Managing native and non-native sea lamprey (*Petromyzon marinus*) through anthropogenic change: a prospective assessment of key threats and uncertainties

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Abstract

Sea lamprey (*Petromyzon marinus*) are a species of conservation concern in their native range of the Atlantic coasts of Europe (Near Threatened to Critically Endangered) and North America (Secure to Critically Imperiled), and an invasive species of great economic and ecological concern in the Laurentian Great Lakes. Despite differences in life history strategy (anadromous natives vs adfluvial non-natives), the biology of sea lamprey is sufficiently similar to expect comparable responses to large-scale environmental change. We take a prospective look at the future (50 to 100 years) of sea lamprey management in an era of considerable environmental disturbance, and consider biological responses, management actions, and the future status of populations across the native and non-native ranges. Based on facilitated discussion by a diverse group of international experts, two major but poorly characterized classes of threats to sea lamprey were identified: climate change and socio-political issues. We discuss how climate induced changes affect growth, bioenergetics, and phenology of sea lamprey, and associated effects on control tactics (pesticides and barriers) and conservation. We consider tensions surrounding improving connectivity in the Great Lakes while controlling invasive sea lamprey, and discuss supplements and alternatives to pesticides and their wider effect, as well as the effects of new invasive species. To prevent the extirpation of native sea lamprey populations, or the re-expansion of non-native populations, we conclude with a call for new and ongoing dialogue and collaboration among all sea lamprey biologists and managers across the native and invasive range.

Key words: climate change, conservation, control, fish, management, socio-political.

Introduction

The sea lamprey (*Petromyzon marinus*) is a species that exemplifies duality. Larvae are filter-feeding and sedentary in streams, whereas juveniles are parasitic and highly mobile in open water. Some populations are freshwater resident showing an adfluvial life history, while yet more are anadromous, and maximum size of mature adults ranges from ~600 mm TL to ~1200 mm TL. Moreover, geography itself reveals another dualism of sea lamprey; they have both a native and non-native range, which requires often radically different approaches to their management. In the major Atlantic watersheds of Europe, where sea lamprey are native, their conservation status ranges from "Near Threatened" to "Critically Endangered" as a consequence of habitat loss, declining water quality and quantity, and overexploitation (Maitland et al., 2015; Clemens et al., this issue; Figure 1). For many of the same reasons, in the Atlantic watersheds of North America where the species is also native, their conservation status ranges from "Secure" to "Critically Imperiled", and the American states of Connecticut, Massachusetts, New Hampshire, and Vermont recently designated it a "Species of Greatest Conservation Need" (Renaud et al., 2009; CRASC, 2018; Figure 2). In response, management actions such as barrier removal and remediation, translocation, and habitat restoration seek to improve their outlook (CRASC, 2018; Lucas et al., this issue). By 1921, sea lamprey penetrated inland from the Atlantic coast, gained access to the upper Laurentian Great Lakes (Erie, Huron, Michigan, and Superior), and became a widespread and destructive invasive species in this region (Figure 3). Despite their putative native status in Lake Ontario, New York Finger Lakes, and Lake Champlain (Eshenroder, 2014), sea lamprey populations are currently managed by a joint U.S. and Canadian control program in the Great Lakes (Great Lakes Fishery Commission [GLFC]), by the New York State Department of Environmental Conservation (NYSDEC) in the Finger Lakes, and by the NYSDEC and Vermont Department of Fish and Wildlife (VDFW) in Lake Champlain. Control strategies include the use of barriers to restrict adult access to spawning grounds, and the application of pesticides to reduce larval abundance (Marsden and Siefkes, 2019).

Regardless of the antecedent events that now necessitate their management (conservation or control), sea lamprey biology remains sufficiently similar in native and non-native ranges that we should expect comparable responses to large-scale environmental change. Anthropogenic stressors such as human population growth, climatic influence, and an often rapidly oscillating socio-political landscape are affecting the aquatic environment now more so than at any point in human history (e.g., Best, 2019). Species are going extinct (Ceballos et al., 2015), ranges and phenology are shifting (Shuter et al., 2012), and organismal interactions are being generated and destroyed as species respond to rapid human-induced change (Winder and Schindler, 2004; Budria and Candolin, 2014). Lampreys are not immune to these stressors; record-setting warm temperatures and more frequent droughts in some parts of the world (e.g., California U.S.A., southern Europe, Iran, and southeastern Australia) will result in substantial range contractions and local extinctions (Lucas et al., this issue; Wang et al., this issue). In many parts of the sea lamprey distribution (e.g., North America), a large proportion of dams are > 50 years old and need replaced (National Inventory of Dams https://nid.sec.usace.army.mil/ords/f?p=105:1), and in Portugal new barriers require the provision of fish passage. Ageing barrier networks are an opportunity to aid sea lamprey management as without suitable fishway designs (Moser et al., this issue) or the removal of lower-most barriers, migratory lampreys and other native species will continue to be restricted to the lower reaches of rivers where spawning habitat is lacking or suboptimal. In the Great Lakes, the legacy of six decades of successful invasive sea lamprey control is under threat. Not only is there reduced public and stakeholder tolerance of an ageing network of barriers intentionally fragmenting river networks to reduce sea lamprey access to spawning habitat, but reliance on chemical pesticides leaves the program vulnerable to a change in political ideology and public support.

Support for management of both native and non-native sea lamprey may also suffer from a “shifting baseline” effect, whereby the public and policy makers alike have forgotten their recent history (Papworth et al., 2009). Sea lamprey are a critical part of ecosystem functions in their native range, and were a highly valuable fisheries resource; in the Great Lakes region they contributed to the collapse of the ecosystem, and caused significant economic harm to the fishery. Management decisions made in the next 50 years could be instrumental in determining the future of sea lamprey globally. To address this concern and bring research and management communities to a common plateau of understanding regarding lamprey biology, the Great Lakes Fishery Commission sponsored the third Sea Lamprey International Symposium in the summer of 2019. As part of that effort, a diverse international group with expertise in lamprey biology, conservation, as well as sea lamprey control practice and policy convened to discuss the question "*How will anthropogenic changes affect sea lamprey, their prey, and predatory-prey interactions in the future?*" Through facilitated discussion, two major classes of threats were identified that may have the greatest effects on sea lamprey globally: climate change and socio-political issues (Figure 4). Our aim in this paper is to broadly discuss key aspects of climate change and socio-political decisions, and uncertainties surrounding them, that will impact sea lamprey in the coming decades. We take a prospective look at how sea lamprey might biologically respond to those issues, how management of populations will consequently be affected, and speculate on their future status.

The approach to this paper, and conclusion presented, differ from previous related contributions (e.g., Lennox et al. (2020)) in two primary ways. First, we contrast the primary anthropogenic effects on sea lamprey populations in both the native and non-native ranges, which necessitates a review of several topics covered independently for each part of the distribution. Second, by bringing together the conservation and control communities, we hope to inspire cross-cutting research that leverages the knowledge from both communities to better manage sea lamprey globally.

Sea lamprey status and distribution

Sea lamprey are native to a large extent of western Europe, and are regionally abundant in countries with large rivers discharging to the Atlantic Ocean (Figure 1), but this distribution is rapidly changing in response to habitat availability. Juvenile and sub-adult sea lamprey are infrequently encountered near the mouths of some north African, eastern Mediterranean, and Icelandic streams (not shown in Figure 1) but have not yet established spawning populations in these areas (Mateus et al., this issue). A major threat to the species in Europe is restricted access to freshwater habitats, especially in the Iberian Peninsula during the last century (Mota et al., 2016). In Spain, sea lamprey no longer have access to ~75% of habitat in some major watersheds, and in Portugal sea lamprey can access only 588 river km, a reduction of ~84% in some major drainages (Mateus et al., 2012). In France, populations have been in decline in the largest watersheds (Garonne-Dordogne and Loire) for three decades, yet exploitation rates in a commercial fishery for the species in these catchments remain high or are increasing (Beaulaton et al., 2008; Legrand et al., 2020). In the coming decades, increasing temperatures are projected to result in a loss of suitable watersheds from the Iberian Peninsula, Italy, Bosnia and Herzegovina, and Poland (Lasalle et al., 2009).

The sea lamprey is native to the western Atlantic Ocean, and their distribution in this region is similarly extensive as it is in Europe (Figure 2). The mid-Atlantic region of the North American coastline and the Connecticut River in particular appear to be strongholds (Figure 2). There is no evidence that juvenile sea lamprey currently disperse across the Atlantic Ocean in either direction, which suggests ongoing reproductive isolation (Rodríguez-Muñoz et al., 2004). Based on mitochondrial DNA, Genner et al. (2012) concluded that European sea lamprey populations were founded by an older North American lineage around 125,000 years ago, and the effective population size of native North American sea lamprey is five times greater than that of Europe (Genner et al., 2012). Since 1955, access to > 70% of the Connecticut River mainstem and tributaries has been re-established via dam removal and mitigation (CRASC, 2018) and the population appears stable. In the south Atlantic region of North America's coastline, sea lamprey are rare in Florida and Georgia, with only ~10 confirmed observations of adults in the last century (Florida Fish and Wildlife Commission). The species may never have established consistent spawning populations in this region, or it may have been recently extirpated. In the north Atlantic region of North America, sea lamprey are also rare in Labrador, and ranked Critically Imperiled in Newfoundland (Figure 2). However, the biology and status of native North American sea lamprey is generally not well quantified and management plans are lacking. The narrative of managing the species in these watersheds is regularly over-shadowed or conflated with the need to control the species in their non-native North American range.

At some point early in the 20th Century, sea lamprey gained access to, and became established within the upper Laurentian Great Lakes (Erie, Michigan, Huron, and Superior) of North America. The species is unquestionably non-native in these lake basins. Whether or not they should be considered native to Lake Ontario, the New York Finger Lakes (Cayuga and Seneca), Oneida Lake, and Lake Champlain is debatable and likely impossible to resolve using currently available ecological and genetic evidence (Docker and Potter, 2019). Regardless, sea lamprey populations are managed by the GLFC in all five Great Lakes, by the NYSDEC in lakes Cayuga and Seneca, and by the NYSDEC and VDFW in Lake Champlain (Marsden and Siefkes, 2019). Sea lamprey populations are now widely established in watersheds throughout this region of North America (Figure 3). Sea lamprey also reproduce within the connecting channels of several lakes, including the St. Mary's, Detroit, and St. Clair rivers. However, of the ~5750 tributaries of the Great Lakes, sea lamprey have been recorded only in ~10%, and ~6.5% of those are treated annually with pesticides to control larval populations (Marsden and Siefkes, 2019). To restrict access to this vast potential habitat, the GLFC maintains 50 purpose-built barriers and an additional 27 "de facto" barriers (waterfalls, hydropower structures, etc., Siefkes et al., 2013; Zielinski et al. 2019). These 77 structures reduce access to ~1400 river km and an estimated 15% of the total preferred larval habitat (Marsden and Siefkes, 2019). Moreover, an additional ~1000 de facto barriers have been identified in the Great Lakes region that act to prevent sea lamprey accessing a further 300,000 river km (Miehls et al., 2019; data.glfc.org). This network of barriers constrains sea lamprey to ~50% of potential spawning and rearing habitat in this region. Without barriers, the cost of managing sea lamprey in their non-native range of North America will rapidly become untenable, as the area of infestation will exceed treatment capacity.

Climate Change

Change in distribution caused by shifts in temperature and precipitation

In recent decades, consensus has formed that species will shift their range poleward and into higher elevations in response to increasing global temperatures (Chen et al., 2011). Increases in water temperature and shifts in seasonal precipitation patterns will interact with physical habitat at multiple spatial scales and affect all sea lamprey life stages in their native and non-native ranges. Maximum stream temperature and availability of suitable substrates are the primary drivers of larval habitat selection in sea lamprey. Where temperatures approach tolerance limits, shifts in both larval distribution and growth rate are likely (Young et al., 1990; Rodríguez-Muñoz et al., 2001; Dawson and Jones, 2009).

