolic rate (MMR, dashed red line) of fishes, with corresponding effects on aerobic scope, the difference between MMR and RMR (bottom panel). Within a fish's thermal niche (e.g., 17.8–21.8°C for larval sea lamprey; Holmes & Lin, 1994), the toxicity of phenols, such as TFM, may decrease with increasing temperature below the upper pejus temperature (temperature at which performance begins to decline), where aerobic scope begins to decline. Beyond the upper pejus temperature, tolerance to TFM could decrease with the collapse of aerobic scope (lower panel), and corresponding decreases of ATP supply. Under this scenario, requirements for effective treatments will be expected to increase as climate change results in warmer waters for longer periods, provided temperatures are below the upper pejus temperature of sea lamprey, beyond which less TFM would be required. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

flowing rivers such as the St. Marys' River between Lake Superior and Lake Huron. Granular Bayluscide sinks in the water column, making it highly effective in waters where treatments with TFM would be ineffective due to the depth (lentic areas off stream mouths) or impractical due to high discharge (St. Marys' River; Dawson, 2003; Wilkie et al., 2019).

Warmer (24°C) water (compared to cooler 6°C) decreases TFM toxicity to sea lamprey larvae but increases uptake rate (Hlina, Tessier, & Wilkie, 2017; Muhametsafina, Birceanu, Hlina, Tessier, & Wilkie, 2019). Larger size also decreases the uptake; therefore, larger larvae succumb to TFM later during treatments (Tessier, Long, & Wilkie, 2018). Longer growing seasons could accelerate sea lamprey larval growth unless other processes (e.g., other invasions, density dependence, stress) compensate for these conditions. More TFM may be required to treat warmer streams due to increases in TFM tolerance. Increasing TFM tolerance of larval lamprey acclimated to progressively higher temperatures of 6, 12, or 24°C (Muhametsafina et al., 2019) suggests it would be prudent to compile temperature and toxicity data from treated streams to determine if the temperature–toxicity relationship observed in the laboratory extends to the field.

Another major concern is the potential for larval sea lamprey to enter metamorphosis younger than they currently do and emigrate from the streams before TFM treatments because of either warmer temperatures or increased winter and spring precipitation. Treatments are scheduled based on timing of metamorphosis; if metamorphosis is accelerated by a year or more due to climate change, metamorphosed sea lamprey may escape to the lakes before lampricides are applied.

To compensate for accelerated rates of metamorphosis, sea lamprey assessments of larval habitat and treatment cycle frequency may have to be accelerated, increasing the costs of sea lamprey control due to greater labor requirements and lampricide consumption. Projected changes to storm intensity and timing could result in more frequent occurrences of fine sediment scour in downstream reaches of tributaries that could lead to larval populations in lentic environments (Fodale, Bronte, Bergstedt, Cuddy, & Adams, 2003), where chemical treatment is more difficult. Whereas lower flows in the summer and fall may reduce the amount of TFM needed to reach required concentrations, shifts in the distributions of larvae resulting from altered sediment transport and deposition may ultimately make treatment more difficult. The control program has noted increased frequency of high springtime flows when lampricides are applied due to extreme rain events, which risks faster dispersal of the lampricide, decreased effectiveness, and a greater demand for lampricide in these areas. Lower water discharges in summer and fall could reduce total lampricide requirements, but this could be offset by the need for greater treatment effort.

### 2.1.3 | How does the degradation of lampricides in the environment change with climate?

The impact of climate change upon lampricide degradation rates is expected to be modest, but differences exist between TFM and niclosamide. Photodegradation and biodegradation are the primary degradation processes for TFM and niclosamide in



tributaries of the Great Lakes. TFM is susceptible to direct photodegradation, whereas niclosamide undergoes both direct and indirect photodegradation (McConville, Hubert, & Remucal, 2016; McConville, Mezyk, & Remucal, 2017). Under conditions encountered during typical treatment applications, TFM could undergo significant photodegradation in approximately 10% of treated tributaries (McConville, Cohen, et al., 2017). Niclosamide photodegradation is too slow to influence its fate on the timescale of a lampricide application, but could result in degradation once niclosamide reaches the Great Lakes (McConville, Cohen, et al., 2017). Biodegradation is faster under anaerobic conditions for both lampricides and is generally faster for niclosamide than TFM (Bothwell, Beeton, & Lech, 1973; Fathulla, 1996; Kemp, 1973; Muir & Yarechewski, 1982). Neither lampricide undergoes abiotic hydrolysis under environmentally relevant conditions (Dawson, 2003; Hubert, 2003).

Although the influence of water temperature on TFM or niclosamide photodegradation rates has not been evaluated (Ellis & Mabury, 2000; McConville et al., 2016), direct photodegradation reactions are distinct from thermal reactions and are typically independent of temperature across environmentally relevant ranges (Leifer, 1988). Direct photodegradation of both chemicals is strongly pH dependent (McConville et al., 2016) and acidification could affect photodegradation rates. The direct photodegradation of TFM increases with increasing pH, so a decrease from pH 8 to 7.7 pH units (what is expected across the Great Lakes by 2100; Phillips et al., 2015) could decrease the TFM direct photodegradation rate by ~15%. More primary production due to increased photosynthesis or increased turbidity after storm events could reduce water clarity, which would further decrease photodegradation rates of TFM due to increased light screening (McConville, Cohen, et al., 2017). The same pH change could increase the direct photodegradation rate of niclosamide by a factor of 3 because it has an opposite pH dependency than TFM; notwithstanding, niclosamide photodegradation may still be minimal in tributaries of the Great Lakes (McConville, Cohen, et al., 2017).

Biodegradation rates of TFM and niclosamide are likely to increase in response to a changing climate. A large portion of applied lampricides is temporarily stored in the hyporheic zone (i.e., the sediment region alongside and below the riverbed). For example, 19%–30% of TFM was stored in the hyporheic zone in two small (i.e., <2 km long) tributaries as the lampricide block moved downstream over the course of 1–4 hr (McConville, Cohen, et al., 2017). Thus, biodegradation of both lampricides is expected primarily under anaerobic conditions in sediments in Great Lakes tributaries (Dawson, 2003; Hubert, 2003). Warming water temperatures may stimulate microbial activity and result in hastened biodegradation rates. For example, the anaerobic degradation of TFM increased with temperature across the range of 6–60°C (Kemp, 1973). Anaerobic degradation rates in sediment/water mixtures are approximately twice as fast for TFM (Fathulla, 1995, 1996) and niclosamide (Graebing, Chib, Hubert, & Gingerich, 2004) compared to aerobic degradation rates measured under similar conditions.

