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Review

Impacts of a changing climate on native lamprey species: From physiology to ecosystem services

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ABSTRACT

Lampreys are jawless fishes that evolved hundreds of millions of years ago and exhibit multiple and varied life history strategies. Rapid changes in the current climate are clear, and warming temperatures and changes in precipitation patterns over the past several decades are projected to continue into the foreseeable future. The effects of our changing climate may impact lamprey species worldwide in ways already recorded for other taxa including range contractions. In order to manage and conserve the varied native lamprey species and mitigate for the potential impacts from climate change, it is necessary to understand how lampreys and their communities could be affected. We use the potential pathways of community change identified by Hughes (2000) to evaluate whether lampreys and their aquatic and human communities are already being affected by climate change. Evidence supports the likelihood that climate change will affect the physiology and phenology of lampreys as well as their distribution and contributions to communities and ecosystems. However, when considering their length of time on the planet, evolutionary history resulting from that time, multitude of life history expressions and range of distribution, it is possible that lampreys may be relatively resilient to climate change.

Contents

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Introduction

Lampreys are jawless fishes that evolved hundreds of millions of years ago. Modern lampreys have been called living fossils because their mouth anatomy and specialized parasitic feeding style has remained since the late Devonian Period (Gess et al., 2006). There are 44 species of native resident and anadromous lampreys recognized worldwide (Maitland et al., 2015). Lampreys are found on all continents; though, all but four of these species inhabit the Northern Hemisphere. Lampreys have co-evolved with their prey and host organisms over millennia and thus wherever native lampreys are found, they play an important role in aquatic ecosystems. Additionally, lampreys have played an important role in human culture as a traditional food. Threats impacting lamprey species vary depending on geographic location and life history strategy (e.g., Aronsuu, 2015; Boeker and Geist, 2016; Close et al., 2002; Lucas et al., 2020; Maitland et al., 2015; USFWS, 2019). The status of lampreys worldwide ranges widely from 'threatened' to 'least concern' according to the IUCN (International Union for the Conservation of Nature) classification with many falling under the 'data deficient' category (Clemens et al., 2021; Maitland et al., 2015). Many resident species of lamprey have a conservation status of 'least concern' while anadromous lampreys can be classified at elevated risk due to factors such as passage barriers blocking their migratory pathways (Clemens et al., 2021; Maitland et al., 2015). Other threats impact both resident and anadromous lamprey species, such as essential habitat loss and degradation, including deterioration of water quality and hydrological alteration (Costa-Dias et al., 2009; Maitland et al., 2015; USFWS, 2019). Though climate change has been identified as a potential threat to lamprey species worldwide, the degree to which it is impacting them (or may impact them in the future) is just beginning to be understood (Lassalle et al., 2008; Maitland et al., 2015; Wang et al., 2020) .

Climate change

Rapid changes in the current climate are clear and future projections have been intensively modeled (Meehl et al., 2014). The underlying drivers of our changing climate are increasing concentrations in greenhouse gases (i.e., water vapor, carbon dioxide, methane, nitrous oxide and ozone), giving rise to what is commonly known as the greenhouse effect (Dlugokencky et al., 2019; IPCC, 2013). This phenomenon has resulted in rising air temperatures and changes in precipitation patterns over the past several decades which are projected to continue into the foreseeable future (IPCC, 2013). These primary effects of our changing climate influence secondary effects such as increased water temperature, decreased snowpack, altered hydrology, and increased frequency and intensity of wildfire and other extreme events (IPCC, 2014). Cumulatively, the effects of our changing climate may impact lamprey species in ways already recorded for other taxa including significant range contractions and changes to species interactions (Parmesan, 2006; Parmesan and Yohe, 2003). The changing climate is likely to impact lampreys worldwide, though we mainly focus here on studies analyzing the changing climate and its impacts to lamprey species in three regions of the northern hemisphere: Western Europe, the Northwestern United States, and Japan. Examples from other regions are presented when relevant (e.g., Australia, Middle East).

The average temperature in Europe has increased in recent decades and warming trends are expected to continue under all emission scenarios (IPCC, 2014, 2013). High temperature extremes have become more frequent and low temperature extremes less frequent (EEA, 2012; IPCC, 2013). Annual precipitation has increased in northern Europe and decreased in parts of southern Europe and regional precipitation extremes are also evident (Berg et al., 2013; EEA, 2012; IPCC, 2014, 2013). Precipitation is expected to decrease in summer and increase in winter south of Sweden, with more rain than snow in mountains resulting in a decrease of long-term mean snowpack (IPCC, 2014; Räisänen and Eklund, 2012; Schmidli et al., 2007; Steger et al., 2013). The results of these and other parameters of the changing climate in Europe is that aquatic habitats and connectivity in the riverscape may become increasingly fragmented (e.g., Blaustein et al., 2010; Gómez-Rodríguez et al., 2010; Harrison et al., 2008; Hartel et al., 2011; IPCC, 2014; Morán-López et al., 2012).

Temperatures across the Pacific Northwest of the United States have increased over the past century (Kunkel et al., 2013; USGCRP, 2017, 2014). Annual precipitation has generally increased over this time period, but both increasing and decreasing trends are evident depending on specific location, season and time period (USGCRP, 2014). However, snowpack in the Cascade Mountains, a major mountain range of western North America, has decreased by approximately 20% since the 1950s (USEPA, 2016). Changes in extreme temperature and precipitation events in the Pacific Northwest, while evident and potentially increasing in recent years, have not been statistically significant (USGCRP, 2017, 2014). Annual mean temperature is expected to continue to increase in the Pacific Northwest through the end of century (USGCRP, 2017, 2014). Precipitation changes are expected to result in wetter winters and drier summers, with more precipitation in the form of rain rather than snow at higher elevations, resulting in decreased snowpack (USGCRP, 2017, 2014). The results of projected changes in the climate of the Pacific Northwest of the United States will affect stream flow and water quality due to less winter snow accumulation, higher winter stream flows, earlier spring snowmelt, earlier peak streamflow and lower summer streamflow, likely impacting aquatic habitats and connectivity among them (USGCRP, 2018, 2014).