Lennox et al. (2020) concluded that in Great Lakes tributaries in the southern part of the distribution of non-native sea lamprey, where summer stream temperatures will more frequently exceed thermal tolerance, there will be a reduction in the number of suitable watersheds and corresponding declines in recruitment. Sea lamprey presence is also projected to decrease in the southern portion of their native European range, particularly Italy, Bosnia and Herzegovina, and the Iberian Peninsula (Lassalle et al., 2009; Lassalle and Rochard, 2009). As many as 30 basins currently occupied by European sea lamprey are projected to become unfavorable by 2100. Sea lamprey will remain in the mid to northern part of their present European distribution, with strongholds in western Europe and Scandinavia, and a possible expansion into Icelandic watersheds as they warm (Lassalle et al., 2008; Lassalle and Rochard, 2009). Distributional data from the native range of North America are scant for sea lamprey, but they have been found widely dispersed in Atlantic tributaries from Florida in the U.S.A. to Labrador in Canada (Beamish, 1980; Figure 2). Increased stream temperatures will likely result in loss of larval sea lamprey populations from southern American states of Florida, Georgia, the Carolinas, and Virginia, but potentially the establishment of permanent populations in Canadian provinces such as Newfoundland and Labrador.

The magnitude of climate shifts that will occur by the end of this century is uncertain. However, current projections of climate-induced temperature and stream flow alterations, in combination with other anthropogenic stressors discussed here, increase the probability that native lamprey distributions in Europe and North America will indeed shift and possibly contract even in the most optimistic scenarios (e.g., Wang et al., 2020). More basic research is required to establish thermal tolerance of larval sea lamprey and their capacity for avoiding unfavorable environmental conditions. This is particularly important in the native North American range, where uncertainty surrounds the true extent of stable spawning populations vs the occasionally documented vagrant sub-adult migrating upstream. But similarly, in their non-native range, a better understanding of how the population will respond to warming streams could enable predictions of tributaries that will likely need to be managed in the next few decades.

Interactions between temperature-precipitation and other stressors

Large-scale changes in temperature and precipitation are expected to result in altered flow, sedimentation, and nutrient export within watersheds (Verma et al., 2015). With this will come changes to stream substrate composition (e.g., loss of fine sediment under high pulsed flows), which may change the distribution and proximity of suitable sea lamprey spawning and larval habitat within streams. The magnitude and frequency of peak flows could impact sea lamprey recruitment by increasing larval mortality during more frequent flood events, potentially changing production and dispersal of the larval migratory cue that mediates stream-localizing behavior in sub-adults (Lennox et al., 2020; Fissette et al., this issue). In the Great Lakes region, pH is predicted to decrease by nearly 0.5 by the year 2100 due to increased acidification (Phillips et al., 2015). Perception of semiochemicals by fish may be reduced with decreasing pH (Leduc et al., 2013), and this could lower the ability of sub-adult invasive sea lamprey to locate favorable spawning habitat. Therefore, sea lamprey may enter more streams as they lack an honest signal of past reproductive success. While a broader distribution of spawners could manifest as increased mortality (e.g., when spawning occurs in an unsuitable stream) and therefore benefit control of invasive sea lamprey populations, it could also result in more widespread colonization of streams that lack barriers or are difficult to treat with pesticides. In their native range, a more dispersed spawning population could exacerbate mate-finding challenges associated with reduced population sizes. However, it seems equally likely greater dispersal of sub-adults could result in the colonization of new rivers where populations could become established.

Sea lamprey range shifts could be exacerbated by increased urbanization and agricultural land use, which have a lower capacity to buffer temperature and precipitation changes than do forested or wetland-dominated watersheds. Besides reinforcing direct effects of temperature and altered hydrology, human-impacted watersheds are often a source of fertilizer runoff and other pollutants, and tend to see higher bank erosion and sedimentation. Where agricultural and urban land use increases, higher nutrient-loading and warmer temperatures could increase primary productivity within streams (Whitehead et al. 2009; Collingsworth et al. 2017). In streams where larval survival severely limits production, higher stream productivity may allow for higher concentrations of food, leading to lower mortality and faster growth. This will also affect dissolved oxygen concentrations, as higher productivity increases system biomass while warmer temperatures increase decomposition and decrease oxygen solubility (Collingsworth et al., 2017, Guo et al., 2017). In summer months when stream temperatures are highest and flows are at their minimum, hypoxic conditions in the sediment may cause larvae to smother (Guo et al., 2017). Increased bank erosion from deforestation coupled with pulses of high storm runoff could greatly increase sedimentation within streams, altering the distribution of suitable habitat for spawning and larval growth (Beamish, 2001; Guo et al., 2017). Measures to limit point-source pollution and bank erosion could largely mitigate these compounding effects. Where new streams are subject to dredging and channelization for greater navigability, larval habitat might be completely destroyed, and areas of suitable spawning habitat covered with sediment (Guo et al., 2017).

Changes in land-use and vegetation cover will also significantly affect the magnitude of hydrological changes through more rapid conversion of precipitation into surface runoff (Thodsen et al., 2007; Gomez et al., 2009). In their native range, higher flows could wash larval sea lamprey from rivers into estuaries with greater frequency in the future, and salinity intrusion in lower river reaches is possible with rising sea levels. Larvae of anadromous sea lamprey cannot tolerate salinities of > 10‰ (Beamish et al., 1978; Resi-Santos et al. 2008), therefore salinity intrusion, which is expected to increase from a combination of sea level rise and reduced runoff, could decrease habitat available for larval rearing in many watersheds important to native sea lamprey populations (Lassalle et al., 2008; Mateus et al., 2012). Older larvae of anadromous sea lamprey, and those already undergoing the process of metamorphosis that are washed from natal streams, may not suffer complete mortality though (Reis-Santos et al., 2008), so the timing of extreme floods relative to the onset of metamorphosis could determine overall impact. In their non-native range, higher precipitation and associated terrestrial runoff could result in increased sedimentation of river deltas. Larval sea lamprey displaced from streams and deposited in these environments may find themselves in extensive areas of suitable habitat that are difficult to assess and treat (Fodale et al., 2003; Johnson et al., 2016a). Consistently treating more river mouths or deltas with granular pesticides could become a necessary additional cost to the control program.

Predicting where sea lamprey will spawn and larvae settle in the future will be a challenge where funds for monitoring and assessment are limited. In regards to controlling non-native sea lamprey, stream treatment prioritization currently employs expert judgement to identify streams that are difficult or expensive to assess, but which have previously been large producers of larval sea lamprey. Predictive models incorporating expected changes in stream hydrology and climate could reduce the cost of monitoring through improved stream treatment prioritization. Prioritization exercises by those tasked with sea lamprey conservation can employ the same methodology to reveal rivers in need of legislation protecting nascent populations of sea lamprey (e.g., Cowx et al., 2009), and ensure colonization proceeds with as few impediments as possible.

Effect on sea lamprey-host relationships

In the coastal marine environment, which is warming faster than the global rate (Mackenzie and Schiedek, 2007), climate change is expected to alter fish community structure and species abundance, indicating the potential for large-scale ecological alteration in the coming century (Cheung et al., 2009). Juveniles of native sea lamprey populations forage over extensive areas of the continental shelf of the Atlantic Ocean (Mateus et al., this issue), and this habitat has been warming steadily for 50 years (Figure 5). Several important hosts for juvenile sea lamprey, including Atlantic horse mackerel (*Trachurus trachurus*), pollack (*Pollachius pollachius*), saithe (*Pollachius virens*), haddock (*Melanogrammus aeglefinus*), Atlantic cod (*Gadus morhua*), and common sole (*Solea solea*) (Nye et al., 2009; Lenoir et al., 2011; Hare et al., 2016), are vulnerable to ocean warming and are predicted to shift their range northward, occupy deeper water, and perhaps even experience range contractions. If juvenile anadromous sea lamprey must travel further to locate hosts, or in doing so are dispersed further from the coast, then at-sea mortality may increase as a consequence of higher predation rates, increased energy expenditure, or an inability to locate suitable hosts and/or spawning rivers. However, juvenile sea lamprey have low host-selectivity (Silva et al., 2014) and commonly forage at depths of 0 to 200 m in the marine environment (Mateus et al., this issue), so it seems unlikely they will fail to locate suitable hosts in the future. For example, other parasitic lampreys appear adept at responding to novel host species introductions (Inger et al., 2010; Hume et al., 2013). Furthermore, a widely dispersed juvenile sea lamprey population could lead to encountering new river systems at the end of the feeding period, resulting in the establishment of additional populations.

Climate-induced changes to sea lamprey host abundance are a particular concern. The abundance of Pacific salmonids (*Oncorhynchus* spp.), common hosts for parasitic lampreys in the North Pacific Ocean, fluctuates with the ocean-atmosphere climate (Maitland et al., 2015). Maitland et al. (2015) concluded that parasitic lampreys are sensitive to changes in host abundance, even if they are not affected by the distribution of a particular host species. Host abundance had the strongest modeled effects on return of anadromous Pacific lamprey to the Columbia River Basin (Murauskas et al. 2013). Therefore, watersheds currently serving as source populations of native juvenile sea lamprey could be shifted by the movement, decline, and decreased fitness of preferred hosts. Behavioral responses of juvenile sea lamprey to novel or “less desirable” hosts, or a loss of the host species from sink areas, could further change coastal food webs (Eriksson et al., 2011; Doney et al., 2012).

Like the marine environment, in the Great Lakes both air temperature (0 to 10°C) and precipitation (15 to 25%) are expected to rise, with knock-on effects for the fish communities inhabiting those lakes (Lynch et al., 2010). Great Lakes surface temperatures have increased steadily over the past 60 years (Figure 6), and host species for juvenile sea lamprey (cold, cool, and warmwater species) are all expected to respond positively through increased growth and survival by moving northward and into deeper water to access thermal preferenda (Lynch et al., 2010; Cline et al., 2013). In Lake Superior, sea lamprey body size has increased by 12% since 1980, perhaps in response to increased optimal thermal habitat for hosts (Cline et al., 2014). Lake Superior sea lamprey are generally smaller than those from Lakes Erie and Ontario, potentially because of warmer overall lake temperatures in the latter (M. Docker, personal communication 2020). Juvenile sea lamprey foraging in certain lake regions during the spring and summer prefer lake whitefish *Coregonus clupeaformis* (Hume et al., this issue a) or cisco *C. artedi* (M. Ebener, unpublished data), but lake trout *Salvelinus namaycush* are often touted as the preferred host for Great Lakes sea lamprey populations in general. Yet juvenile sea lamprey can and do select from almost all available fishes (Christie and Kolenosky, 1980; Harvey et al., 2008; Happel et al., 2017). By relying solely on wounding rates recorded from lake trout, it will be exceedingly difficult to detect any change in host selection in the coming decades (Adams and Jones, 2020; Hume et al., this issue a). Limited wounding data from host species may negatively affect the ability to manage invasive Great Lakes sea lamprey as it could potentially decouple metrics used to assess control program success (lake trout wounding rates and index of adult sea lamprey abundance). If lake trout wounding rates decline but adult sea lamprey abundance increases, then causation will be difficult to establish. Furthermore, if warming lakes result in establishment of additional invasive fish species that could potentially act as hosts (Mandrak, 1989), it would be wise to develop a robust sampling program to assess juvenile sea lamprey interactions with all potential hosts to predict demographic responses.