#### 2.1.4 | Will warmer water temperatures increase impacts of lampricide on non-target species?

Climate change has the potential to affect the specificity of control efforts by altering the vulnerability to lampricides (Lu et al., 2015). Native species including other lampreys (e.g., northern brook lamprey *Ichthyomyzon fossor*), lake sturgeon (*Acipenser fulvescens*), ictalurid catfishes (e.g., *Ictalurus punctatus*), centrarchids (e.g., *Lepomis cyanellus*, *L. macrochirus*), (e.g., anurans), and many invertebrates, including some molluscan species at risk (e.g., *Elliptio complanata*, *Pyganodon cataracta*), depend on the freshwater systems invaded by sea lamprey and they are not immune to the toxic mechanisms of TFM (Boogaard et al., 2003). Small animals with faster metabolic rates are more sensitive to toxicants due to accelerated rates of uptake. Younger life stages are generally also more sensitive (Boogaard et al., 2003; Newton, Boogaard, Gray, Hubert, & Schloesser, 2017). Compared to larval lamprey (both sea lamprey and native lampreys), most non-target fishes are exposed to less toxic concentrations of TFM due to their greater capacity to detoxify the compound and larger individuals may have the mobility necessary to avoid prolonged exposure (Bussy et al., 2018a,b; Kane, Kahng, Reimschuessel, Nhamburo, & Lipsky, 1994; Lech & Statham, 1975). In some cases, non-target organisms, especially relatively sessile organisms such as bivalve mollusks, could lack the mobility to seek out refuge when exposed to lampricide (Newton et al., 2017). This was recently shown in larval sea lamprey, in which the rates of lampricide uptake, measured by radiolabeled TFM (<sup>14</sup>C-TFM), increased by more than twofold as water temperatures were increased from 6 to 22°C (Hlina et al., 2017).

Studies assessing the temperature and pH dependence of lampricide toxicity and respiratory rates of non-target species are clearly needed so that informed predictions can be generated about how these animals will respond to lampricides in warmer waters. Mortality of age-0 lake sturgeon was increased in colder water (O'Connor et al., 2017). The risk of mortality was significantly greater when sturgeon were exposed to concentrations of TFM 1.4× the 9 hr minimum lethal concentration (i.e., concentration at which 99.9% of lamprey die; MLC) for sea lamprey, a typical application concentration (Bills et al., 2003), in waters of higher alkalinity (O'Connor et al., 2017). However, most research on non-target impacts focuses on present conditions and future scenarios should be more thoroughly explored, particularly in field simulations. Further work must necessarily account for differences in ontogeny and mobility. For relatively sessile organisms such as bivalves, Waller, Rach, and Luoma (1998) showed that even valve closure was not sufficient to avoid lampricide exposure and resultant toxic impacts, including mortality, whereas increased mobility of species such as fish, particularly larger fish, could permit refuging to avoid treatment assuming they can detect it. Further research to develop models that integrate temperature could assist evidence-based treatment strategies to minimize harm to non-target species and assessment of long-term changes in aquatic communities could help determine how lampricide treatment affects the long-term trajectory of stream communities.

## 2.2 | Growth and maturation in lakes

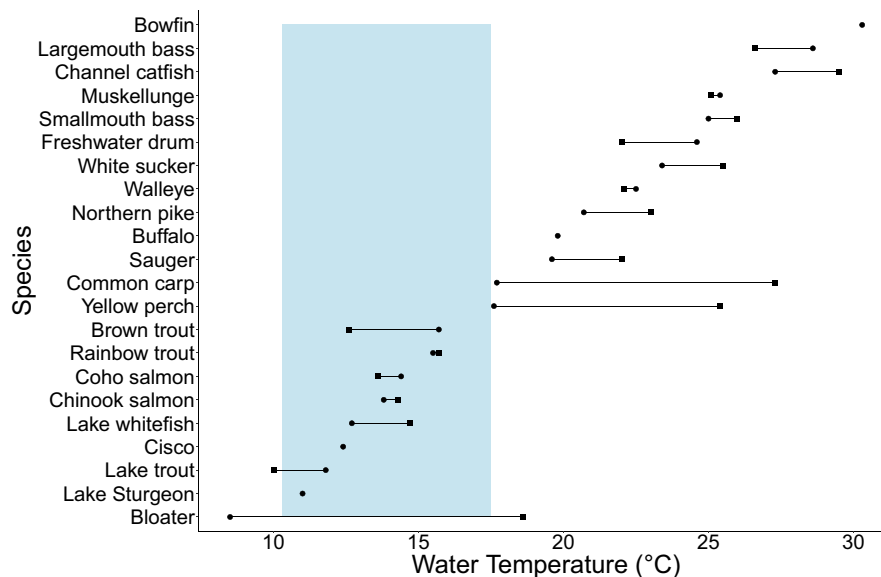
### 2.2.1 | How will climate-induced shifts in the fish assemblage alter host availability and preferences of sea lamprey?

Fish physiology, behavior, growth, and maturation are temperature-sensitive and climate change is positioned to greatly influence the distribution of Great Lakes fishes, which may influence the distribution and hosts available to sea lamprey. Juvenile sea lamprey that enter lakes during spring are generally found in the cold hypolimnion (~4°C) until summer, when they move into shallower, warmer (6–15°C) water during which time growth, and ostensibly feeding, accelerate (Applegate, 1950). Although lake trout are often attacked by sea lamprey in the Great Lakes, other fish species are also exploited by sea lamprey as hosts. Indeed, sea lamprey hosts vary intra-annually and Bence et al. (2003) suggested that species in warmwater guilds were more frequently parasitized by sea lamprey during spring and fall with a switch to cooler water species during the summer. This suggests that sea lamprey are generalists with respect to their preferred hosts, but shift their distribution corresponding to their thermal preferences throughout the year.

The optimum temperature for larval sea lamprey growth is about 17.3°C and the final preferendum is 10.3°C (Farmer, Beamish, & Lett, 1977; Kitchell & Breck, 1980). These values overlap with salmonines including bloater (*Coregonus hoyi*), cisco (*Coregonus spp.*),

lake whitefish (*Coregonus clupeaformis*), lake (*Salvelinus namaycush*), brown (*Salmo trutta*), and rainbow trout, and coho (*Oncorhynchus kisutch*) and chinook (*Oncorhynchus tshawytscha*) salmon (Hasnain, Minns, & Shuter, 2010; Figure 2). However, cold-water (4–6°C) lake trout morphs are more common sea lamprey hosts than warmer water morphs (8–12°C), suggesting that the lamprey thermal exposure can depend on the hosts and that they do not consistently or reliably occupy water at their preferred temperature (Moody, Weidel, Ahrenstorff, Mattes, & Kitchell, 2011). Warming air and water temperatures also may prolong the growing season; historical warming in Lake Superior has corresponded to increased size at maturity of sea lamprey (Cline et al., 2014), suggesting that habitat suitability has increased in that lake. Our bioenergetics simulation of growth suggested that warmer temperatures will enhance growth in Lakes Michigan and Huron (Box 2).