Annual mean temperatures in Japan have risen over the past century at a rate higher than the global average (JMA, 2020; Ministry of the Environment et al., 2018). The frequency of extremely high temperature events (those historically occurring once every 30 years or longer) has increased during this timeframe (1901–2019), with the number of extreme temperature events increasing at a higher rate in the past 30 years. The frequency of extremely low monthly temperatures has decreased over the same period. Precipitation over Japan has been variable over the past century, with deviations both above and below the baseline (i.e., 1981–2010 average) (JMA, 2020; Ministry of the Environment et al., 2018). The number of extremely dry months has increased over this timeframe, while the change in number of extremely wet months is not statistically significant. Changes in precipitation patterns have resulted in decreased snowpack over the past century (Kawase et al., 2016; Ministry of the Environment et al., 2018). Projections under all scenarios indicate that annual mean temperature will rise throughout Japan by the end of the 21st century (JMA, 2020; Ministry of the Environment et al., 2018). The trends of increased number of days with heavy rain and decreased number of days with precipitation are expected to continue through the end of the century. The trend of decreasing snowpack is expected to continue, while the occurrence of decadal heavy snowfall events in inland areas of Honshu and Hokkaido in northern Japan are expected to increase (Kawase et al., 2016; Ministry of the Environment et al., 2018). The results of projected changes in the climate of Japan are expected to largely change river flow conditions, particularly in areas on the coast of the Sea of Japan (Ministry of the Environment et al., 2018). These changes in the hydrography will likely impact water quality and other habitat parameters due to increased sedimentation from slope failures and other impacts of flooding.

Lamprey life histories

Lampreys exhibit multiple and varied life history strategies including both anadromous and resident life histories. Anadromous forms of lampreys, such as Pacific lamprey (*Entosphenus tridentatus*), begin their life in freshwater where buried embryos transition into burrowing larvae (Clemens et al., 2010). After a variable period of time in freshwater, a true metamorphosis occurs where larvae transform into juveniles which, in turn, migrate to sea. Juveniles eventually transform into adults and return to freshwater to spawn. Certain species of lamprey, such as Arctic lamprey (*Lethenteron camtschaticum*), may express a life history where juveniles migrate downstream but remain in freshwater (Kucheryavyi et al., 2007). Resident lampreys, such as western brook lamprey (*Lampetra richardsoni*), also begin their life in freshwater where buried embryos transition into burrowing larvae (Renaud et al., 2009). However, after a variable period of time in freshwater, the larvae of resident forms metamorphose into adults, typically exhibit an upstream migration and do not exhibit an extensive downstream migration, and prepare to spawn. In general, freshwater resident forms are believed to have arisen from anadromous forms and, in some cases, are believed to have become differentiated to the extent that they are distinct species (Bracken et al., 2015).

Lampreys also exhibit parasitic and non-parasitic forms (Evans and Limburg, 2019). During larval development, all lampreys derive their nutrition through filter and deposit feeding. After their larval transformation, parasitic forms of lampreys, such as European river lamprey (*Lampetra fluviatilis*), develop teeth as well as the ability to attach to hosts and use a rasping tongue to derive their nutrition from the fluid of host organisms (Lasne et al., 2010). After non-parasitic forms of lampreys, such as European brook lamprey (*Lampetra planeri*), transform, they become adults and begin sexual maturation for imminent spawning without any feeding (Lasne et al., 2010). The parasitic and carnivorous species are associated with migratory forms (approximately half of these species go to the ocean while the others remain in freshwater) while non-parasitic species that do not feed as adults remain in freshwater (Renaud et al., 2009). In general, non-parasitic species have been assumed to have evolved from a parasitic species (Docker, 2009) and most have been paired with a congeneric parasitic species (Potter et al., 2015). For example, European river lamprey and European brook lamprey are paired species that have accumulated more variation and attained higher reproductive isolation in southern Europe (Spain and Portugal) than their more recently diverged northern counterparts (Mateus et al., 2016; Rougemont et al., 2015). An example of paired species in North America would be western brook lamprey and western river lamprey (*Lampetra ayresii*) (Docker, 2009). Whether the two species of a pair should be considered an expression of phenotypic plasticity within a single species or they have diverged into two distinct species is often unclear (Mateus et al., 2013; Bracken et al., 2015). Lamprey evolution over the past 300–500 million years (Clemens et al., 2010) has resulted in numerous life history expressions and adaptations to a range of conditions making it difficult to predict how lamprey taxa will respond to a globally changing environment.

In order to manage and conserve the varied native lamprey species worldwide and mitigate for the potential impacts from climate change, it is necessary to understand how lampreys and their biological communities could be affected. Hughes (2000) described how species and communities might be affected by human-induced climatic and atmospheric changes resulting from the enhanced greenhouse effect. Hughes categorized these predicted impacts into potential pathways of community change. First, increased CO_2 concentrations will act directly on species via physiology and indirectly via other climate change components/parameters (increasing temperatures, changes in precipitation, changes in frequency and severity of extreme events). Second, there will be changes in phenology and/or geographic distribution of individual species with potential in-situ microevolutionary changes. Third, because of these changes at the individual species level, changes in species interactions will occur. Finally, further shifts in distribution and/or extinctions may cause changes in community structure and composition. We use the potential pathways of community change identified by Hughes (2000) to evaluate whether native lampreys and their aquatic and human communities are being or will be affected by climate change (Fig. 1). Evidence of such might be useful in designing and framing future research for native lamprey conservation.

This paper focuses on the impacts of climate change to native lamprey species, but climate change will also certainly impact invasive lamprey species such as the sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes. Native to the Atlantic Ocean and tributaries of the east coast of the United States and west coast of Europe, sea lamprey were observed in Lake Ontario in 1835 and invaded the remaining Great Lakes in the early 20th century (GLFC, 2021). The juxtaposition of native versus invasive sea lamprey and how climate change may impact them and their communities is intriguing. The very changes in physiology, phenology, and distribution we describe as potential negatives to native lampreys, including sea lamprey, may very well benefit invasive lamprey species (Lennox et al., 2020). Lennox et al. (2020) discusses the issues surrounding sea lamprey management in a changing climate and should be considered a useful companion piece to this paper.

Response of lamprey species to climate change

As noted previously, in the aquatic environment, climate change is likely to have an impact on temperature as well other environmental characteristics (e.g., hydrology, snowpack). Increasing temperature is likely the most direct, measurable and possibly predictable result of climate change. While their potential impact to lampreys should not be discounted, characteristics such as altered hydrology are relatively uncertain as well as difficult to understand and predict. In addition, the literature relating the biology of lampreys to temperature is relatively robust whereas the literature on other, indirect environmental changes from a warming climate is relatively scarce. Thus, the following discussion primarily focuses on impacts to lampreys associated with changes to water temperature.