Effect on growth and bioenergetics of sea lamprey

Thermal variation has a strong influence on the metabolic processes of ectothermic organisms such as fish because they cannot maintain a constant body temperature, and it can significantly alter growth rates (e.g., Boltaña et al. 2017). For example, larval sea lamprey growth rate is correlated with stream temperature and varies with latitude. In their native range, larvae of sea lamprey populations from Portugal grow faster than those from France or Canada (Quintella et al., 2003), and larvae of non-native populations in lakes Erie and Ontario grow faster than those from Lake Superior (Dawson et al., 2015). An increase in growing degree-days within streams as a result of warming water temperatures is likely to result in higher larval growth rates (Neuheimer and Taggart, 2007), provided negative density-dependent effects do not also occur (Jones et al., 2003). It is not known if or how growth rate or maximum size at metamorphosis in larval lamprey transfers to later life stages. However, should larval lamprey growth positively influence juvenile fitness (e.g., reduced mortality due to greater energy stores prior to first feeding; faster growth rates due to increased metabolism) then host mortality may be greater due to larger juvenile sizes or increased feeding rate, and subsequent increased sea lamprey fecundity could become a concern for invasive sea lamprey control program managers (Lennox et al. 2020).

The effects of climate change are not uniform in the aquatic environment, particularly in regards to depth. For example, shallow-water marine species (< 250 m) have exhibited significant growth rate increases during the last century, whereas deep-water species (> 1000 m) have not (Thresher et al., 2007). These differences are correlated with rapidly increasing surface water temperatures. For native juvenile sea lamprey in the Atlantic Ocean, estimating growth is stymied by a lack of repeat observations on individuals and a large variation in size observed in collections. For example, native juvenile sea lamprey captured in or near North American rivers discharging to the Atlantic range from 150 to 400 mm TL, which could reflect either variance in the onset of feeding, or different juvenile cohorts being sampled (Beamish, 1980). Comparing sample means of native juvenile sea lamprey from North America, Beamish (1980) estimated a growth rate of ~0.7 g day^{-1} over 23 – 28 months, with a slower growth rate during winter. Beamish's data indicated that water temperature does influence juvenile sea lamprey growth rate in the marine environment. However, Silva et al. (2014) individually marked 408 juvenile sea lamprey from Spain and recaptured a single specimen 13.5 months later; growth was estimated as ~1 g day^{-1}, increasing from 218 mm TL and 20 g to 895 mm TL and 1218 g. Colder winter temperatures were either not affecting the growth of that particular juvenile sea lamprey, it was able to rapidly compensate for a slow growth period, or it avoided cooler waters. Juvenile growth rates under natural conditions are a significant knowledge gap in sea lamprey biology, which could aid in better predicting their responses to warming seas and lakes. Furthermore, in the

Great Lakes, growth rates of sea lamprey could be accounted for in feeding models used to better estimate annual and seasonal damage to the fishery.

In their non-native range, juvenile sea lamprey growth rate is similar to populations from the Atlantic Ocean basin, and potentially also influenced by temperature. Applegate (1950) estimated a growth rate of ~0.9 g day^{-1} in Lake Huron, but a laboratory study suggested growth is slower in colder temperatures (minimal growth at 5°C, maximum growth at 15 to 20°C; Farmer, 1977). Hume et al. (this issue a) concluded that variation in growth rate observed in a long time-series (1983 to 2017) of juveniles from Lake Huron was partly explained by host selection and sex, as well as temperature. Furthermore, the authors of that study concluded it may be the relative rate of warming in the spring that more strongly influences growth rate of juveniles, rather than absolute differences between winter and summer temperatures. For example, non-native juvenile sea lamprey from Oneida Lake are ~90 mm longer than juveniles from Lake Ontario by July, which may be a consequence of the shallower overall depth of Oneida Lake resulting in more rapid warming of water during spring (Forney, 1986). Regardless, increased growth of juvenile sea lamprey from non-native populations is expected in the coming decades as surface water temperatures of the Great Lakes and Finger Lakes continue to rise (Hansen et al., 2016; Lennox et al., 2020; Figure 6).

A longer growing season will lead to greater blood consumption by sea lamprey juveniles in their non-native range and, consequently, increased sea lamprey-induced mortality could be inflicted on host fish populations (Cline et al., 2014; Kitchell et al., 2014). Host mortality increases non-linearly with the size of the attached juvenile, and the largest sea lamprey have a disproportionately higher rate of mortality on hosts (Kitchell, 1990). Furthermore, temperature is a dominant factor explaining mortality in a range of laboratory feeding studies (Swink, 2003). Climate change effects on lake trout growth in lakes Michigan and Huron (and probably Lake Superior as well) are likely to be minimal during the next 50 years, although these predictions are partly dependent on prey availability (Kao et al., 2015). Lennox et al. (2020) concluded higher sea lamprey growth during the juvenile life stage is expected to result in increased sea lamprey fecundity, which may lead to greater population sizes and increasingly severe pressure on host populations. All else being equal, a trend toward warming lakes will likely require additional control effort to prevent sea lamprey recruitment to the juvenile stage and greater damage to the fishery.

In general, there is a need for more directed research into the juvenile life stage of sea lamprey in both their native and non-native ranges (Hume et al. this issue a; Quintella et al. this issue). Such studies could help better explain the relationship between growth, thermal profiles, host selection, mortality, and sex. Mark-recapture studies using individual tags combined with commercial fishery surveys of potential hosts and sub-adult sea lamprey assessment during the spawning migration are one potential route to resolving uncertainty surrounding juvenile growth rates. However, tagging studies will require capture of 100's if not 1000's of out-migrating juvenile sea lamprey to achieve a reasonable rate of return captures of sub-adults, and out-migrants are currently difficult to collect in the wild (Evans et al., this issue). Another option is the use of acoustic telemetry tags with temperature sensors, to directly associate sea lamprey feeding bouts with spatial data and environmental conditions, but again tag costs may be prohibitive and tags with sufficient battery life to address the question are typically too large for juvenile sea lamprey. Ample opportunity exists for research and development of lamprey-specific monitoring strategies and technologies, such as miniaturized tags or sampling gear designed to lure feeding juveniles.

Effect on survival rates

In their native range, effects of climate change on the survival of adult sea lamprey, developing embryos, and larvae are not readily identifiable given a general lack of data. Potentially, if sea lamprey spawning occurs earlier in the year, then a mismatch between optimal habitat characteristics for spawning, embryonic development, and larval emergence could occur (Clemens et al., 2009; Maitland et al., 2015; Lennox et al., 2020). Southern Europe is predicted to experience warmer (1 to 5.5°C), and drier, summers by the end of the century (Giorgi et al., 2004). Because of lower flow rates in streams, warming of interstitial water within the substrate (Isaak et al., 2012) could result in reduced survival of developing embryos and larvae of sea lamprey occupying the southern extent of their native range (Maitland et al., 2015; Tutman et al., 2020). Excessively warm spring stream temperatures decrease survival of developing Pacific lamprey embryos, and a similar effect is expected for anadromous sea lamprey (Meeuwig et al., 2005). Optimal temperatures for developing anadromous sea lamprey larvae range between 17.8 and 21.8°C (Holmes, 2011), and populations from Portuguese rivers are apparently subjected to temperatures exceeding the fundamental thermal niche upper limit during summer months (e.g., July to August, 2012 to 2015 water temperatures: Vouga River, mean = 19.6ºC, maximum = 25.2ºC; Mondego River, mean = 19.8ºC, maximum = 24.2ºC). A possible explanation to this contradiction is the fact that Atlantic drainages of both North America and Europe sea lamprey typically spawn in the mainstem of large rivers, where embryos and larvae would be somewhat buffered thermally due to the relatively large volumes of water these large rivers carry (Maitland et al., 2015). Moreover, thermopeaking (the intermittent sharp change in stream temperatures associated with a release of stored water upstream of hydropower facilities) may moderate these effects, since the turbines' intake is located in the hypolimnion (the deeper, cool part of the water body) (Greimel et al., 2018).

Increased larval sea lamprey growth rates due to warmer streams could potentially enhance recruitment to the juvenile population by speeding-up metamorphosis, thus the duration of the larval phase may be substantially reduced. Overall mortality experienced by sea lamprey larvae may be reduced accordingly, and survival is already high after the onset of exogenous feeding (0.44 to 0.95, Moser et al., 2019). Without methods to directly suppress invasive juvenile sea lamprey that avoid pesticide treatments as larvae, Lennox et al. (2020) conclude more frequent treatments may be required as additional streams become infested and metamorphosis occurs earlier. More research is required to reduce uncertainty surrounding the effects of climate change on larval growth and recruitment to the juvenile life stage.

Effects on assessment of adult non-native sea lamprey

By the end of the century, streams in the Great Lakes are anticipated to experience significantly higher flows during spring (Cherkauer and Sinha, 2010). Coupled with a 37 to 88% reduction in ice cover on the lakes and overall warming lake waters (Wang et al., 2012; Mason et al., 2016), the spawning migration of sea lamprey is likely to occur progressively earlier (McCann et al. 2018). As a consequence, Lennox et al. (2020) surmised sea lamprey control agents may have to install assessment traps earlier in the spring to match run timing. Trap efficiencies (in regard to total capture and mark-recapture approaches to assessment, Harper et al., 2018) may also experience declines as water levels rise and traps become clogged by debris during flooding events (Lennox et al., 2020). For example, 2019 was the wettest spring in 100 years, resulting in record high lake levels across the Great Lakes. In the Cheboygan River, situated in northern Michigan, the total number of adult sea lamprey captured by the index trap at this site was 4305 (vs 14,123 on average, 1977 to 2018) and trap efficiency estimated at 41% (vs 65% on average, 1986 to 2018) (USFWS, unpublished data). Reduced trap efficiency will further increase uncertainty in the evaluation of control effectiveness. If adult indices of sea lamprey abundance cannot be robustly calculated, reductions in the estimated sea lamprey population size cannot be attributed confidently to management actions.

Duration of the sea lamprey spawning migration may increase with earlier warming springs. An extended spring migration would require trapping for assessment be extended to cover the duration of the migration. Currently, traps are operated for ~2 months beginning in late-March in the lower Great Lakes and mid-late April in the upper Great Lakes. Costs will likely increase proportional to the length of time that traps are operational; an additional month could amount to a 50% increase in the annual cost of adult assessment (Peter Hrodey, USFWS, personal communication 2020). Population genomic approaches (e.g., single nucleotide polymorphism genotyping) provide one alternative to traditional mark-recapture estimates of abundance and may provide some ability to account for reduced accuracy or precision of trap estimates resulting from altered sea lamprey phenology. Genomic resources for sea lamprey are becoming increasingly available (Smith et al., 2018; Sard et al., 2020), permitting accurate estimation of the number of reproducing adults contributing to the larval population (John Robinson, Michigan State University, personal communication 2020).

Effect on control of larval non-native sea lamprey

Pesticides (TFM 3-trifluoromethyl-4-nitrophenol, and niclosamide 2′,5-dichloro-4′-nitrosalicylanilide) have been applied to ~106 streams annually in recent years (range = 93 to 120; 2015 to 2019) to control invasive sea lamprey in the Great Lakes. Based on the probability of metamorphosis of the majority of larvae in a stream the following year, these applications occur on a regular cycle (3 to 4 years years). These pesticides are metered into infested streams at a target concentration 1.5x the minimum lethal concentration (MLC, 99.9% mortality in 9 hr), such that a "block" of pesticide moves downstream through target reaches (Dawson, 2003). Treatments are, therefore, most effective under stable flow. More frequent and increasingly erratic precipitation events associated with climate change (Cherkauer and Sinha, 2010) may increase the amount of monitoring, amount of pesticide, or both required to treat streams on an annual basis, amplifying the cost of management. Precipitation that occurs during a treatment can significantly increase the amount of pesticide required to maintain MLC (Brege et al., 2003). In some cases, terrestrial runoff can dilute pesticide concentrations sufficiently to render the entire treatment ineffective, necessitating retreatment. In addition, some streams require cooperation with hydropower facilities to maintain stable flow for the treatment's duration. Following a substantial precipitation event in a watershed, logistical and legal requirements can prevent hydropower operators from accommodating the discharge required for treatment.