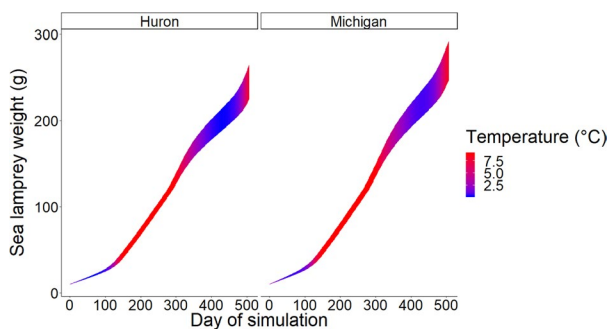
Growth potential of sea lamprey also depends on their forage supply and food conversion efficiency, which are temperature dependent; therefore, increased size of sea lamprey may also correspond to increased parasitism or increased mortality on Great Lakes fishes (Cline et al., 2014). The prey supply is dependent on the assemblage, which may fluctuate with climate change. Fish distributions and relative abundances could shift as the climate changes in the Great Lakes, altering the exposure of some species to lamprey. Significant changes in the fish community in the coming years are possible as non-native alewife (*Alosa pseudoharengus*), the primary prey supporting the non-native salmonid assemblage and lake trout in Lakes Ontario and Michigan, are declining (Madenjian et al., 2008). Alewives were also the primary prey of



**FIGURE 2** Selected Great Lakes fish thermal niches. Data are the optimum growth temperature (squares) and final preferendum (circles) of fish based on data compiled by Hasnain et al. (2017). The spread of sea lamprey (shaded area) overlaps with salmonines, coregonines, and lake sturgeon. Species key: bowfin (*Amia calva*), largemouth bass (*Micropterus salmonides*), channel catfish (*Ictalurus punctatus*), smallmouth bass (*Micropterus dolomieu*), freshwater drum (*Aplodinotus grunniens*), white sucker (*Catostomus commersonii*), walleye (*Sander vitreus*), northern pike (*Esox lucius*), buffalo (*Ictiobus cyprinellus*), sauger (*Sander canadensis*), common carp (*Cyprinus carpio*), yellow perch (*Perca flavescens*), brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), coho salmon (*Oncorhynchus kisutch*), chinook salmon (*Oncorhynchus tshawytscha*), lake whitefish (*Coregonus clupeaformis*), cisco (*Coregonus artedii*), lake trout (*Salvelinus namaycush*), lake sturgeon (*Acipenser fulvescens*), bloater (*Coregonus hoyi*) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**BOX 2 Application of the sea lamprey (*Petromyzon marinus*) bioenergetics model to observed growth in Lake Huron and Lake Michigan, and predicted sea lamprey growth in both lakes under future climate scenarios based on application of the bioenergetics model. The inset figure depicts the forecasted increase (wedge of color) in sea lamprey growth with climate change. The lower edge of the wedge represents observed growth and the upper edge of the wedge represents forecasted growth under climate change. Note that estimates are not sex specific and future efforts should focus on identifying differences between males and females for improved models. Sea lamprey growth was modeled using the R (R Core Team, 2018) Shiny (Chang, Cheng, Allaire, Xie, & McPherson, 2018) app Fish Bioenergetics 4.0 (Deslauriers, Chipps, Breck, Rice, & Madenjian, 2017).**

For the baseline run, the sea lamprey bioenergetics model was fitted to growth observed during the historical (years 1964–1993) period, and the proportion of maximum consumption ( $p$ -value) was recorded. Next, this  $p$ -value was used in a simulation with the temperature regime predicted for the projected (years 2043–2070) period to forecast sea lamprey growth during the projected period. Temperature regimes were taken from Kao, Madenjian, Bunnell, Lofgren, and Perroud (2015) for both the historical and projected periods. The simulation duration was from 1 January to 21 May of the following year (506 days), based on data for the lake residency time and migration timing of sea lamprey in the Great Lakes (Madenjian, Cochran, & Bergstedt, 2003). Bioenergetics model coefficients were taken from Kitchell and Breck (1980). As a hematophagous animal, prey energy density was assigned a value of 3,200.8 Joules/g wet weight that was reflective of a whole blood diet. Sea lamprey energy density was modeled as a function of sea lamprey weight (Madenjian et al., 2003). A starting weight of 10 g and a final weight of 225 g (Lake Huron) and 248 g (Lake Michigan) were specified (Ted Treska, U.S. Fish and Wildlife Service, unpublished data).  $p$ -values derived from baseline runs



### BOX 2 (Continued)

were equal to .8235 and .8349 for Lake Huron and Lake Michigan, respectively.

Projected weights of sea lamprey were 117% and 118% of the historical weight for Lakes Huron and Michigan, respectively. The weight gain was supported by an increase in blood consumption of 20% in Lake Huron and 21% in Lake Michigan, implying that sea lamprey parasitism would be expected to increase with climate change. These simple bioenergetics simulations illustrate the host-impact changes that can be expected as climate change may increase the parasitic demands of sea lamprey in Lake Huron and Lake Michigan.

[Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

salmonids in Lake Huron until 2003, when the alewife population completely collapsed. Although sea lamprey marks are observed on many species, lake trout are considered the principal host of Great Lakes sea lamprey (Farmer, 1980), although why this is the case is unclear.