Physiology

An organism's physiological response to climate change is likely a significant factor mediating the overall impact of climate change (Hughes, 2000). Generally, physiology focuses on the biochemical processes associated with the function of organs (e.g., liver) or systems (e.g., endocrine) and, relative to climate change analysis, on metabolic and developmental rates. In the context of lampreys, however, we are considering a broad suite of characteristics that may be influenced by climate change. These include traditional physiological characteristics that may be directly impacted by climate change (e.g., respiration rate) as well as characteristics that may be impacted by climate change indirectly through physiological processes (e.g., burrowing behavior). Some physiological processes also have marked annual cycles (e.g., metamorphosis), and we address impacts associated with timing in the Phenology section (below). Based on general principles in environmental physiology, it is reasonable to anticipate a physiological response from lampreys to increasing temperatures. For example, Q10 is a concept that stems from observations on a variety of organisms that

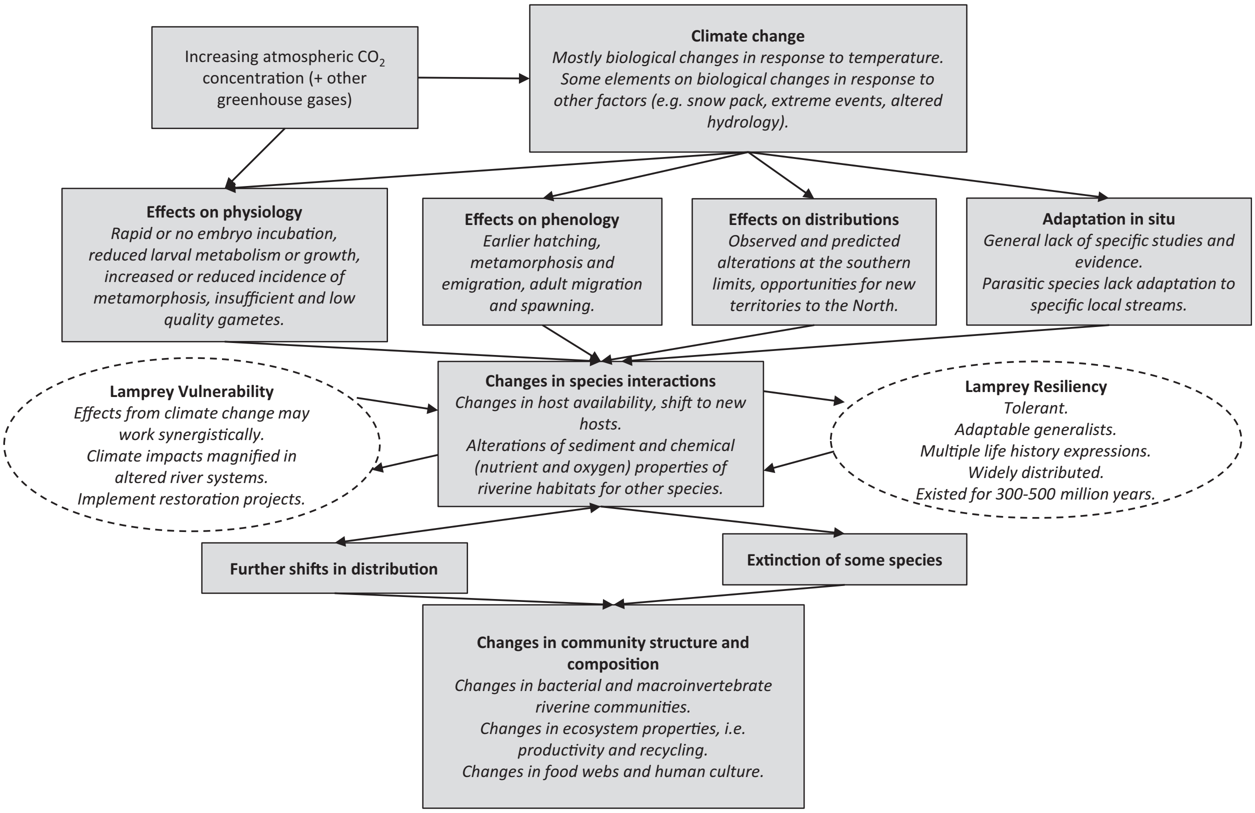

Fig. 1. Potential pathways of impacts from climate change for native lampreys and their aquatic and human communities. Text in italics were the main conclusions derived from the present literature review for the different categories of impacts. Vulnerability and Resiliency were added to the initial structure proposed by Hughes (2000).

the rate of physiological processes increases for each 10 °C of temperature increase (Bron et al., 2005). The increase may be from >1 to 10 fold, varying by species and process. It is likely that the rate of physiological processes in lampreys, at least to some extent, increases with increasing temperature. In addition, it is also important to consider that climate change has the potential to affect all four developmental stages of lampreys (embryo, larva, juvenile and adult).

The embryonic stage of lampreys generally has the shortest duration of any stage but is an incredibly sensitive stage, where lampreys may experience up to 85% mortality (Smith and Marsden, 2009). In sea lamprey, successful incubation of embryos and subsequent hatching occurs over a relatively narrow range of water temperature (approximately 15–25 °C) (McCauley, 1963). Within that range, survival from fertilization to hatching appears to have a positive relationship with temperatures up to 23 °C (Rodríguez-Muñoz et al., 2001). However, increased incubation temperatures may have a delayed effect after hatching, where survival to the burrowing stage appears to have a negative relationship with temperature (Piavis, 1961). Similarly, in a study conducted by Meeuwig et al., (2005) with Pacific lamprey and western brook lamprey, exhibit increases in survival from fertilization to hatching at temperatures up to 18 °C (see Table 1). However, temperatures warmer than 18 °C were suboptimal, resulting in reduced survival. In addition, Meeuwig et al., (2005) found that relatively warm incubation temperatures may have a sublethal effect, resulting in a greater rate of larval abnormalities than cooler temperatures. This information suggests that we may expect to see climate-related changes to the embryonic development of lampreys, especially in areas where spawning and incubation take place in relatively warm months of the year. For example, when compared to current conditions, warming water temperatures may result in a relatively rapid incubation process or, ultimately a complete disruption of embryonic development.

Table 1
Effective temperature (E_T), days required to reach 50% hatch (D_{H50}), days required to reach 95% hatch (D_{H95}), and days to the larval stage (D_L) for Pacific lamprey and western brook lamprey reared at four temperatures. The values of D_{H50} and D_{H95} were estimated independently for each replicate by means of logistic regression. Reproduced from Meeuwig et al. (2005) with permission.

Species	Temperature (°C)	E_T (°C)	D_{H50} (±SE)	D_{H95} (±SE)	D_L
Pacific lamprey	10	5.15	26.22 ± 0.57	29.26 ± 0.50	56
	14	9.15	16.95 ± 0.20	18.85 ± 0.36	35
	18	13.15	11.10 ± 0.03	12.22 ± 0.10	23
	22	17.15	8.38 ± 0.05	9.08 ± 0.08	17
Western brook lamprey	10	5.03	26.93 ± 0.53	29.34 ± 0.60	56
	14	9.03	15.82 ± 0.18	17.00 ± 0.19	33
	18	13.03	10.84 ± 0.10	11.90 ± 0.06	23
	22	17.03	8.05 ± 0.10	9.03 ± 0.09	17

The larval stage of lampreys, which generally comprises the longest duration of any stage (summarized in (Whitesel et al., 2020)), is subject to numerous annual rearing cycles and physiological processes (see Docker, 2015). The larval stage is, perhaps, the most well studied in lampreys, including investigations related to freshwater temperature and flow. Increased temperature can influence various physiological characteristics of larval lampreys. Leatherland et al. (1990) found that increasing the temperature from 16 °C to 25 °C resulted in lower serum thyroxine and triiodothyronine levels in the pouched lamprey (*Geotria australis*). In pouched lamprey, although their blood has a relatively high affinity for oxygen, it also exhibits a reduced oxygen affinity as temperatures increase (Macey and Potter, 1982). In sea lamprey, metabolic rate has been shown to peak from 15 to 18 °C but experience a significant reduction after water temperatures exceeded 21 °C (Holmes and Lin, 2011). Increased temperature has been shown to influence larval growth and morphology. At temperatures over 18 °C, Arctic lamprey exhibit decreases in growth rate as temperature increases (Arakawa and Yanai, 2021). All growth rates were positive in temperatures up to 18 °C, but at 29.5 °C growth rates became negative and larvae shrank.