While the overall effects of a changing climate on sea lamprey control are extremely complex, it is conceivable that an increase in stream temperatures will require the use of more pesticide to treat infested streams on an annual basis (Lennox et al. 2020). The toxicity of sea lamprey pesticides has long been recognized as being strongly dependent on stream pH and alkalinity (e.g., TFM toxicity is ~5x greater at pH 7 vs pH 8, Wilkie et al., 2019). However, Muhametsafina et al. (2019) concluded that temperature could also significantly influence TFM toxicity. Under laboratory conditions, larval sea lamprey are less vulnerable to TFM in 24°C than 12°C water. The effectiveness of pesticide applications does appear to be affected by seasonality, with TFM toxicity 1.5 to 2x greater in May-June than July-August (Scholefield et al., 2008). Treatments typically occur between late-April and mid-October but complex systems (e.g., with strong diel pH cycles, low base flows) are treated earlier in the season. Streams that are rescheduled for pesticide treatment due to heavy precipitation or unexpected warming could therefore be treated during a sub-optimal period (low flow, high water temperature), reducing toxicity to sea lamprey and increasing risk to non-target species, including native lampreys (Marsden and Siefkes, 2019). Similar to the phenological shifts anticipated in adults and the need to manage them earlier, by the end of the century pesticide treatments may also need to occur earlier when stream temperatures remain cool (Muhametsafina et al., 2019; Lennox et al., 2020). The challenge will be in treating streams under more frequent high spring flows, and the acquisition and application of greater quantities of pesticides.

Not all climate-induced effects may negatively impact sea lamprey control in the Great Lakes. Treatments with TFM and niclosamide to kill sea lamprey larvae are typically halted by mid-October, primarily due to freezing air temperatures that can damage scientific equipment and prevent pesticide applications. The effectiveness of both TFM and niclosamide is reduced at low water temperatures. However, if under a warming climate scenario air and water temperatures increase sufficiently that they do not fall below freezing at night, it is possible that larval control operations could be extended into November-December. Larval assessment is also halted by mid-October, when sampling becomes constrained by freezing air and water temperatures as well as reduced daylight hours restricting the number of sampling sites. Larval sea lamprey are slower to emerge in response to electrofishing sampling at low water temperatures and therefore catch-per-unit effort is reduced under low temperature conditions. If water temperatures significantly increase under a warming climate, it is possible that larval sea lamprey surveys could also be extended later in year, albeit with a higher degree of uncertainty surrounding sampling effcieincy.

Effects on contaminant accumulation

Organisms accumulate organic and inorganic contaminants that they encounter in their environment and subsequently store in tissues. In fishes, this occurs through dietary uptake (ingesting contaminated material) or aqueous uptake (water-borne compounds), and the bioaccumulation of contaminants has a range of direct and indirect effects. Mercury (Hg) is a global environmental toxicant that readily enters aquatic food webs when Hg is methylated (Boening, 2000; Driscoll et al., 2013); this methylated form is referred to as methylmercury (MeHg). Concentrations of Hg in sea lamprey body tissues are likely to increase in the coming decades for several reasons. The rate that MeHg is formed by bacteria tends to increase in warmer water temperatures (Matilainen and Verta, 1995; Paranjape and Hall, 2017), thus, greater availability of MeHg in the aquatic ecosystem is expected under climate change. Furthermore, top predators tend to accumulate Hg in greater concentrations than species at lower trophic levels through dietary uptake (biomagnification) and many of these species (e.g., Atlantic bluefin tuna *Thunnus thynnus* in the Atlantic Ocean), are predicted to increase in Hg concentration by the end of the century (Schartup et al., 2019). Juvenile sea lamprey in the Atlantic Ocean and the Great Lakes have a tendency to feed on top predators (Drevnick et al., 2006; Pedro et al., 2014), such as lake trout, thus will likely accumulate higher Hg concentrations in the future.

Increased Hg concentrations detected in sea lamprey tissues could affect consumption advisories for communities that regularly consume adults in their native European range (Beaulaton et al., 2008; Braga et al., 2019). At present, more than half of adult sea lamprey from Atlantic Ocean and Great Lakes watersheds exceed the 500 ng g^{-1} European Union (EU) guideline for Hg concentration in fish consumed by people (Madenjian et al., this issue). Any further increase in Hg concentration will likely trigger a response from management agencies to impose stricter regulations on the consumption of sea lamprey by people. Furthermore, blood consumption by sea lamprey in the Great Lakes is predicted to increase ~20% by 2070 (Lennox et al., 2020), and this is thought to be the primary route of mercury bioaccumulation in this species (Madenjian et al., this issue). However, it is unlikely invasive sea lamprey will ever be marketed for human consumption in North America due to their already high mercury concentration and lack of historic importance as a food item.

Evidence for a significant increase in concentrations of organochlorine contaminants (e.g., polychlorinated biphenyls, PCBs) in sea lamprey in response to climate change is not apparent. Concentrations of PCBs in sea lamprey from the Great Lakes have in fact substantially declined between the 1970s and 2011 (Madenjian et al., this issue). Furthermore, whereas Hg concentration in lake trout in some of the Great Lakes has increased between the 1990s and 2010, PCB concentration decreased from the 1970s through 2010 in all five Laurentian Great Lakes. Dietary uptake of PCBs by juvenile sea lamprey may therefore not represent a meaningful threat in the future.

Influence on loss and creation of barriers to sea lamprey migration

Barriers to upstream migration (dams, waterfalls, dry river bed sections, etc) are, probably, the main cause for sea lamprey habitat loss in Europe and North America (Renaud, 1997; Almeida et al., 2002; Gardner et al., 2012; Hogg et al., 2013; Hansen et al., 2016), with reductions of up to 96% of habitat in a certain watersheds, such as the Douro River basin in the Iberian Peninsula (Mateus et al., 2012). Very few data exist for anadromous sea lamprey adult spawning runs in North America, however in the Connecticut River there is large variation in run size (17,000 to 97,000 annually) suggesting adults may be responding to river conditions (CRASC, 2018). Sedgeunkedunk Stream, a small (~ 5 km) tributary of the Penobscot River in Maine that recently benefitted from barrier removal efforts, attracts around 250 sub-adult sea lamprey each spring suggesting even relatively small, unobstructed streams can support anadromous sea lamprey populations (Hogg et al., 2013). Besides altering the natural flow regime, barriers can also result in an increase in sea lamprey mortality in their native range caused by natural predators, which take advantage of the accumulation of sub-adults downstream of barriers (Quintella, 2006; Maitland et al., 2015). Sea lamprey that are delayed during their upstream movement from estuaries and lower river reaches because of barriers are also susceptible to over-exploitation by local fisheries and poaching in Europe (Mota et al., 2016; PR Almeida, unpublished data).

Increasing river regulation and water abstraction for agricultural, industrial, and domestic uses reduces river discharge, and is expected to decrease attraction of migrating sub-adults of anadromous sea lamprey from the marine environment (Maitland et al., 2015). Furthermore, in their native range of Europe and North America, low flow conditions during the spawning migration could hinder sea lamprey recruitment and threaten population stability by preventing upstream movement. In the Mondego River, Portugal, a reduction in the abundance of adult sea lamprey passing the Coimbra Açude-Ponte dam appears correlated with drought conditions. Typically, ~10,000 adults pass the dam annually, yet in 2017 and 2019 (both drought years) only ~700 and ~300 adults were recorded using the dam's fishway, respectively (PR Almeida, unpublished data). Reduced flow and warmer temperatures appear to hamper upstream movement, so the number of sea lamprey approaching the dam may be low, rather than the fishway being ineffective (Pereira et al., 2017, 2019). Those sea lamprey that initiate upstream movement late in the season could fail to travel as far as the dam (43 river km from the mouth), with annual reproduction in this watershed restricted to just 15 river km of freshwater downstream of the barrier. With warmer, drier summers predicted to become more frequent in southern Europe (Giorgi et al., 2004), maintenance of adequate quantities of water in mainstem rivers will be crucial to ensure successful spawning of sea lamprey.

Southern Europe has been identified as a "critical region" in regard to the risk of drought, with 100-year droughts expected to occur every 10 to 50 years by 2070 because of greenhouse gas emissions (Lehner et al., 2006). Drought is likely to exert extreme pressure on sea lamprey populations by reducing the available habitat for long-lived, multi-generational larval populations. For example, in some tributaries of the Guadiana River in southern Portugal, significant reductions in water availability during dry years are already threatening sea lamprey. Because of dewatering, larvae accumulate in deep natural pools, or in temporary impoundments made from earthen embankments. However, due to conflict with local farmers and cattle ranchers for water reserves, sea lamprey there are imperiled (Mateus et al., 2012). Recently observed behavioral adaptations by other lamprey species provide some hope larval sea lamprey may tolerate short-term (< 30 days) dewatering events. In California, a region prone to periodic droughts, larval lamprey have been observed surviving within remnant pools (Bogan et al., 2019) and even buried within the sediment of a dry stream bed (Rodríguez-Lozano et al., 2019).

To halt the spread of sea lamprey in their non-native range, many hundreds of barriers are employed to restrict access to spawning habitat in the Great Lakes basin (Marsden and Siefkes, 2019). However, like all in-stream barriers they are vulnerable to periodic inundation or complete failure during high flows (Lavis et al., 2003). If dam failure occurs coincident with the spawning migration, then upstream escapement of sea lamprey can be severely costly (Jensen and Jones, 2018). Hydrological modeling informed by regionally downscaled climate projections predict large increases in peak streamflow in the Great Lakes by the end of the century (Cherkauer and Sinha, 2010; Byun et al., 2019). Seasonally, this will occur earlier during winter and spring in northern watersheds, where greater rainfall and earlier snowmelt drive the majority of observed runoff. In southern watersheds, peak streamflow will be more dependent on unpredictable summer storms (Byun et al., 2019). Barrier efficacy is likely to be negatively affected by this increased frequency of high streamflow events, as well as the continued physical degradation of barriers as they age; most barriers in the Great Lakes are already exceeding their 50-year lifespan (Miehls et al., 2019). Taken together, climate change puts great strain on ageing infrastructure critical to sea lamprey control, and priority will have to be given to some barriers over others. Given the extent of potential sea lamprey spawning and rearing habitat blocked by barriers (~50%), even a moderate increase in the frequency of barrier failures could prove prohibitively expensive to rectify. For example, removing the lowest dam on Michigan's Grand River could cost an additional $200,000 to $360,000 annually in pesticide treatments should sea lamprey utilize just 10 to 50% of available habitat (Jensen and Jones, 2018).