### 2.2.2 | Will accelerated growth and increased size of sea lamprey increase the lethality of parasitism to hosts?

Increased parasite to host size ratios generally enhance the lethality of parasitism (Swink, 2003). We predict an accelerated growth rate of sea lamprey in the Great Lakes in a changing climate (Box 2). Although sea lamprey parasitism is not necessarily lethal, parasitism is nonetheless associated with significant host mortality (Bergstedt & Schneider, 1988). Indeed, sea lamprey-induced mortality has been cited as an important contributor to collapses of some Great Lakes fish populations, especially lake trout (Muir, Krueger, & Hansen, 2012), but also lake whitefish (*Coregonus clupeaformis*; Ebener, 1997) and burbot (*Lota lota*; Stapanian et al., 2010). Lethality depends on host size (Patrick, Sutton, & Swink, 2009; Swink, 1990, 2003), parasite size (Kitchell, 1990), and water temperature (Bence et al., 2003; Farmer et al., 1977; Patrick et al., 2009; Swink, 2003; Swink & Hanson, 1986). The average size of sea lamprey in the Great Lakes has increased in correspondence with water warming and abundance of non-native salmonid hosts (Kitchell, 1990), potentially increasing the parasite–host size ratio and thereby the lethality of sea lamprey interactions with hosts. Warming temperatures in Lake Huron and Lake Michigan (2043–2070) may enlarge sea lamprey by about 20% with a corresponding increase in feeding activity (Box 2). Even without a corresponding change in food consumption (Kao et al., 2015), our projections indicate that the relative increase in growth with climate change for sea lamprey would exceed that of lake trout. These models that predict growth to larger size presume that lamprey will have enough food available, or enhanced ability to find or convert food, to allocate to growth, however, we do not have data to support or refute this.



The rasping disk of sea lamprey slices through host scales and flesh to access bodily fluids and can cause significant physical damage to the host. Parasitism by sea lamprey can inhibit feeding and accelerate energy depletion by generating drag on the swimming host (Cooke et al. Unpublished Data; Renaud et al., 2009). Interestingly, sea lamprey appear less motivated to parasitize an animal already burdened by another sea lamprey (Bence et al., 2003; Swink, 2003). Following detachment of a sea lamprey from its host, secondary infection of the wound site may lead to mortality, particularly for small fish (Swink, 1990; Swink & Hanson, 1986). Pathogenicity of bacteria increases with water temperature (Holt, Sanders, Zinn, Fryer, & Pilcher, 1975), and experiments to understand whether sea lamprey parasitism will increasingly be lethal through increased secondary infections as the climate changes could be beneficial in this area. Changes to blood physiology are likely to have unknown sublethal effects on hosts, particularly with respect to reproduction, and more research on this is needed.

### 2.2.3 | What pathogens could affect sea lamprey growth or survival?

Marine populations of sea lamprey develop different pathogen communities than in the Great Lakes, where their endofauna tend to be similar to salmonids including *Aeromonas* spp., the etiological agent of furunculosis (Appy & Anderson, 1981). Wilson and Ronald (1967) revealed eight species that were previously unknown to be parasites of sea lamprey, and in 2003 and 2004, bacterial kidney disease (*Renibacterium salmoninarum*) was observed in Lake Ontario sea lamprey (Eissa, Elsayed, McDonald, & Faisal, 2006). Other sea lamprey pathogens include fungi such as *Scopulariopsis* spp. invading tissue of migrating adult sea lamprey in the Great Lakes, which was anecdotally associated with higher vulnerability to handling-related mortality than those sea lamprey that showed no symptoms. Additionally, viral hemorrhagic septicemia has been confirmed as an infectious agent affecting sea lamprey in the lakes, and analyses by Coffee et al. (2017) suggested that the effects are predominantly sublethal in nature despite its lethality in other species. A more complete list of pathogens found to affect sea lamprey is presented in Appy and Anderson (1981). Research on synergies between sea lamprey disease and thermal stressors could assist managers in interpreting the role of disease, climate, and management strategies on lamprey populations.

The existence of sea lamprey pathogens in the Great Lakes suggests potentially dynamic changes to sea lamprey populations as the climate changes. Sea lamprey share pathogenic species with salmonids; if the sea lamprey diet shifts to other species due to shifts in abundance or distribution of hosts in the Great Lakes, there is a potential for changes to the pathogen community, and on this topic, more research is needed (Appy & Anderson, 1981). Additional research is needed to understand sea lamprey infection prevalence, fitness costs, and potential changes to infection dynamics with warming Great Lakes.

## 2.3 | Phenology and spawning migration

### 2.3.1 | Will sea lamprey reproductive phenology track climate change or become mismatched?

Maturing sea lamprey migrate into streams during spring when water temperatures reach 3–4°C (Applegate, 1950). Binder and McDonald (2008) observed that migration was not initiated until temperatures attained 7°C, but early entrants may begin migrating as soon as ice off (McCann, Johnson, Hrodey, & Pangle, 2018). Most movement is nocturnal until temperatures exceed 20°C, after which it can occur at any time (Binder & McDonald, 2008). Nest construction and spawning of sea lamprey occur during June–August when water temperature exceeds 11.7°C (Manion & McLain, 1971). Sea lamprey are not philopatric (i.e., they do not return to their river of origin with high fidelity) and instead follow semiochemicals upriver to spawning grounds (Brant, Li, Johnson, & Li, 2015; Waldman, Grunwald, & Wirgin, 2008). The sex pheromone 3-keto petromyzonol sulfate stimulated migratory activity even at suboptimal temperatures (15°C), suggesting an interaction between the two cues (Brant et al., 2015). However, given that migration and maturation are correlated to water temperature (McCann, Johnson, & Pangle, 2017), the bioavailability of these sex pheromones may advance earlier in the season because of temperature changes rather than independently. Therefore, sea lamprey control efforts would need to adapt to track an earlier run.

Effective prediction of spawning runs and manipulation of stream conditions could enhance the success of some management actions such as trapping (used for monitoring but not control), given that trap encounter rates are flow- and temperature-mediated (Binder, McLaughlin, & McDonald, 2010). Storm intensification may increase the frequency with which barriers are inundated, allowing adult sea lamprey to swim upstream past them. The earlier shift in elevated flows toward winter and spring also could increase the likelihood barriers are inundated during the sea lamprey spawning migration. Furthermore, shifts in storm intensity and timing could alter the abundance and distribution of preferred sea lamprey spawning habitat characterized by swift flowing, unidirectional flow over coarse gravel (Applegate, 1950). Treatment of streams with lampricide has inhibited the recruitment of adult sea lamprey to spawn as the semiochemicals used by adults to select spawning streams are eliminated or reduced (Moore & Schleen, 1980). Shifts in precipitation patterns and changes to stream discharge could alter the conveyance of these semiochemicals from streams into the lakes and may alter the information available to sea lamprey for their migration or their ability to perceive it (Leduc, Munday, Brown, & Ferrari, 2013). Particle distribution models in Great Lakes rivers could be used to investigate the distribution of semiochemicals in currents under different flow scenarios. Perception of semiochemicals may also be altered by acidification; trials with cyprinids and salmonids suggest that small (0.5 pH units) decreases in freshwater pH can disrupt olfactory-mediated behaviors (Leduc et al., 2013). No research has been conducted on the influence of acidification

on the integration of hormones by sea lamprey but given that projections suggest up to a 0.49 unit decrease in pH by 2100 (Phillips et al., 2015) in some areas of the Great Lakes, this is a worthwhile topic for future research.