Water temperature and flow have also been shown to influence various larval behaviors. Kirillova et al. (2011) reported that during periods of increased flow, relatively young Arctic lamprey burst out of burrows to surface. This behavior is presumably associated with larvae interacting with the flow to facilitate a passive movement downstream, preserve energy reserves and avoid predators (Kirillova et al., 2016; 2011). Pacific lamprey exhibited impaired burrowing behavior at a non-lethal temperature of 27 °C (Tim Whitesel, USFWS, personal communication). When given a choice, sea lamprey have been shown to tolerate temperatures up to 19 °C, but prefer cooler temperatures near 14 °C for burrowing (Reynolds and Casterlin, 1978). When compared to current conditions, warming water temperatures may inhibit the ability to burrow and result in greater mortality from predation. It has also been demonstrated that water temperature can influence filtration rate and, thus, affect filter feeding in European brook lamprey (Malmqvist and Brönmark, 1982).

One of the most thoroughly studied aspects of increased temperature influencing larvae is relative to their survival. Potter and Beamish (1975) investigated the thermal tolerance of four species, northern brook lamprey (*Ichthyomyzon fossor*), landlocked sea lamprey, American brook lamprey (*Lethenteron appendix*) and European brook lamprey. They determined that the incipient lethal levels (for larvae acclimated to 15 °C) ranged from approximately 28–31 °C. They also estimated the ultimate incipient lethal levels (the highest temperature to which fish can acclimate) to be approximately 31 °C for sea lamprey and approximately 29 °C for European brook lamprey. Similarly, essentially 100% of Arctic Lamprey (Arakawa and Yanai, 2021) and Pacific lamprey (Tim Whitesel, USFWS, personal communication) survived to temperatures of 27–28 °C, and exhibited reduced survival in temperatures above 28 °C until no larvae survived in a temperature of 33 °C (Fig. 2). For Pacific and Arctic lampreys, the ultimate upper incipient lethal temperature was estimated to be from 29 to 30 °C (Arakawa and Yanai, 2021; Timothy Whitesel , USFWS, personal communication). For sea lamprey in laboratory experiments, larval survival has increased at warmer temperatures, so improved recruitment might occur in suitable habitats (Rodríguez-Muñoz et al., 2001). As suggested by the survival studies, the larvae from various species of lamprey may express similar responses to climate change based on these seemingly well conserved traits related to thermal inflation. In any event, taken as a whole, this information suggests that we may not expect to see climate-related changes to the larval stage of lampreys unless water temperatures reach the highest levels projected by climate models or at the warmest extremes of lamprey distribution.

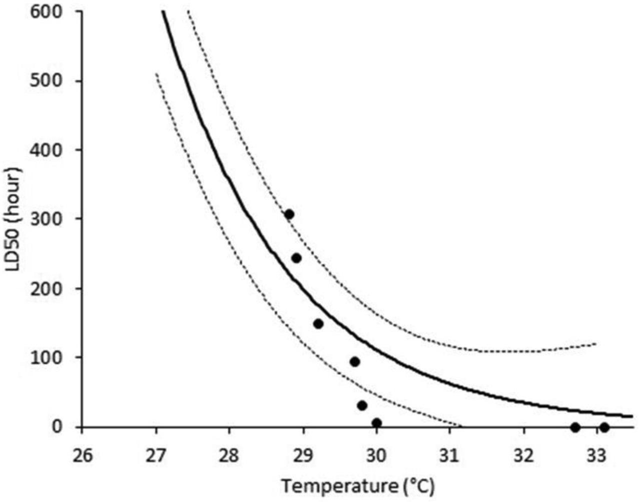

Fig. 2. The relationship between water temperature and LD50 (temperature inducing 50% survivorship) for larval Arctic Lamprey. LD50 = 3.855 * $10^9 e^{-0.5787 * temperature}$. The ultimate incipient lethal temperature was estimated to be 29.3 °C. Reproduced from Arakawa and Yanai (2021) with permission.

The juvenile stage of lampreys is most obvious in parasitic species. It is a transitional but important life history stage that begins with a larval metamorphosis and ends with a transition into an adult. Transformation to the juvenile stage is a true metamorphosis which involves cellular reorganization and numerous physiological changes (Manzon et al., 2015) as well as changes in feeding ability, behavior, morphology and a natural change in their habitat or environment. In parasitic species, juveniles migrate downstream to relatively large bodies of freshwater or, in many cases, to the ocean. Anadromous forms that enter the ocean also undergo physiological changes that allow them to osmoregulate in seawater (Richards and Beamish, 1981). The relationship between temperature and metamorphosis may be the most extensively investigated aspect of juvenile biology, especially in sea lamprey. Water temperature has been shown to have a clear effect on larval metamorphosis (Binder et al., 2010; Holmes et al., 2011; Youson et al., 1993). It has been suggested that, as temperatures increases from 7 to 21 °C, so does the incidence of metamorphosis (Purvis, 1980; Youson et al., 1993). Temperatures near 21 °C have been proposed as possibly optimal for larval metamorphosis while cooler temperatures (9–13 °C) and warmer temperatures (25 °C) result in a reduced incidence of metamorphosis (Holmes and Youson, 1998), sometimes precluding metamorphosis (Purvis, 1980). Changes in temperature appear to be particularly significant, and the effects may be mediated through metabolic processes (Holmes and Youson, 1994). Similar to the effects of temperature on survival, larval metamorphosis appears to be a fairly consistent process in many species of parasitic lamprey (Manzon et al., 2015). This information suggests that we may expect to see climate-related changes associated with the physiology of larval metamorphosis and the juvenile stage of lampreys. For example, as water temperatures warm, there may be an increase in the incidence of larval metamorphosis or, if temperatures become too warm, a reduced incidence or no metamorphosis at all.