Socio-Political Issues

Improving river connectivity

Hydroelectric dams, weirs, and other anthropogenic barriers disconnect the marine or lacustrine feeding grounds of sea lamprey from their freshwater spawning and larval rearing habitats, and they are potentially the greatest threat to native sea lamprey populations on both sides of the Atlantic (Maitland et al., 2015). Barrier removal efforts have realized impressive, and often rapid, conservation gains for sea lamprey; sustained colonization of previously inaccessible habitat by spawning and larval sea lamprey can occur in a matter of years and has been observed in both European and North American watersheds recently (Docker and Hume, 2019). Where barriers cannot be removed, mitigation via the installation of technical fishways is the typical approach (Moser et al., this issue). However, most fishways are not effective at passing native sea lamprey and may cause a serious impediment to upstream passage. For example, fishways in the Connecticut River (Massachusetts, U.S.A.) pass only 29 to 55% of anadrmous sea lamprey, and cause delays of up to 14 days in upstream migration phenology (Castro-Santos et al., 2017). In the Mulkear River (Ireland), retrofitting weirs with studded tiles to aid sub-adult sea lamprey passage was found to pass only 8% of radio-tagged individuals (Rooney et al., 2015). Both the Connecticut and Mulkear rivers list sea lamprey as a species of conservation concern. Connectivity, therefore, remains a significant threat to sea lamprey in their native range, but efforts are currently underway to help inventory barriers in both their North American (e.g., North Atlantic Aquatic Connectivity Collaborative https://streamcontinuity.org/naacc) and European ranges (Adaptive Management of Barriers in European Rivers https://amber.international/). Datasets such as these will be invaluable not only in characterizing the extent of fragmentation caused by barriers (Jones et al., 2019), but also in revealing watersheds where remediation efforts would result in the greatest gains in terms of available habitat to support sea lamprey (Barry et al., 2018; CRASC, 2018). Specific to Europe, the EU Water Framework Directive (WFD) has made river connectivity a prime criterion in achieving “good status” in European rivers. The WFD has, in part, prompted the genesis of multiple non-governmental organizations dedicated to the removal or mitigation of barriers (e.g., Dam Removal Europe https://damremoval.eu/; European Rivers Network https://www.rivernet.org/ern.htm), which is expected to aid native sea lamprey in their European range in the coming decades.

Tributaries of the Great Lakes are fragmented by an extensive network of natural and anthropogenic barriers. These barriers, particularly the lower-most in watersheds, often prevent sea lamprey from utilizing critical habitat to complete their life cycle. However, these same barriers also restrict desirable and native fishes from accessing critical spawning habitat, creating a tension among stakeholders who differentially value sea lamprey control and fish passage (McLaughlin et al., 2013); the so called “connectivity conundrum” (Zielinski et al. in press). More than $1 billion has been spent to remove barriers in the basin, but new barriers continue to be proposed and modified to maintain control of sea lamprey in some key tributaries (Lavis et al., 2003; Neeson et al., 2015; Marsden and Siefkes, 2019). Decision support tools (computer-based models to facilitate decision making in complex environmental scenarios) and structured decision making can provide objective and transparent support for potentially divisive decision-making. However, automated decision making still requires critical human thought and expert judgement. For example, when prioritizing barriers for removal in Michigan's northwestern lower peninsula to support fish passage - while accounting for climate change scenarios, future species distributions, and land use - similar sets of barriers were identified; whereas, including sea lamprey control within this prioritization framework resulted in a different portfolio of barriers selected for removal (Lin et al., 2019b). Many other factors must also be considered in barrier removal decisions, including barrier age, public safety, historic preservation, costs, ownership, and user satisfaction (e.g., anglers and boaters, Lin et al. 2019a). Decisions regarding barrier removal and remediation, including prioritizing those for removal and determining best practices for doing so, are fraught with difficulty due to the multiple, often conflicting, value sets and objectives of the stakeholders involved.

Regardless of the social tension surrounding the removal of tributary barriers terminal to the Great Lakes, research has shown that an increase in habitat for spawning sea lamprey will result in larger lake-wide population sizes (Jensen and Jones, 2018; Lin and Robinson, 2019). Sea lamprey do not natally home and can disperse widely within the lakes (Bergstedt and Seelye, 1995), which results in a rapid increase in simulated population abundance when new habitat becomes available (Lin and Robinson, 2019). When barrier removal is not accompanied by increased funds for pesticide treatment, the intensity of lake-wide control is reduced as funds become reallocated to treat the newly available habitat, again leading to overall increases in population abundance (Jensen and Jones, 2018). This predicted result could be exacerbated by projected faster larval growth and larger sexually mature sea lamprey if the climate continues to warm, which could necessitate more frequent lampricide treatments at greater cost (Lennox et al., 2020). Ultimately, decisions about removal, remediation, or replacement of sea lamprey-blocking barriers will require careful consideration of ecological trade-offs among native, desirable, and invasive species, buoyed by predictive modeling of the effects of any management actions (Kočovský et al., 2009, McLaughlin et al., 2013, Jensen and Jones, 2018, Lin and Robinson, 2019).

The tension between fish passage and invasive species control can lead to creative solutions and technologies for optimizing competing outcomes (Zielinski et al. in press). Selective fragmentation of river networks relies on a kind of biological filtering, separating species along behavioral or ecological axes (Rahel and McLaughlin, 2018). For example, seasonal barriers or barriers with an adjustable crest have been implemented with varying success, blocking invasive sea lamprey during their spawning run but permitting passage of desirable species based on run-timing or jumping ability (Zielinski et al., 2019). Species-specific chemical cues to attract and repel sea lamprey downstream of barriers (Hume et al., 2015, 2020) may promote the use of trap-and-sort fishways, potentially enabling the removal of sea lamprey from mixed assemblages of migratory fishes using species-specific designs (Hume et al. 2020). Smart fishways that allow partial connectivity for native and desirable fishes and blockage or removal of invasive or undesirable fishes could provide a potential solution to the connectivity conundrum. One such structure is currently being designed for the Boardman River, Michigan, U.S.A. where a suite of sorting technologies and techniques will be optimized for automated or semi-automated fish sorting and passage (http://www.glfc.org/fishpass.php). Although these methods have yet to prove as effective as barrier removal in terms of desirable fish passage, they highlight the drive to resolve tensions between the sea lamprey control program and other stakeholders (Zielinski et al., in press). Paired with decision-making processes that involve all stakeholders and explicitly consider all competing objectives (e.g., decision analysis, Lin et al., 2019a), we may yet develop optimal fish passage solutions to restore natural stream flow and habitat connectivity for native fishes while preserving the need to control sea lamprey in the Great Lakes.

Alternatives or supplements to sea lamprey pesticide and their potential impact

The sea lamprey control program has adopted the integrated pest management concept in recent decades, with the goal of suppressing populations to a level that minimizes economic harm caused by the pest, while also minimizing the adverse impacts of management actions (Sawyer, 1980; Hubert et al., 2019). While a combination of lower-most barriers and pesticide applications is the most effective means of controlling sea lamprey, these methods can conflict with natural resource management goals and the intrinsic value sets of Indigenous Nations, communities, and organizations. Protecting the natural environment, particularly water quality, during sea lamprey control operations is of utmost importance, and the introduction of pesticides into a stream may disrupt the use of rivers by Indigenous people. Likewise, the construction of barriers that do not allow adequate fish passage may prevent fishes such as lake sturgeon (*Acipenser fulvescens*), from accessing their native range on Inigenous people's land where they are a culturally important food (Runstrom et al., 2002, Beck et al., 1995). Understanding and respecting the values of Indigenous Nations, communities, and organizations - and encouraging open dialogue with Indigenous people - is vital to maintaining a cooperative relationship, and therefore an active social license to conduct sea lamprey control throughout the Great Lakes basin. In some cases, this may mean that alternative or supplemental controls are needed in place of barriers or pesticides, even if they are not as effective at controlling sea lamprey.

The sea lamprey control program remains, however, heavily reliant on the application of TFM and niclosamide to kill sea lamprey prior to metamorphosis, and has been for 60 years. The concentrations applied to kill sea lamprey are reasonably selective, do not pose a risk to the public, and are not persistent in the environment (Wilkie at al., 2019). Currently, TFM is only manufactured by two companies and there is some risk attached to such a limited supply (Fredricks et al., 2019). Theoretically, sea lamprey populations could evolve resistance to current pesticides within 40 to 80 years of the first appearance of a resistant individual (Christie et al., 2019), which suggests the process may have already begun. However, despite no evidence of resistance thus far (Dunlop et al., 2018), coupled with a generally negative view of applying organic pesticides to the environment since the 1950s, the need for a "green" alternative to sea lamprey control has never been felt more keenly.

Alternatives to chemo-sterilants designed to alter sex ratios, such as can be mediated by genetic manipulations, are possible future sea lamprey control tactics (Siefkes, 2017; Siefkes et al. this issue). Such tactics are species-specific and environmentally benign, thus they are attractive alternatives (if not outright replacements) for organic pesticides such as TFM. Several "genetic control" options are feasible, including gene drives, gene knockdown, and genetically modified hosts (Thresher et al., 2019a). Gene drives involve the transmission of alleles through a population at a higher rate than normal, which could be developed to alter sex ratios or induce negative fitness consequences for individuals, whereas gene knockdown prevents the expression of particular genes during development. There is broad stakeholder support for the research and development of these technologies (~85 to 95%, Thresher et al., 2019b), and these approaches appear biologically feasible (Heath et al., 2014; McCauley et al., 2015; Thresher et al., 2019a). If it is possible to gain access to suitably biosecure infrastructure, and the completion of the sea lamprey life cycle ex situ is achievable, research and development of genetic manipulation will be a logical next step in the evolution of sea lamprey control.

If genetic controls for invasive sea lamprey were found to be feasible, considerable international dialogue would be required prior to considering implementation. The greatest risks in deploying genetic controls is the lack of an "off switch", coupled with transfer across political boundaries and out of the target area causing unintended ecological effects (Marshall and Hay, 2012; David et al., 2013; Harvey-Samuel et al., 2017). The unintended spread of gene drives out of the target area are, at least theoretically, able to be controlled under certain circumstances (e.g., on islands with limited gene flow, Noble et al., 2019). The escapement of deleterious genes to sea lamprey in their native range via Lake Ontario and the St. Lawrence River is certainly possible, as is transfer to the gene pool of sympatric native lampreys in the Great Lakes through inter-specific spawning (Cochran et al., 2008). Estimating the movement of sea lamprey in the St Lawrence and Lake Ontario watershed or the Erie Canal and Hudson River (e.g., through the use of telemetry, Holbrook et al., 2016), and testing for meaningful levels of ongoing gene flow between these populations will be necessary prior to implementation. A contingency plan is also required should any undesirable manifestation of genetic control occur in non-target populations.

Non-native species in the sea lamprey geographic range

Freshwater ecosystems have historically been heavily pressured by introduced non-native fishes, and severe ecological and evolutionary impacts have been observed in recent decades (Coucherousset and Olden, 2011). In the Garonne and Dordogne rivers, declines in native sea lamprey abundance potentially coincides with the proliferation of invasive wels catfish (*Silurus glanis*) in the country (Libois et al., 2016; Guillerault et al., 2018). In a study using newly developed predation tags, Boulêtreau et al. (2020) estimated that 80% of tagged adult sea lamprey in the Garonne and Dordogne rivers were consumed by what is most likely to be wels catfish during the spawning migration. Sea lamprey abundance in this region of France has significantly declined in the past decade (Legrand et al., 2020), while wels catfish abundance has increased (Boulêtreau et al., 2020). Predation of sea lamprey by an invasive species on a massive scale poses a major threat to possibly the largest population of sea lamprey in Europe. Wels catfish have also recently established in the Tagus River, Portugal, where it consumes among other prey items adult sea lamprey (Ferreira et al., 2019). Boulêtreau et al. (2020) speculate that low flow conditions in France in recent years have been responsible for greater predation rates on sea lamprey by wels catfish, because sea lamprey reduce activity levels in low flow conditions while catfish increase activity, resulting in greater rates of encounter. With warming stream temperatures and reduced precipitation in southern Europe in coming decades, wels catfish in the European range of sea lamprey may require management intervention to prevent regionalized extirpations of sea lamprey populations.