### 2.3.2 | How will environmental changes affect barrier and trap effectiveness?

Warmer water may facilitate stronger swimming ability of sea lamprey but increase anaerobic demands of swimming. Higher water levels could inundate some barriers to facilitate circumvention by migrating sea lampreys, but in general, climate change is not expected to reduce barrier effectiveness. Sea lamprey barriers physically disconnect adult sea lampreys from suitable spawning and larval habitat (Figure 1; Zielinski et al., 2019). Sea lamprey barriers do not always reduce the number of larvae produced in a tributary because spawning can occur below barriers; instead, sea lamprey barriers exclude upstream areas from the need for costly lampicide treatments. Most barriers are permanent or semipermanent structures that are not dynamic to account for fluctuations in water levels, but some are inflatable and therefore capable of adjusting to the water level. Inflatable barriers that move up and down with water levels and low-head barriers with electrical barrier backups for high water events have been installed on a few Great Lakes tributaries, but these technologies have not been widely used due to higher failure rates (Zielinski et al., 2019). The probability of adult sea lampreys escaping upstream of a barrier depends on site-specific conditions including barrier crest height, the presence of a “lip” that overhangs the crest, flow, and temperature, and the interplay between these factors and the sea lamprey’s physical and physiological capabilities (Lavis, Hallett, Koon, & McAuley, 2003; McLaughlin et al., 2003, 2007). Increased flooding associated with climate change could result in low-head barriers becoming less effective. Kemp, Russon, Vowles, and Lucas (2011) studied passage by adult river lamprey (*Lampetra fluviatilis*) at experimental weirs in controlled flumes and showed that fish approached and passed the obstacles more frequently at relatively lower discharges and associated velocities. However, under field conditions, adult river lamprey approach and passage of low-head barriers have been found to be increased at high discharge, especially under conditions when obstacles, with or without fishways, are drowned (Lucas, Bubb, Jang, Ha, & Masters, 2009; Tummers et al., 2016). Fishway entry and passage of pre-spawning adult sea lamprey was also negatively related to river discharge, ascribed to a reduction in relative attraction flow from the fishway as proportionately more water was released over the dam at high river discharge (Pereira et al., 2017). Climate change-mediated alterations to river discharge and local flow patterns at lamprey barriers in the Great Lakes may alter behavioral responses of adult sea lamprey compared to current conditions. These observations suggest that long-term data are needed to investigate how effective barriers are for Great Lakes sea lamprey for a range of barrier structures, temperatures, and discharge

scenarios. Monitoring data will be valuable for making effective determinations about the deterioration or enhancement of barrier effectiveness given different environmental regimes (Bravener & McLaughlin, 2013). Establishing the nature of relationships among sea lamprey spawning escapement above barriers, water temperature, flow, and time of year will facilitate the generation of predictions about barrier effectiveness.

Deployment of lamprey traps is a monitoring tool that exploits the sea lampreys’ strong instincts to swim upstream to find suitable habitat and spawn, to take refuge by day during the pre-spawning period when they are nocturnal, and to explore structured habitats (Moser, Butzerin, & Dey, 2007). In the Great Lakes, sea lamprey traps are normally hard-engineered steel structures placed below lamprey barriers or other river infrastructure. Effectiveness of traps in smaller tributaries could be influenced to a greater degree by changes in climate. For example, when flooding occurs, many traps are ineffective because they become clogged with debris, and cannot be emptied safely because they are inundated with water. When new traps are constructed, designs should consider more frequent high water levels, perhaps by increasing the height of the traps or building curb-like walls around the top of the trap. Trap operators may need to adapt to rising air temperatures resulting in earlier snow melt and earlier adult sea lamprey migrations, by installing traps earlier in the spring. Emerging tools that could improve trap performance, such as electric currents and semiochemicals to guide adult sea lamprey into traps, depend on environmental conditions for their success and will need to be designed to accommodate climate change.

Designing effective sea lamprey traps and barriers clearly relies on a detailed understanding of encounter probability and capture success. Temperature is a primary factor that greatly affects lamprey swimming performance (Beamish, 1974). As sea lamprey migrate up rivers toward spawning grounds, they swim steadily and constantly through slow flowing reaches but convert to a punctuated series of (probably anaerobic) swimming bursts to overcome areas of high flow, attaching to the substrate with the oral disk in between bursts to rest (Quintella, Póvoa, & Almeida, 2009). Critical swimming speeds of anadromous adult sea lamprey are near 1.0 m/s (Almeida, Póvoa, & Quintella, 2007) up to a maximum of 3.9 m/s (Hunn & Youngs, 1980). According to Reinhardt, Binder, and McDonald (2009), sea lamprey have limited capabilities to ascend even small, smooth-surfaced, unlippered barriers and must have the dorsoventral fins fully submerged in order to produce the burst needed to scale a barrier. Height ascended by sea lampreys was positively correlated with temperature up to 17.2°C, with gains measuring a few centimeters on average. However, Hume et al. (unpublished data in review) recorded 98% passage of sea lamprey over a 45° ramp and they suggest that ramp design and water flow may influence the passability of such structures (J. Hume, personal communication). We project that climate change will facilitate faster growth and larger size of sea lamprey spawners (Box 2) and research could determine whether a 0.45 m (18 inch) minimum barrier height will require adjustment in the future.

## 2.4 | Abundance, distribution, life history

### 2.4.1 | Will climate change complicate sampling and challenge abundance estimation?

The ability to accurately assess the status of larval sea lamprey populations is an essential tool to effectively allocate control efforts and exert an effect on the sea lamprey invasion (Christie et al., 2003; Slade et al., 2003). Many methods have been tested for sea lamprey stock assessment (Moser et al., 2007), but larval sea lamprey surveys are predominantly conducted using electrofishing and granular Bayluscide. Bayluscide deposited into rivers sinks to the bottom, forces larvae out of burrows, and kills them, allowing them to be counted. Efficient sampling in terms of spatial coverage and effective removal is necessary to ensure that larval population assessments are conducted using a method that reflects true abundance so that treatment efforts can be effectively allocated (Slade et al., 2003). Steeves, Slade, Fodale, Cuddy, and Jones (2003) investigated effects of temperature on sampling efficiency of backpack electrofishing, but found no evidence that monitoring larval abundance would be complicated by rising temperatures. Conductivity did, however, affect electrofishing sampling efficiency and higher productivity in streams causing greater conductivity could affect catchability and challenge abundance estimation if not properly accounted for. Warmer temperatures could, however, extend the period available for larval assessment as the season extends earlier in the spring and later into the autumn months.