All lamprey species transition into semelparous adults where they spawn and die in freshwater (Potter et al., 2015). For parasitic species, this transition typically involves juveniles increasing in size significantly while feeding over a relatively short period of years (Potter et al., 2015). For non-parasitic species, this transformation occurs relatively quickly from the larval stage, there is no feeding after the transformation and adults are typically not much larger (Potter et al., 2015), and sometimes smaller, than larvae. There are numerous physiological processes associated with the transition to an adult and spawning (e.g., gonadal development and sexual maturation). Water temperature can affect the traditional physiology of adult lampreys. A positive relationship between water temperature (from 1 to 20 °C) and oxygen consumption rate has been observed in adult sea lamprey (Beamish, 1973) and Far Eastern brook lamprey (Lethenteron reissneri) (Renaud and Naseka, 2015; Wang et al., 2011). In sea lamprey, the circadian rhythm of melatonin production has been shown to have a larger amplitude at 20 °C than at 10 °C (Bolliet et al., 1993). In addition, temperature has been shown to influence dermal light receptors in sea lamprey, where those at 22 °C had a reduction in dermal photosensitivity and displayed less search activity than those at 7 °C or 15 °C (Binder and McDonald, 2008).

Water temperature and flow can also have an effect on the growth of adult lampreys. Water temperature and river discharge are generally believed to be major factors influencing the activity of sea lamprey and European river lamprey (Baer et al., 2018). Cline et al. (2014) conducted an analysis on sea lamprey that suggested warmer water results in increased feeding rates and leads to larger, more fecund sea lamprey. The length at maturity for sea lamprey also increased over the last two decades for the Adour, Dordogne (Garonne Basin) and Vienne (Loire Basin) rivers in France. No causal relationship was provided, but a potential link with increased water temperatures was cited as an explanation among others (Beaulaton et al., 2008).

Water temperature may be particularly important to spawning. For example, in European river lamprey, temperature was found to have a negative relationship with sperm production and also influenced ovulation (Cejko et al., 2016). Specifically, 7 °C was the best temperature for males to produce mature sperm with high motility whereas the majority of those held at 10 °C and 14 °C did not spermiate. This information suggests that we should expect to see climate-related changes associated with the physiology of the adult spawning lamprey as well. When compared to current conditions, warming water temperatures may impact the ability of lampreys to produce sufficient and high-quality gametes.

Phenology

Climate change affecting the phenology of an organism is likely a significant factor mediating the overall impact (Hughes, 2000). Phenology is associated with the timing of annual events or life cycle events ((Demaree and Rutishauser, 2011)). A focus of phenology is the dates at which biological events first occur in their annual cycle, or seasonal biological phenomena, as triggered by environmental cues (Hughes, 2000). Relative to climate change, phenology effects have the potential to result in disrupted synchronization (match-mismatch hypothesis) between species-species or species-habitat relationships (Hughes, 2000). Based on climate change models, we may anticipate changes to water temperature and flow events, both of which may act as environmental cues, or 'zeitgebers' (Ehlers et al., 1988), for the life cycle events of lampreys. In the context of lampreys, phenological characteristics would include the time at which a life cycle event begins or ends as well as its duration. For example, degree-days, which are an expression of thermal units as a result of integrating temperature and time, is an example of a general concept associated with temperature influencing phenology (see Neuheimer and Taggart, 2007). Many phenological characteristics of various organisms are associated with the accrual of a certain number of thermal units (e.g., length of incubation). Additionally, organisms take their cues from the annual hydrograph to determine the best times to spawn and migrate. Variation in the hydrograph, measured in deviation from the hydrologic mean date (the date representing when 50% of the volume of the river for the water year passes a specific location) also has the capacity to affect phenological characteristics (Wang et al., 2020). It is reasonable to anticipate a phenological response from lampreys to environmental cues such as increasing temperatures or altered flows. In addition, it remains important to consider that climate change has the potential to affect the phenology of all four developmental stages of lampreys (embryo, larvae, juvenile and adult).

The most commonly studied phenological characteristic of the embryonic stage is time from egg fertilization to the hatching of embryos (duration) in fresh water. The duration of incubation in Pacific lamprey and Western brook lamprey has been shown to be negatively related to water temperature (Lampman et al., 2016; Meeuwig et al., 2005). Warmer incubation temperature has also been associated with quicker times to hatching and burrowing in sea lamprey (Rodríguez-Muñoz et al., 2001; Moser et al., 2019). Accordingly, we may expect to see climate-related changes to the timing of embryonic development of lampreys with a potential for warming water temperatures to result in earlier hatching.

Regarding the larval developmental stage, Potter (1980) proposed that at warmer water temperatures one could expect an increased larval growth rate in sea lamprey and a relatively shortened larval phase. Unfortunately, studies that could relate to phenological characteristics of larval lampreys were found to be less frequent than studies on the other developmental stages.

During metamorphosis, cellular reorganization typically begins in the fall, followed by changes to morphology that become apparent the following spring and summer, then completion of the transformation the subsequent fall or winter (Manzon et al., 2015). While there is some variability in the specific timing of individuals from a given metamorphic cohort (McGree et al., 2008), the timing of the process is generally similar across species (see Manzon et al., 2015). Once transformed, juveniles generally migrate during that fall or ensuing winter and spring (Baer et al., 2018). The relationship between metamorphosis and cues from the environment has been relatively well investigated, especially in sea lamprey (e.g., Holmes et al., 2011; Manzon et al., 2015; Youson et al., 1993; Youson and Manzon, 2012). Temperature appears to be an especially important cue for various metamorphic events. In sea lamprey, low winter temperatures followed by increasing temperature in the spring as well as the rate at which the temperature changes in the spring have been identified as important cues for larvae to initiate and complete metamorphosis (Holmes et al., 1994; Potter and Beamish, 1977). The springtime rise in water temperature has been described as a particularly important trigger for final metamorphosis (Youson et al., 1993). Metamorphosis in the Australian lamprey occurred 4–5 weeks earlier due to elevated winter temperatures (Potter, 1970).

The initiation of juvenile downstream migration has also been shown to be related to temperature (reviewed by Kirillova et al., 2016). In sea lamprey, the majority of downstream migration was observed to occur in the spring of each year when water temperatures were between 9 °C and 12 °C (Baer et al., 2018). It has been suggested that warmer than normal temperatures can lead to a seaward migration at earlier ages than normal, presumably because of accelerated growth (Potter, 1980). Furthermore, the initiation of juvenile migration has also been shown to be related to flow (reviewed by Kirillova et al., 2016). A primary cue for seaward migration appears to be associated with specific flow conditions (e.g., high or increasing flow) that often vary on an annual basis. As a result of the variability in flow, migration does not appear to occur at precise times each year and may extend through fall into the following spring (Potter, 1970). Goodman et al. (2015) found that both days from a rain event and stream flow were associated with emigration timing in Pacific lamprey. Baer et al. (2018) also found juvenile migration in sea lamprey was related to discharge peaks between December and February. Specific flow conditions that trigger migration may vary across species. Nonetheless, we may expect to see climate-related changes associated with the phenology of larval metamorphosis and the juvenile stage of lampreys. For example, as water temperatures warm and the flow patterns change, lampreys may initiate metamorphosis sooner, complete the process more quickly as well as emigrate earlier in the year, than they do presently.