The loss of access to, or degradation of, spawning habitat is likely to be the principal cause of declines in sea lamprey abundance in native populations of North America, but data are scarce (Limburg and Waldman, 2009; CRASC, 2018). However, invasive species are the second most prominent threat for freshwater fishes in Canada (Dextrase and Mandrak, 2006), and they likely threaten fishes to a similar extent in the U.S.A. Another potential threat to the persistence of native sea lamprey populations on the east coast of North America is the establishment of round goby *Neogobius melanostomus*; this highly successful invasive species inhabits a range of temperate freshwater and brackish-water ecosystems, including small and large rivers, where they often consume the eggs and larvae of native fishes (Kornis et al., 2012). The interactions of lampreys and round goby in their native or non-native range are not known, but direct observation of predation of sea lamprey eggs by round goby (e.g., stomach contents, predation trials) would clarify the severity of this threat. For example, streams where round goby and sea lamprey are sympatric, such as in tributaries of Lake Michigan (Jordan River), would provide a natural laboratory for observational studies of interactions between these species. Freshwater invasions by non-native crustaceans are a similar concern, as invasive species from taxa such as crayfish and crabs could also potentially directly consume sea lamprey eggs or larvae. For example, in experimental studies crayfish *Orconectes* spp. were found to consume more sea lamprey eggs than several fish species (Smith and Marsden, 2009), and larval pouched lamprey *Geotria australis* in Chile are possibly predated by freshwater crabs *Aegla denticulata* (Catchpole and Ruiz, 2018). Any invasion of important North American sea lamprey habitats (e.g., Connecticut River) by invasive species should be monitored closely to detect potential negative effects on sea lamprey abundance.

The sea lamprey control program in the Great Lakes has effectively reduced the population by ~90% over the past six decades (Marsden and Siefkes, 2019). Consequently, as each human generation passes, fewer individuals recall the collapse of the commercial fishery, rise of a sport-fishing industry, and the ensuing basin-wide ecological and economic changes. The major risk inherent in the passing of time is the perception that sea lamprey no longer represent a threat to the Great Lakes. This phenomenon, known as “shifting baseline syndrome”, could jeopardize public, political, and therefore financial support for continuing suppression efforts (Papworth et al., 2009; Soga et al., 2018). Furthermore, the number of non-native species invading the Great Lakes continues to grow; 24 aquatic non-native species have become established since 1993, taking the basin-wide total to 188 (Sturtevant et al., 2019). The estimated cost of these invasions is $134 billion by 2050 (Krantzberg and De Boer, 2008). Recently, the specter of four species of Asian carp establishing within the basin has received considerable media and scientific attention, and support for costly control options of these new invaders is high should that occur (Kahler et al., 2020). While the risk of new aquatic invasive species should not be minimized at the expense of protecting a fishery valued at ~$7 billion annually (Krantzberg and De Boer, 2008), neither can the threat of sea lamprey be marginalized because of successful control implementation thus far. If funding for sea lamprey control was reallocated to address new invasive species, there is a consensus among the scientific community that sea lamprey populations will respond quickly by increasing in abundance (e.g., Jensen and Jones, 2018).

Support for sea lamprey restoration in their native range

In Europe and North America, sea lamprey are generally considered to benefit from support of habitat restoration projects that aim to protect other anadromous species, namely allis and twaite shad (*Alosa alosa* and *A. fallax*) and Atlantic salmon (*Salmo salar*). The construction of fishways to reestablish the longitudinal continuity of rivers attempts to account for the physiological capacity of the different species that potentially use them, and some of these are moderately effective for sea lamprey (e.g., Pereira et al., 2017; CRASC, 2018). In general though, ineffective passage of lampreys via fishways remains a substantial challenge to overcome (Docker and Hume, 2019; Moser et al., this issue). Despite the fact that "good status" or higher of all EU watersheds by 2027 is a long way from being achieved in many countries (Carvalho et al., 2019), there is consensus that the implementation of the EU Water Framework Directive will improve the ecological status of aquatic ecosystems and their diadromous fish populations, sea lamprey included (Brevé et al., 2014). In the Connecticut River watershed, four American states (Connecticut, Massachusetts, New Hampshire, and Vermont) have agreed that sea lamprey are a "Species of Greatest Conservation Need", and the first management plan for native sea lamprey in North America has recently been drafted (CRASC, 2018).

Due to their anadromous life cycle and high economic value in several European countries (Portugal, Spain, and France), sea lamprey can be considered an early responder to large-scale environmental disturbance that affects the management and conservation of diadromous fish species in general (Stratoudakis et al., 2016). In Portugal, concerns have been raised regarding overharvesting of adult sea lamprey, particularly because there has been a substantial reduction in access to critical habitat in recent decades. For this reason, since 2013, commercial fisheries regulations were amended in Portugal, primarily the implementation of a 5 to 10-day closure of the fishery adjusted to cover the estimated annual peak of the sea lamprey spawning migration (Stratoudakis et al., 2016). In France, a long-term decline in the number of adult sea lamprey passing fishways has occurred in all major watersheds (Legrand et al., 2020). Declines in sea lamprey abundance could result from overfishing in these watersheds, where more than 100 tons is harvested each year (Hansen et al., 2016; Legrand et al., 2020). The long-term availability of sea lamprey in these European watersheds will depend on science-based management, and decision makers should not ignore the larger warning signs of a declining population of a long-lived diadromous fish species such as sea lamprey.

Successfully conserving sea lamprey in their native range will rely on sound management decisions, but broader public and stakeholder support can fuel this effort. Positive attitudes toward uncharismatic species such as lampreys can provide the impetus for large-scale social license to conduct management actions (e.g., barrier removals), and result in meaningful legislative protection (Docker and Hume, 2019). In the case of sea lamprey in their native range, there is no doubt that the public's imagination has been strongly negatively influenced by the need to control the species in the Great Lakes, and unfortunately this too often translates to sensationalized, emotive, and often factually incorrect language when describing sea lamprey observations in the press or social media. Sea lamprey are also cryptic throughout the majority of their life cycle, and are not fished artisanally or commercially in most regions, therefore the public are not routinely made aware of their existence or status. Yet sea lamprey are of great importance to the healthy functioning of the watersheds they inhabit, and their population declines appear largely the result of our actions. Consequently, managers of freshwater ecosystems are strongly encouraged to consider sea lamprey as a key part of restoration efforts (Almeida et al. this issue; Moser et al. this issue). But beyond that we must engage more with the public and any stakeholder groups that value the presence of sea lamprey. Specific examples to engender support could include: the creation of citizen science programs to generate distributional data; classroom programs designed to introduce future generations to the complex lamprey life cycle; production of positive social media messaging and engagement with the press; and the correction of factually inaccurate or emotive articles.

Conclusions

Due to a warming climate, sea lamprey will likely be lost from the southern extent of their native range, but potentially expand northward as they track favorable habitats and hosts. Evidence from birds, another highly mobile group of organisms, indicates that individual species can track rapidly changing temperature and precipitation patterns, and suggests climatic niche modelling could be a strong predictor of future distributions (Tingley et al., 2009). Despite potentially losing access to southern tributaries of their non-native range, warming streams and lakes will potentially increase both larval and juvenile growth rates in the north, resulting in larger adults with greater fecundity. Altered flow regimes in tributaries due to frequent, extreme precipitation events could result in changes to larval habitat, potentially reducing recruitment and removing reliable sources of the migratory cue used, in part, by sub-adults to locate suitable spawning rivers. In the Great Lakes, this could equate to greater numbers of more difficult to treat lentic populations of larvae, and a more widely dispersed spawning population. Earlier spawning migrations could occur in response to higher and warmer spring flows from rivers. In their native range, a mismatch might therefore occur between the timing of spawning and embryonic development, resulting in increased mortality in smaller tributaries. In the Great Lakes, shifting phenology will reduce the effectiveness of barriers to block sub-adults, and reduce the efficiency of traps used to assess their abundance. Coupled with external pressures to improve river connectivity and bolster an ageing infrastructure, the need for new methodologies to monitor and mitigate the passage of sea lamprey at barriers in native and non-native ranges is pressing. Erratic precipitation and warming streams are likely to reduce the ability of sub-adult sea lamprey to ascend southern tributaries in both native and non-native ranges. In the Great Lakes, these conditions are expected to reduce the effectiveness of pesticides and necessitate the rapid development of “greener”, less costly, but ecologically risky alternatives.

Although it seems unlikely there is anything we can do to halt or reverse the root causes of anthropogenic stress currently faced by sea lamprey, now is not the time for inaction. We can take steps to mitigate or reduce the impact of many factors outlined herein, and ensure the management of sea lamprey globally is proceeding as best it can. Some of these steps include:

- Continued pursuit of basic and applied research questions regarding the response of sea lamprey to increased temperatures, altered flow regimes, and shifts in community structure;
- Development of new methodologies to monitor sea lamprey throughout their life cycle to reduce uncertainty in assessment of population size and trends;
- Continued development of robust decision making strategies that incorporate multiple stakeholder values for managing fish passage;
- Continued research and development of supplemental and alternative management tactics for the control of invasive sea lamprey;
- Development and pursuit of research questions to address the glaring lack of basic research on native North American sea lamprey populations;
- Foster collaboration with biologists and managers from the entire native range of sea lamprey, as well those managing non-native populations residing in lakes Cayuga, Champlain, Oneida, and Seneca.

Elsewhere within this Special Issue, specific research needs relevant to a range of topics are presented, including those of relevance to sea lamprey control (e.g., Siefkes et al. this issue) and conservation (e.g., Lucas et al. this issue). At a higher level though, to address the knowledge gaps and prominent issues outlined in this paper, as a community we must commit to new and ongoing dialogue, collaboration, and knowledge transfer among those of us working to manage sea lamprey. The meeting of our community at SLIS III in 2019 has the potential to represent a watershed moment in sea lamprey management; the point at which we cease to consider our actions in isolation, and instead recognize the value in sharing our experiences, regardless if they stem from the conservation or control of *Petromyzon marinus*. It is our sincere hope that this will not be a wasted opportunity.

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Figure Legends

Figure 1. Distribution and status of native sea lamprey *Petromyzon marinus* in European watersheds (colored polygons). Watershed boundaries were obtained from the European Environment Agency (WatershedsData, EEA 2012) and cross-referenced with conservation status of the species in each country as derived from the literature (Maitland, 2000; Doadrio, 2001; Cabral et al., 2005; Kålås et al., 2010; King et al., 2011; HELCOM, 2013; Rondinini et al., 2013; Verreycken et al., 2014; ArtDatabanken, 2015; UICN Comité Français, MNHN, SFI and AFB, 2019). Status was ranked according to the criteria of the International Union for Conservation of Nature (IUCN).

Figure 2. Distribution and status of sea lamprey *Petromyzon marinus* in watersheds (colored polygons) of their native North American range, with some key locations mentioned in the text highlighted. Watershed boundaries were obtained from the United States Geological Survey and cross-referenced with the status of the species within American states and Canadian provinces from NatureServe (2019).

Figure 3. Presence of sea lamprey *Petromyzon marinus* in watersheds (colored polygons) of their non-native North American range. Watersheds boundaries were obtained from the Great Lakes Aquatic Habitat Framework (Great Lakes Hydrography Dataset, Forsyth et al., 2016, glahf.org/

watersheds). Data regarding the presence/absence of larval sea lamprey within watersheds were provided by the United States Fish and Wildlife Service and Fisheries and Oceans Canada.

Figure 4. Management of *Petromyzon marinus* relies on our current understanding of their biology, or often derived from historically influential sources. Cumulative effects of anthropogenic stressors are likely to result in changes to sea lamprey biology that will necessitate shifts in management strategy and tactics. These stressors may manifest in different ways, each with attendant impacts on native and non-native sea lamprey populations. Knowledge gained while addressing these impacts may be shared across populations, such as those associated with the development of effective passage/blockage devices, or response to barrier removals and improved water quality. But risks may also be shared, such as the development of genetic control tools to suppress non-native sea lamprey populations.