Warming water temperature may alter wound healing of host species. Temperature has a role in the severity and healing of lamprey wounds with those made at colder temperature being difficult to observe (King, 1980). Wound healing may accelerate in warmer water, but infection rates may increase. Additionally, secondary infections and sublethal effects of parasitism on hosts could be exacerbated under a warming climate. Wounding incidence is an important measure of sea lamprey abundance, distribution, diet; therefore, models using wounding rates will need to be adapted to compensate.

### 2.4.2 | Which rivers will switch from hospitable to inhospitable (and vice versa) for sea lamprey spawning and rearing? Are species distribution modeling exercises needed?

Sea lamprey do not appear to home to their natal streams, and are therefore well-suited to explore, invade, and occupy new areas (Massiot-Granier et al., 2018; Waldman et al., 2008). The expansion of suitable sea lamprey spawning and rearing habitats to current cold-water and northern rivers in the Great Lakes (e.g., Lake Superior and Lake Michigan-Huron basins) might be expected. Estimating this could be accomplished by an approach similar to the predicted disappearance from some Iberian, Mediterranean, and southern Baltic areas and potential appearance in Iceland

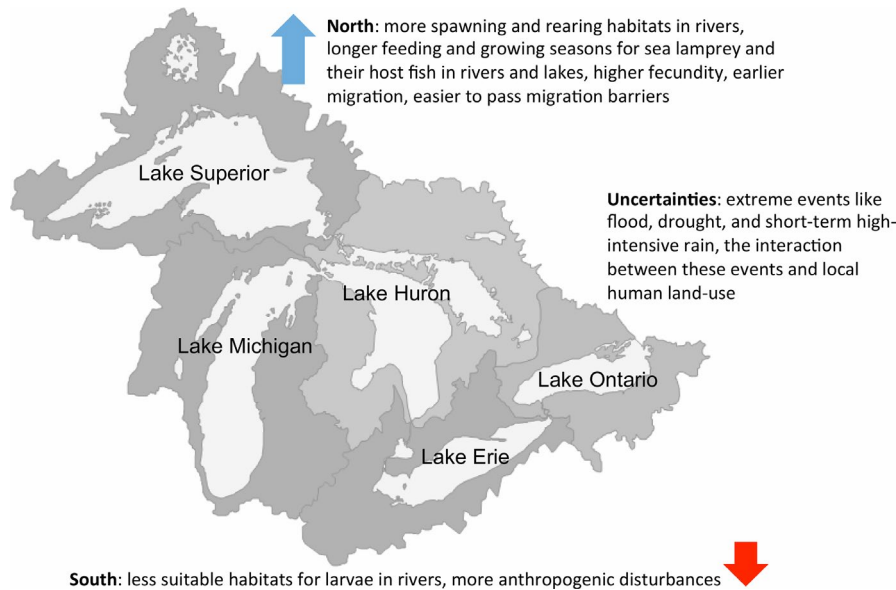
and northern Baltic drainages based on biogeographical models (Lassalle, Béguer, Beaulaton, & Rochard, 2008). Although sea lamprey seem to have effectively colonized many Great Lakes streams, in general their migration ecology in which they home to chemical cues may make them less effective at colonizing new areas than other migratory fishes, as suggested by Pess, Quinn, Gephard, and Saunders (2014).

Warmer temperatures might provide longer feeding seasons and thus increase the growth rate of larval sea lamprey in current cold-water rivers (Cline et al., 2014; Hansen et al., 2016). Increasing water temperature and the number and frequency of extreme hot days (>35°C) during early development (e.g., summer), however, could negatively affect early survivorship because the young life stages of sea lamprey have relatively stenothermal tolerance (e.g., 17.8–21.8°C for larval sea lamprey; Dawson & Jones, 2009; Rodríguez-Muñoz et al., 2001). Therefore, current warm-water rivers and some streams in southern watersheds (e.g., basins of Lakes Erie, Ontario, and southern Lake Michigan) may become less suitable for sea lamprey in the future if summer water temperature exceeds their thermal tolerance (Figure 3). In addition, more intensive anthropogenic disturbances, such as riparian clearing, channelization, and damming in the southern Great Lakes basin (Robertson & Saad, 2011), could weaken the ability of riparian vegetation and groundwater seeps to buffer rising temperature (Poole & Berman, 2001).

Assessing the spatial distribution of suitable sea lamprey habitats is the key to identifying where to implement control actions like migration barriers and lampricides (Jones, 2007). Young, Kelso, and Weise (1990) successfully applied discriminant analysis to classify Great Lakes' tributaries where sea lamprey spawn, revealing significant effects of substrate and temperature on lamprey distribution. Looking forward, it will be crucial to model possible changes in future sea lamprey distribution using mechanistic models that consider the thermal physiology of these animals, at different life stages. Additional research may predict changes to sea lamprey distribution based on known features correlated to their presence, especially the availability of critical habitats such as spawning gravels and larval soft-sediment habitat. Furthermore, models that could explicitly account for uncertainties in climate models and control actions (e.g., Bayesian networks) could improve the flexibility of decisions when facing a changing climate (Lynch, Varela-Acevedo, & Tayler, 2015).