The adult stage has numerous phenological components (e.g., migration timing). Water temperature and stream flow can affect the migration of adult lampreys. Malmqvist (1980) estimated that the European brook lamprey need to experience a temperature of 7.5 °C to initiate their spawning migration. In Pacific lamprey, the migration timing has been found to be earliest in warm years (Keefer et al., 2009; reviewed in Moser et al., 2015). Warmer water has also shown a positive relationship with increased upstream movement in sea lamprey (Brant et al., 2015). Not only is migratory activity in sea lamprey apparently related to mean stream temperature, but it may peak at a temperature near 15 °C (Binder et al., 2010; Lampman, 2011). Evidence that migratory activity may be triggered when temperatures increase between days, but be inhibited when temperature decreased between days, suggests that patterns in temperature may be important as well (Binder et al., 2010). In its native European range, a slight advancement in the migration dates of sea lamprey (−0.2 day per decade) was found based on data collected on fish counting devices in France (40 sites) over 10–30 years (Legrand et al. 2021). For Pacific lamprey in the Columbia River (west coast of the USA), at Bonneville Dam, Keefer et al. (2009) found that lamprey run timing shifted progressively earlier from 1939 to 2007 (−0.26 day per decade), coincident with decreasing Columbia River discharge and increasing water temperature. This time period also coincides with the operation of Bonneville Dam, which was completed in 1938, and has accelerated flow and temperature changes in the river that we expect to continue based on climate modelling. Furthermore, based on a 41-year time series of adult lamprey counts at Bonneville Dam, migration timing was earliest in warm, low-discharge years and latest in cold, high-flow years.

Water temperature and stream flow can also affect the timing of adult lamprey spawning. As described for European brook lamprey (Hardisty, 1944), water temperature has been suspected to have a relationship with the timing of spawning. The initiation of spawning in American brook lamprey (Seagle and Nagel, 1982) and chestnut lamprey (*Ichthyomyzon castaneus*) (Cochran, 2014) appears to be associated with temperature. Warmer than normal temperatures during early 2012 resulted in spawning up to one month earlier than typical by the American brook lamprey in five streams in southeastern Minnesota (north-central region of the USA)(Cochran et al., 2012). Stream flow can also influence spawning, as high discharge events have been shown to prevent spawning in chestnut lamprey (Cochran, 2014). This information suggests that we may expect to see climate-related changes associated with the phenology of adult lampreys. For example, when compared to current conditions, warming water temperatures and changes to flow patterns may lead to earlier migrations and spawning attempts.

Shift in distribution range

Hughes (2000) predicted that the changing climate would affect the distribution of individual species shifting them towards the poles and upward in elevation. Correlative species distribution models (C-SDMs) have been used for decades to identify which climatic variables are the most constraining for a species distribution and predict the impacts of human-induced climate changes on these distributions (Guisan et al., 2017). Correlative SDMs were applied to European diadromous species on their historical continental distributions (Lassalle et al., 2008; Lassalle and Rochard, 2009). Temperature and precipitations, as a distal proxy of river discharge, were the two climatic variables tested as there were the only one available at the European scale for the early 21st century. Explanatory variables included in C-SDM approaches are selected to balance between data availability and ecological interpretation. Projections in the context of climate change for sea lamprey highlighted a decrease in the species presence in the basins bordering the east coast of the Adriatic Sea, in most of the Italian basins and in the Iberian Peninsula under scenario A2 of the IPCC in 2100 (Lassalle et al., 2008). However, conditions remained suitable in the northern part of its present distribution area and the Icelandic basins became favorable to this species (Fig. 3) (Lassalle et al., 2008). In Rose (2005), the sea lamprey was identified as a warm-water species that would be expected to be new arrivals to Greenland and Iceland waters in a warm period. Sea lamprey will also likely move northward out of the basins in the southern states of the USA and into permanent populations in eastern Canadian provinces as temperatures warm (Hume et al., 2021).

The potential for new sea lamprey populations to appear in northern territories in response to large-scale changes in temperature and precipitation need to be put in the perspective of the suitability of essential habitats at the local scale, e.g., accessible spawning grounds with fine sediments. If management actions are needed to secure such population settlements in the next few decades, the decisions will require the consideration of ecological trade-offs among native and desirable species, particularly Salmonidae, and the assessment of the societal acceptance of these measures for a species that remains ambivalent (Hume et al., 2021).

For the European river lamprey continental distribution, Lassalle et al. (2009) predicted a decrease in habitat suitability mainly in southern France around the Bay of Biscay, but with a stable habitat suitability in other areas, particularly in the British Isles. For both sea lamprey and European river lamprey, a second set of models and projections were run with four classes of abundance (i.e., missing, rare, common and abundant) as the response variable, leading to strengthened previously mentioned conclusions regarding potential impacts of climate change on Western European lampreys (Lassalle et al., 2009). No projections existed for the marine distribution of European anadromous species but knowledge on the current trends have recently improved (Elliott et al., 2021).

The same method was applied to the European brook lamprey in their French distribution range where they inhabit upstream riverine reaches. This resident species was predicted under both IPCC scenarios B1 (more optimistic) and A2 (more pessimistic) to lose more previously suitable sites than to gain newly suitable habitats in 2080 (Buisson et al., 2008).

For the two anadromous European lampreys, maps and probabilities from SDMs were supplemented with an expert-based approach to score their exploratory potential according to their life history traits (Massiot-Granier et al., 2018). The exploratory potential was defined by the authors as “the capacity of species to initiate the act of leaving their current habitats and to reach new ones outside of their range; at a rate fast enough to keep pace with climate change.” The work was done for the North Atlantic diadromous species. Whatever the theoretical and practical backgrounds of the experts were, sea lamprey was always at the bottom of the rankings, meaning poor capacities to explore compared to other diadromous species. For the five life history traits considered in the analysis, sea lamprey had low to intermediate scores relative to the other species attesting to poor biological