Figure 5. Temperature anomaly of the Atlantic Ocean at 0 - 100 m deep, 1955 - 2019. Baseline temperatures derived from 1955 - 2010 data. The blue line represents 3-month averages, and the red line represents the 3-year average. Data were obtained from the NOAA National Oceanographic Data Center (https://www.nhc.noaa.gov/sst/?text).

Figure 6. Average annual surface temperature of the Laurentian Great Lakes, 1948 - 2004. Data were smoothed using a 3-year moving average. The dashed lines represents the linear regression and confidence intervals for each lake's data. Data were obtained from NOAA CoastWatch (coastwatch.glerl.noaa.gov/statistic). Significant increases in surface water temperatures have occurred in all lakes (Superior, $P < 0.001$, Michigan, $P < 0.001$, Huron, $P = 0.03$, St. Clair, $P < 0.001$, and Erie, $P = 0.046$) except Lake Ontario ($P = 0.9$).

Figure 7. Average annual precipitation for Laurentian Great Lakes watersheds, 1882 - 2007. Data were smoothed using a 3-year moving average. The dashed lines represent the linear regression

and confidence intervals for each lakes' data. Data were not available for Lake St Clair. Data were obtained from Michigan Sea Grant (https://www.michiganseagrant.org/lessons/lessons/by-broad-concept/earth-science/data-sets/hydrology-of-the-great-lakes-long-term-trends/). Significant increases in precipitation have occurred in all lakes (Michigan, Huron, Erie, and Ontario, $P < 0.001$) except Lake Superior ($P = 0.07$).

Figures

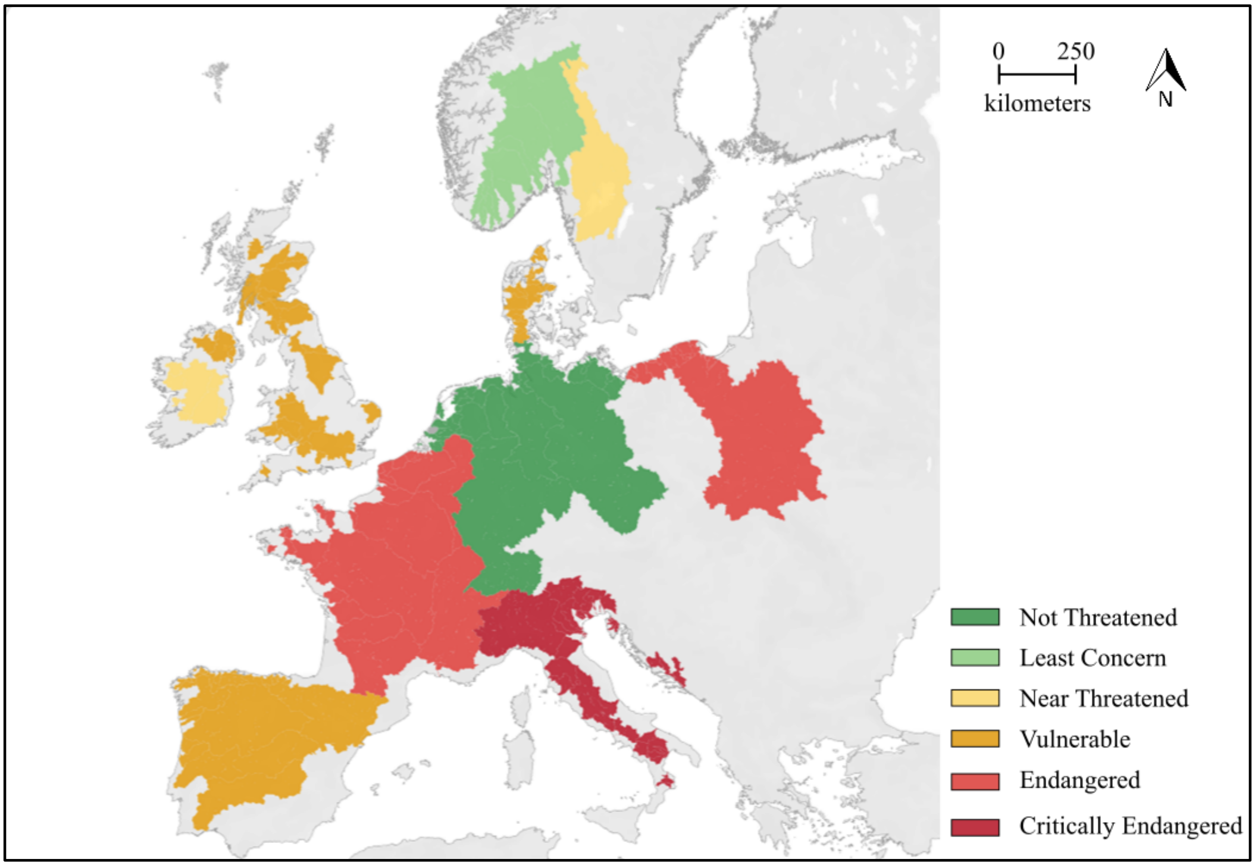

Figure 1.

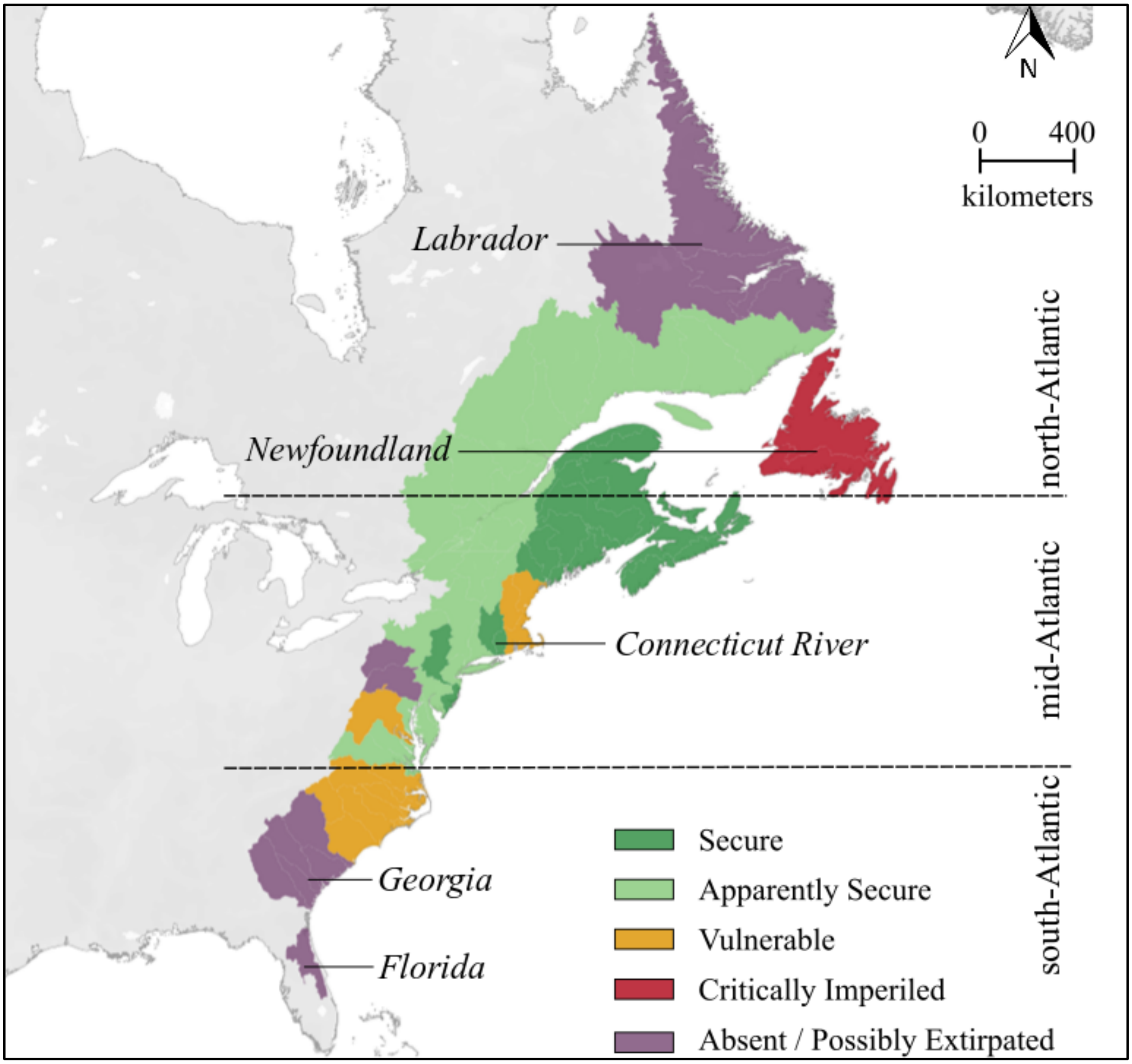
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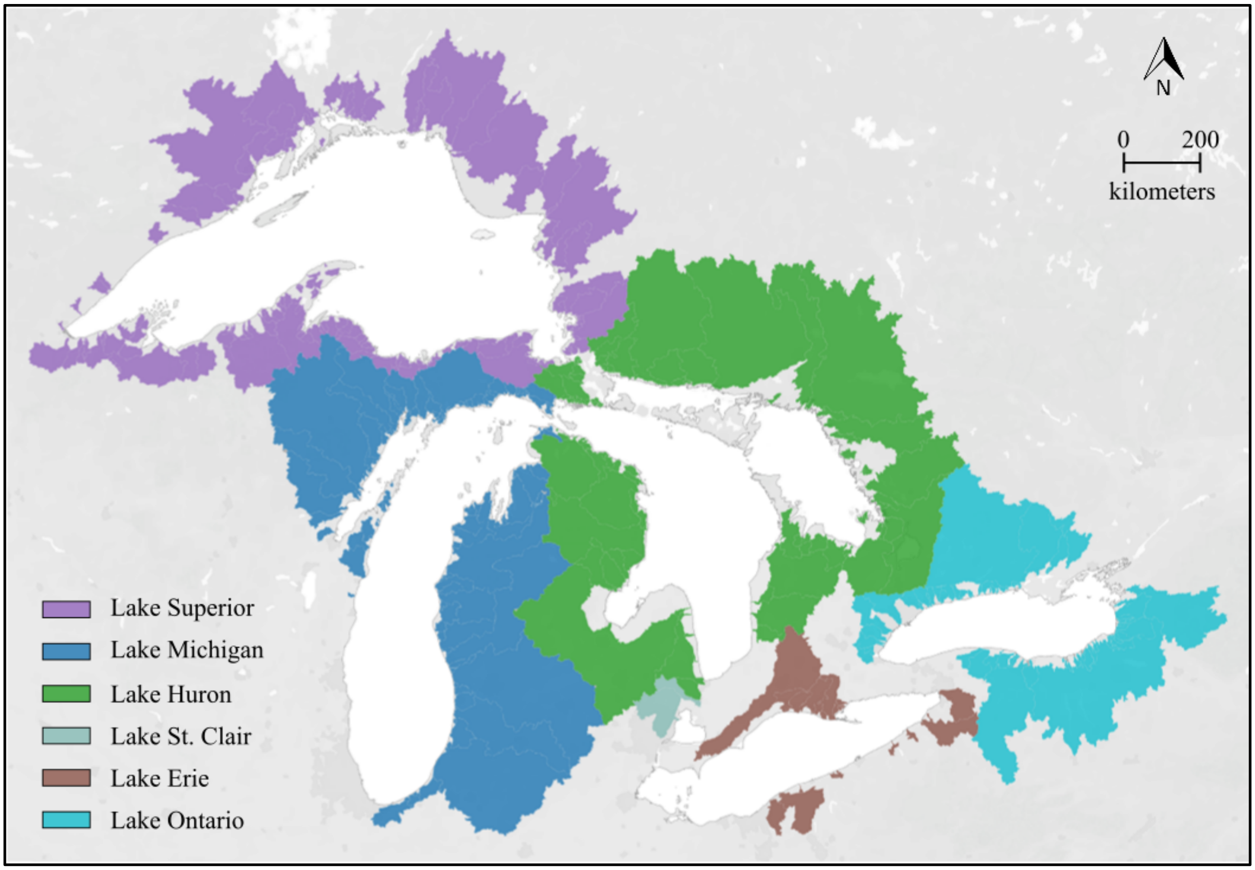
Figure 2.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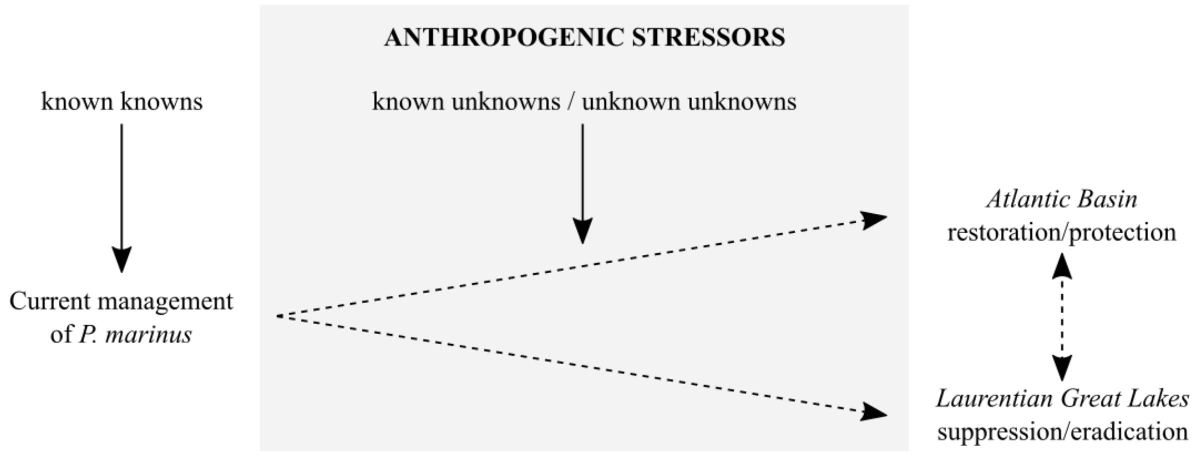
Lake Ontario