### 2.4.3 | How will sea lamprey spawning success and fecundity be affected by climate change?

Within their suitable thermal range, spawning success and fecundity of sea lamprey might also be influenced by climate change. Besides temperature changes, several climate models also predict an overall increase of precipitation in the Great Lakes basin, especially during winter and spring and in the north (e.g., Lake Superior basin, Bartolai et al., 2015; Basile, Rauscher, & Steiner,



**FIGURE 3** The future portends a shift in the suitable habitat available to sea lamprey (*Petromyzon marinus*) within the Great Lakes. Population increases and urbanization/sprawl exacerbate threats to rivers, which may limit productivity to sea lamprey. Warming of the global climate may render northern habitats more hospitable to sea lamprey, potentially increasing the invasive range of the species beyond its present distribution. However, uncertainties remain in terms of the impacts of extreme weather, changes in precipitation and sediment supply and transport patterns, changes in species composition associated with invasions, and other factors that may enhance or degrade that habitat suitability within the basins [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

2017; Byun & Hamlet, 2018; McDermid et al., 2015; Wang et al., 2017), but warmer and drier summers with lower flows. Both warming and increasing river flows, resulting from higher precipitation during the migration season, might enhance upstream movement (Binder et al., 2010; Hogg, Coghlan, & Zydlewski, 2013), help spawning adults overcome migration obstacles (e.g., low-head dams, Rahel & Olden, 2008), and increase the availability and size of spawning grounds (Oliveira, Ferreira, Pinheiro, & Bochehas, 2004). In some locations around the Great Lakes, spawning phenology of sea lamprey has shifted, with peak spawning migration occurring earlier (McCann et al., 2018). More research is needed to understand how temperature fluctuations affect egg development and conditions for larval settlement and growth. This early migration of sea lamprey could provide larvae with a longer growing season before their first winter (McCann et al., 2018), which might allow larvae to accumulate sufficient lipid reserves and reach the critical size for metamorphosis, sooner in their development.

#### 2.4.4 | Will sea lamprey populations increase or decrease in abundance or extent as a consequence of climate change?

Whereas studies indicate that climate change may expand the range of suitable thermal habitats, improve spawning success, and increase fecundity of sea lamprey at broad spatial (e.g., lake basins) and temporal scales (e.g., annual/seasonal temperature or precipitation change), uncertainties in local variables and short-term

extreme events make it difficult to predict changes in population abundance. Although increasing precipitation may create more suitable spawning and larval habitats and facilitate upstream migration, climate change could also increase the intensity and frequency of extreme river discharge events (i.e., flood and drought: Bartolai et al., 2015; Byun & Hamlet, 2018; Cheng, Auld, Li, & Li, 2012; McDermid et al., 2015), which could reduce recruitment. Depending on the time of year, high discharge could cause egg loss from nests (Smith & Marsden, 2009) whereas drought could decrease the size of suitable spawning grounds (Oliveira et al., 2004). In addition, extreme high river discharge may hinder upstream migration and spawning activities (Hogg et al., 2013). In watersheds with more agricultural or urban land cover, climate change may induce more eutrophication (and pollution) events because of intense rainfall in a short time (Collingsworth et al., 2017), which could smother spawning and larval habitats and create anoxic conditions (Maitland, Renaud, Quintella, Close, & Docker, 2015). For species without strict natal homing behavior like sea lamprey, changing sea lamprey production in a certain river may influence many rivers across the lake basin (Jensen & Jones, 2018). Therefore, predicting change in sea lamprey abundance in a lake basin under climate change requires incorporating changes in local reproductive success and recruitment. A model to predict how local recruitment change influences the lake-wide sea lamprey population has been developed (Jones et al., 2009), but more effort is required to incorporate the effect of climate change into the modeling framework. As streams in the present distribution of sea lamprey become inhospitable due to climate change, new ones will be colonized.

### 3 | SYNTHESIS

Our review focused on four categories of individual and population scale dynamics related to the sea lamprey that contribute to their invasiveness and have been focal points of research in their invasive range within the Great Lakes. Knowledge availability appears to be greatest for the larval and migrating adults in stages in lotic habitats, which are relatively easy to access and study. Less information is available for the juvenile parasitic life stage in the lakes, in which the animals are much more elusive. This represents a large knowledge gap that therefore requires new knowledge to assist with control. Telemetry studies would provide important insight into movements. Tagging with small passive integrated transponders is a method to investigate the early phases of the spawning migration (Quintella, Andrade, Espanhol, & Almeida, 2005; Simard, Sotola, Marsden, & Miehl, 2017) and may also detect adults returning to the same stream or nearby streams with PIT antennas. Small acoustic tags (2 mm diameter JSATS) are now available to track outmigration and early lake life of juvenile lamprey (e.g., Mueller, Liss, & Deng, 2019). Filling gaps in understanding the lacustrine life of sea lamprey will be essential to understanding how far individual sea lamprey can travel within the lakes and how they select spawning streams. Knowing how sea lamprey behave in the lakes will also reveal more about their host selection and preferences. The ability to empirically model thermal niche, swimming, and host attachment strategies would reveal more about which species are at highest risk of parasitism by sea lamprey and how fisheries management can be adapted.

Alterations to habitat suitability for Great Lakes ichthyofauna has been discussed for decades (e.g., Magnuson, Meisner, & Hill, 1990) and these changes are now occurring (Lynch et al., 2016; Poesch, Chavarie, Chu, Pandit, & Tonn, 2016). Although changes related to climate are somewhat difficult to project due to interactions with other stressors (e.g., other invasions), available evidence projects that warmer temperatures will accelerate growth, advance migration timing, and expand the range of larval and adult sea lamprey within the Great Lakes (Table 1). However, any temperature-related shifts in sea lamprey physiology and behavior will have to be satisfied by increased foraging availability, success, conversion, or nutritional value (Box 2). Reductions in the effectiveness of sea lamprey control methods are hypothesized to accompany environmental changes. Warmer temperatures, faster growth, and advanced outmigration of larvae may demand earlier, more frequent, and higher volume treatments with lampricide. Meanwhile, we do not know how non-target species such as threatened bivalves and lake sturgeon will respond to lampricides plus temperatures and possible changes to water chemistry. A better knowledge of their sensitivity to lampricides under different climate change scenarios will make it possible to devise strategies to eliminate or minimize potential non-target impacts. Barriers installed to stop migration and spawning of sea lamprey may become slightly more passable under extreme conditions, but it also likely that lamprey will colonize other tributaries where barriers are not present, evading this important control measure (Table 1).

However, the return migration of adults may become more challenging with altered flows and warmer temperatures obfuscating the cues used by lamprey and accelerating energy depletion during the return migration in some instances. Although no species will universally benefit from climate change, sea lamprey is poised to reap many benefits from warming in the Great Lakes, necessitating adaptations to the management program aiming to control them (Table 1).

#### 3.1 | Conclusions

Modern climate change heralds a new era of challenges to the Great Lakes and the managers responsible for this area (Magnuson et al., 1997). The sea lamprey problem is expected not only to persist but also to be exacerbated as lamprey benefit from warming (Table 1). The greatest challenge will be to ensure the effectiveness of lampricide treatments that are essential to the control program as individuals may become larger and streamflow less predictable in dispersing the lampricide while impacts upon non-target species will have to be carefully monitored under the altered flow, pH, and thermal regimes. Heretofore unknown challenges to control sea lamprey could ensue (Mills et al., 2013), including but not limited to the invasion of new species, which may become sea lamprey hosts or predators/parasites themselves. The high rate of invasions in the Great Lakes may further complicate or facilitate control, for example, by diverting resources away from lamprey control.