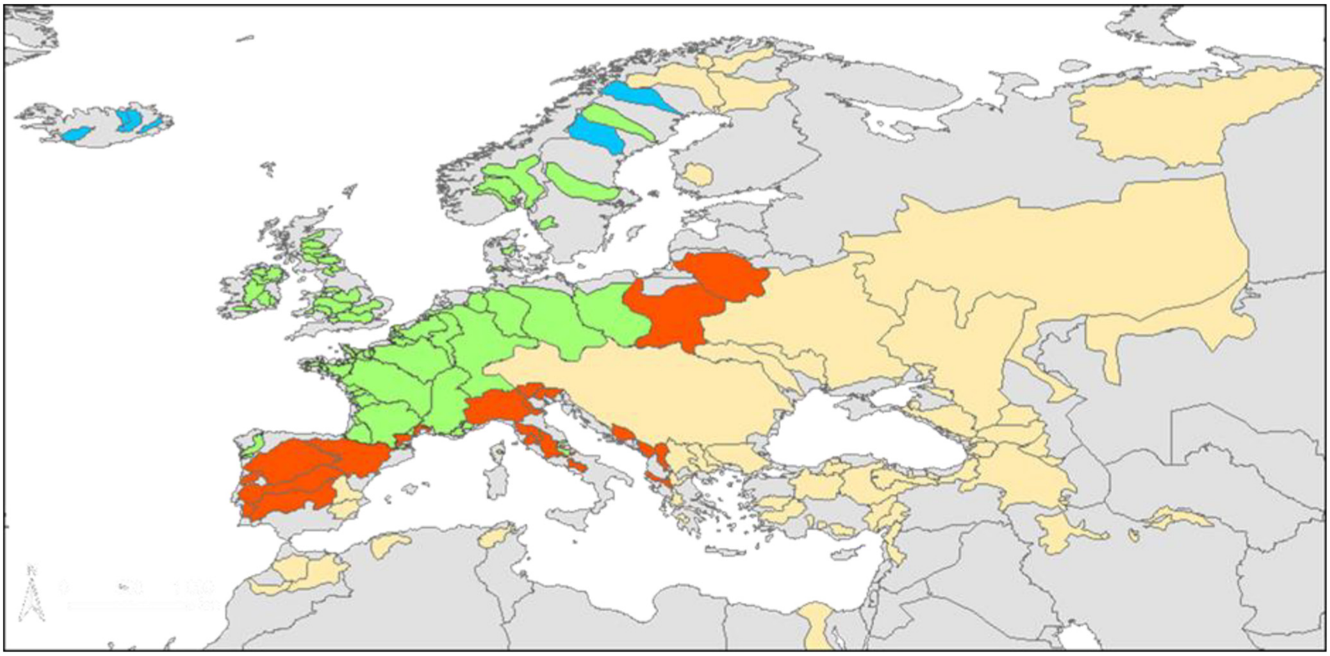

Fig. 3. Suitability of European basins for Sea Lamprey populations by the end of the century under scenario A2 of the IPCC. Pale pink: stable unsuitable; Orange: turning unsuitable; Green: stable suitable; and Blue: turning suitable (Géraldine Lassalle, INRAE, personal communication).

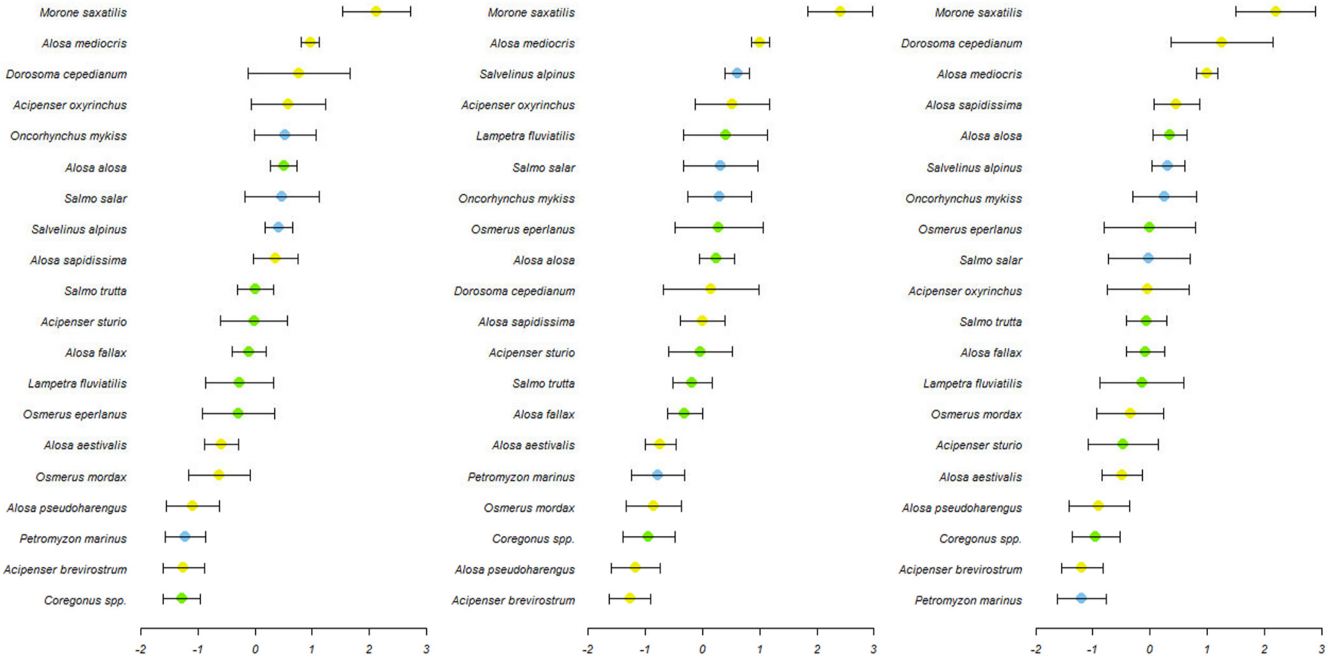

Fig. 4. Exploratory potential index (EPI) distribution values for the diadromous species of the northern Atlantic Ocean according to three groups of experts with different theoretical and practical backgrounds. Means are given with their standard deviation. Yellow indicates North American species, green European species, and blue species occurring on both sides of the Atlantic Ocean. Reproduced from Massiot-Granier et al., (2018) with permission.

characteristics in terms of exploration. In contrast, European river lamprey had a more variable score depending on the expert group (Fig. 4).