Figure 3.



Stressor	**Effect**	**Impact**
Climate change	Increased water temperatures Changes in precipitation patterns	Range shifts (lampreys/hosts) Change in bioenergetics Match-mismatch recruitment Accumulation of contaminants Ineffective barriers/fishways Altered hydrology Ineffective/costly pesticide treatment
Socio-political issues	Reduced tolerance for pesticides & barriers Increased conflict with other management actions/stakeholders	Development of pesticide alternatives (e.g., gene drive) Development of effective/selective fish passage Restoration/addition of suitable habitat Barrier removal Improved water quality Reduced funding for control and conservation actions Overharvest of adults

Figure 4.

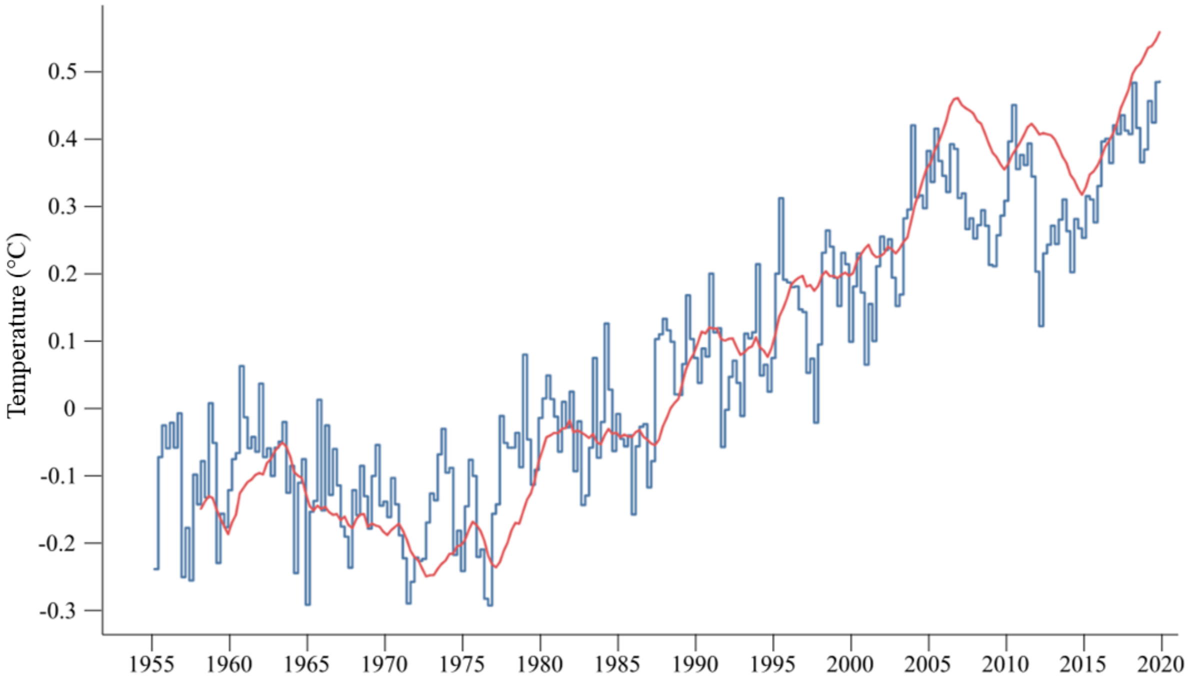

Temperature (°C)
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
2015
2020

Figure 5.

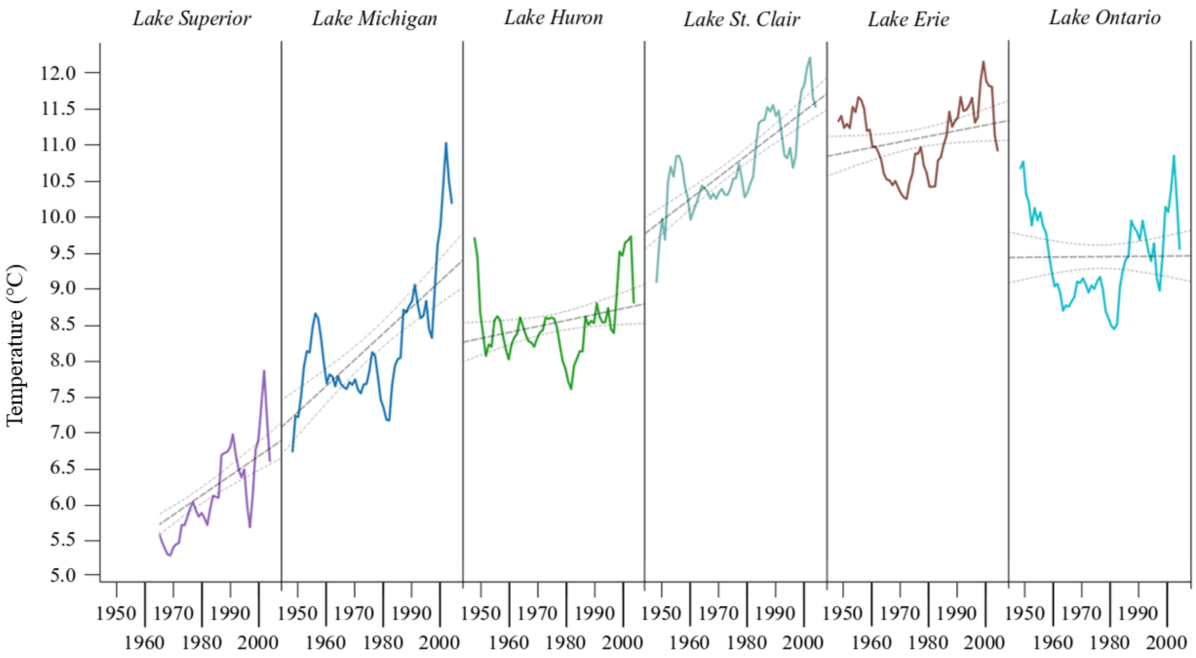

Lake Superior
Lake Michigan
Lake Huron
Lake St. Clair
Lake Erie
Lake Ontario
Temperature (°C)
12.0
11.5
11.0
10.5
10.0
9.5
9.0
8.5
8.0
7.5
7.0
6.5
6.0
5.5
5.0
1950
1960
1970
1980
1990
2000

Figure 6.

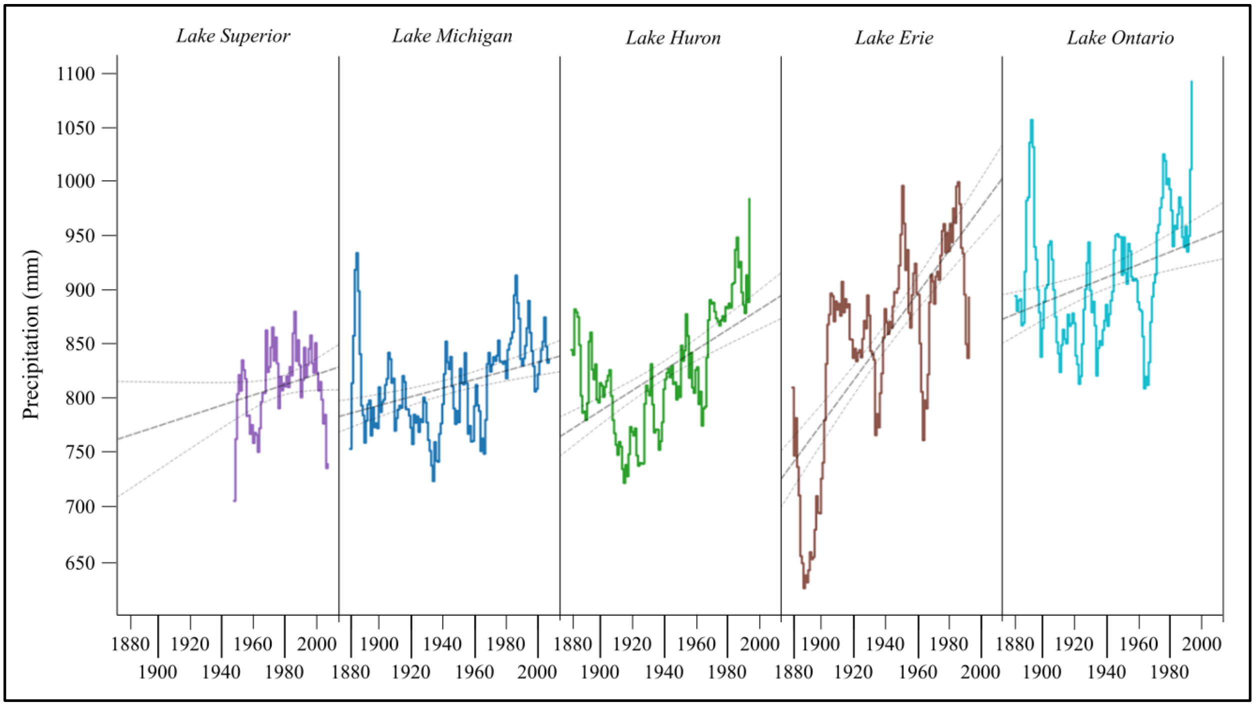

Lake Superior
Lake Michigan
Lake Huron
Lake Erie
Lake Ontario
Precipitation (mm)
1100
1050
1000
950
900
850
800
750
700
650
1880
1920
1960
2000
1900
1940
1980

Figure 7.