The Great Lakes region is a highly important, but vulnerable, ecosystem and climate change will affect many aspects of life in the region. Sea lamprey management has historically been an important aspect of fisheries management, but there are many other ongoing initiatives that may require adaptation to enhance climate change resilience. Changing eco-politics are promoting dam removal projects that could facilitate upstream expansion of sea lamprey and increased need for lampricide treatment, a factor to be balanced against the many important benefits of dam removal for native species conservation (Jensen & Jones, 2018; Lavis et al., 2003). Sea lamprey control efforts may also shift to target downstream migration of larvae (Sotola, Miehl, Simard, & Marsden, 2018). Efforts have been made to rely less upon chemical treatment of streams (McDonald & Kolar, 2007). Future genetic techniques to alter sex ratios or sterilize sea lamprey by genetically modifying food items provide potentially novel options to control sea lamprey, with fewer conflicts with native species (Thresher, Jones, & Drake, 2018). For monitoring, models should be developed to predict what rivers could enter the hospitable range for sea lamprey, as they may be quick to invade previously uninhabitable tributaries once temperature and flow regimes shift and particularly if barriers are removed. Keeping a step ahead of future sea lamprey invasions into additional rivers as their distribution and phenology shift in response to a changing climate is crucial to managing the ecosystem services of the Great Lakes. Early detection of new invasions and the ability to mobilize resources to control them will depend on their nature and extent (Figure 1). Although



**TABLE 1** A scorecard for sea lamprey as a benefit or a cost (or in some cases not certain) when confronting climate change in the Laurentian Great Lakes

Category	Score	Rationale	Confirmatory experiments
Larval growth	Benefit	Longer growing seasons in a warmer climate will accelerate growth and facilitate larger size of sea lamprey larvae	Need to first develop bioenergetics models and aging methods for larval lamprey. Once models have been developed, perform simulations (with validations) of larval metabolism, consumption, and growth at different stream temperatures and flow rates.
Larval survival	Unknown	Larger larvae should have better survival, but density dependent effects are unknown, as are the effects of future changes to precipitation on the distribution and suitability of larval soft-sediment habitat	Factorial comparison of larval growth as a function of food availability, temperature, and conspecific density (ideally in laboratory and field). Model fine sediment supply and redistribution in catchment scale hydrogeomorphological/hydraulic models in response to altered discharge patterns; validate model with data from rivers with different hydrogeomorphic/hydraulic conditions.
Surviving lampricide	Benefit	Lampricidal treatments will be less effective and require earlier treatment, greater volumes, and potentially more frequent treatment to keep pace with accelerated metabolism of the pesticide and faster dilution/dissipation of the chemical in the water; treatment will have to adapt to climate change to level the playing field	Dose-specific comparison of lamprey survival in simulated stream microcosms under factorial temperature and flow regimes; more comprehensive or frequent larval assessments following treatment may be required to confirm effects in the wild.
Outmigration of larvae	Unknown	Sea lamprey larvae appear resilient to migrate from the river to the lake anytime in autumn or spring but may be vulnerable to exhaustion if warm temperatures accelerate depletion of lipid reserves	Comparison of energetic condition of lamprey larvae from streams with different environmental conditions; holding studies where fish are reared under different conditions and then released and tracked to assess fate.
Growth in lakes	Benefit	Lamprey will have ample habitat available to them with potential hosts living at various temperature envelopes throughout the lakes; warmer temperatures will accelerate growth	See Box 1. Also, estimation of interannual variability over the 2043–2070 period, as done for lake trout by Kao et al. (1973)
Success as parasites	Benefit	Lamprey will have access to multiple potential hosts throughout the year; rate of feeding and lethality of parasitism may increase, but this is not likely to affect lamprey up to their carrying capacity	Mesocosm experiments of host–lamprey interactions in different temperature regimes to simulate Great Lakes habitat at different temperature scenarios; experimental studies of parasitic phase lamprey to more diverse range of potential hosts in lab environment. Also, better genetic or observational data on alternate host use (currently wounding data only collected for lake trout) needed
Return migration	Cost	Return migration of sea lamprey will be somewhat more challenging for lamprey as conditions in streams change more rapidly than they did in the past; juvenile scent cues may not entirely accurately reflect habitat suitability. Variation in flows may also challenge lamprey's ability to ascend at certain times	Particle simulation of pheromone distribution from streams with different flow regimes; creative approaches for assessment of lamprey. Lamprey swimming energetics given their use of suction behavior to avoid swimming in high flows.
Overcoming control efforts during spawning migration	Benefit	Expansion of suitable habitat to streams not presently monitored or without barriers installed will allow sea lamprey to be a beneficiary in the short term; warmer water and larger size may also slightly improve the potential to pass barriers or overcome obstacles; efforts to map the potential distribution of sea lamprey and proactive measures could offset any gains sea lamprey are likely to have	Mesocosm or wild experiments using imaging technology, or telemetry to observe barrier passage at different flows and water temperatures
Distribution and abundance	Benefit	Climate change will create new opportunities for lamprey to spawn and thrive in the Great Lakes, particularly in northern areas such as in Lake Superior; southern areas that become inhospitably warm but overall lamprey can be anticipated to become more abundant, increasing the need for vigilance in developing and deploying control efforts	Species distribution or occupancy modeling of lamprey niche given different climate simulations from the International Panel on Climate Change. Occupancy modeling needs to take account of hydrogeomorphic processes.

lampricide applications can easily be redistributed around the basin, issues around treatment timing, accessibility of new systems by treatment crews, and construction of new or modification of existing barriers to confront new threats could require additional resources.

Invasive species are a persistent threat to biodiversity, and therefore, their control is a multibillion dollar effort (Pimentel et al., 2005). These control efforts are inherently challenging and require consideration of costs and benefits of control, particularly with respect to non-target species. Eradication is sometimes impossible, meaning that some control programs must continue indefinitely to sustain the benefits. Control efforts benefit greatly from understanding the biology of the targeted invader, and we attempt to illustrate how such control programs could adapt to climate change in order to keep pace with the dynamic changes that can be expected from an invader. Our review emphasizes where more research is needed to fill knowledge gaps and the importance of considering how control at different life stages is likely to be effective. Proactive evaluation of control programs in a changing climate can prepare resource managers to make effective decisions with resources dedicated to managing the global problem of invasive species.

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