For the Pacific lamprey, western river lamprey and western brook lamprey at the southern end of their range on the Pacific Coast of the USA, Goertler et al. (2020) found that high water temperature constrains lamprey habitat use and considering the projected increases in water temperature with climate change in California, their estuarine use will continue to be restricted in the future. Authors observed differential thermal preferences at sea between the Arctic lamprey and the Pacific lamprey in a zone of potential species interchange, i.e., the Bering Sea at the confluence between the Pacific and Arctic-Atlantic domains. Pacific lamprey were consistently found in warmer waters and were potentially avoiding entry into the cooler waters associated with the “cold pool”, whereas Arctic lamprey did not appear to have a temperature preference in surface waters. Results are strongly linked with the distribution of preferred hosts of each species (Goertler et al., 2020). As such, these two species oceanic distribution will be impacted differently by stressors such as climatic shifts or a warming ocean (Siwicke and Seitz, 2018). The southern boundary for Pacific lamprey distribution in freshwater basins has shifted northward in the last two decades by hundreds of kilometers from northern Baja California to San Luis Obispo creek in South Central Coastal California (USA) (Reid and Goodman, 2016; Damon Goodman, USFWS, personal communication). In Japan, a 1.2 °C increase in temperature since the 1930's has shifted the southern limit of the Arctic lamprey populations northward by 6° in latitude (Arakawa and Yanai, 2021). The results of Bond et al. (2011, 2014) for the freshwater fish fauna in Western Australia suggest there are a number of species predicted to undergo substantial declines in overall habitat suitability by 2030's, including the two anadromous lamprey species, the short-headed lamprey (*Mordacia modax)* and pouched lamprey. The authors used boosted regressions trees (BRTs) to build their SDMs with scenarios A1T (optimistic), A2 (median) and A1FI (pessimistic). A recent paper suggested that Caspian lamprey (*Caspiomyzon wagneri*) populations are currently experiencing a severe constriction of distribution in Iran due to more frequent and severe droughts in the region associated with climate change and the long-term effect of dams and weirs preventing lamprey access to spawning grounds (Nazari et al., 2017).

Genetic adaptation

An organism's ability to adapt to climate change, in situ, is likely a significant factor mediating the overall impact of climate change (Hughes, 2000). In the context of lampreys, adaptation in the typical habitats or areas they occupy warrants several considerations. As discussed previously, all lampreys spend part of their life cycle in freshwater streams and the life cycle of some lampreys includes freshwater migratory corridors as well as an ocean (see Docker, 2015). Occupation of these various habitats intersected by various stages of development create various opportunities for potential adaptation. However, examples of adaptation in lampreys, specifically associated with genetically heritable traits related to selection, and directly attributable to climate change (or change to temperature or flow), are as difficult to find as for any other groups of species.

As a whole, lampreys represent the most ancient group of vertebrates and have existed for ~300–500 million years, surviving through at least four or five mass extinction events (Clemens et al., 2010; Xu et al., 2016). Certainly, as with all species, natural selection and adaptation occur. However, in lampreys, local adaptation through heritable traits may be unlike other species. In anadromous species that do not necessarily return to the natal stream to spawn, it may be unreasonable to expect much adaptation to specific, local conditions (Goodman et al., 2008). Concordant with that idea, Pacific lamprey have been shown to exhibit high levels of gene flow (Spice et al., 2012) and a lack of philopatry or homing (Hess et al., 2013). In contrast, for resident species that generally stay near their origin or in a particular area, it may be reasonable to expect and see adaptation to local conditions (Spice et al., 2011). In either case, investigations related to adaptation, especially of 'rapid' microevolution, are rare. Dunlop et al. (2017) evaluated a relatively closed population (in the Laurentian Great Lakes) of sea lamprey for adaptation to lampricide resistance over a period of 57 years. Although they suggest the data must be interpreted with caution, they found no evidence for selection. Alternatively, Hess et al. (2014) did report Pacific lamprey exhibiting signals of adaptive variation related to broad-scale geography and life history. Specific to climate change, there is little to no evidence of genetic adaptation to temperature or flow changes.

The lack of examples of adaptation may be because the topic has not been investigated thoroughly yet or because such adaptations are rare, especially in migratory lampreys with a long life cycle. For example, the distribution of and streams of origin for Pacific lamprey is incredibly expansive (Close et al., 2002) with little to no evidence of natal homing, local adaptation, or in-situ adaptation (Spice et al., 2012). Alternatively, western brook lamprey which are a resident species sympatric with Pacific lamprey, have relatively limited ranges and do exhibit evidence of selection and adaptation to local conditions (Spice et al., 2011). The majority of lamprey research appears to focus on anadromous or migratory species with cultural (Close et al., 2002) and/or economic (Lupi et al., 2003) importance, with relatively little focus on resident species. To evaluate how lampreys may respond to climate change may require exploring lamprey adaptation by comparing and contrasting migratory and resident species, especially paired species. In particular, paired species may exhibit a level of genetic mixing that is critical to understanding local adaptation and phenotypic plasticity. As described by Hughes (2000), adaptation may be expected from species with short generation times and rapid population growth rates may facilitate microevolutionary changes in-situ. However, relatively speaking, lamprey populations do not necessarily exhibit a short generation time or a rapid population growth rate. Thus, it may not be surprising that examples of in-situ adaptation are relatively uncommon and rarely studied.

Changes in species interactions and community changes

Lampreys of all life history strategies have unique relationships with other species and the communities to which they belong. At every stage, lampreys are prey for other fishes, birds and mammals. As a high-calorie food, they are preferred by many predators (e.g., Close et al., 2002). Their rearing and spawning behaviors also contribute to the health of ecosystems (e.g., Boeker and Geist, 2016; Hogg et al., 2014). Though many changes in species interactions due to climate change have not been specifically studied for lampreys, physiological and phenological changes throughout their life cycles and shifts in distribution have the potential to greatly affect interactions with other species and community composition, including humans.

The larval stage of lampreys is of particular importance to other species and communities. In streams where larval lampreys are abundant, they can comprise a large portion of the biomass where they process, store and cycle nutrients (Beamish, 1980; Close et al., 2002; Kan, 1975; Merritt, 1984). The protracted larval phase ensures a constant source of nutrients to the food web and provide various ecosystem services (Boeker and Geist, 2016; Close et al., 2002; Shirakawa et al., 2013). Filter and deposit feeders, including lampreys, likely alter their habitat conditions including oxygen, organic matter, and nutrient levels (Shirakawa et al., 2013). In a study assessing lampreys' impacts on the physical and geochemical factors in the streambed, Shirakawa et al. (2013) found that the feeding and burrowing behavior of two species of *Lethenteron* lamprey native to northern Japan "increased oxygen levels, maintained softness and increased abundance of fine particulate organic matter in and on the streambed."

Boeker and Geist (2016) explored the contribution of burrowing lampreys to bioturbation and overall ecosystem health. Physical and chemical habitat properties as well as microbial community composition in freshwater substrates were compared in treatments with and without burrowing larval lampreys (*Eudontomyzon* sp.). A strong increase in oxygen availability and nitrate concentrations in interstitial water between sediment particles was observed in the lamprey treatment. Additionally, a shift in microbial community composition to one dominated by aerobic bacteria was observed. Both of these findings were a result of bioturbation of the sediment by lamprey burrowing. Larval lampreys clearly play an important role as 'ecosystem engineers' (Boeker and Geist, 2016; Hogg et al., 2014; Skirakawa et al., 2013). If rearing habitats become unavailable to lampreys due to changing temperatures, hydrologic regime or extreme events, communities that depend on larval lampreys for these ecological ecosystem services could be at risk. Non-anadromous resident lampreys, which do not migrate to the ocean as juveniles, are particularly at risk of impacts from climate change as they cannot migrate into cooler climes (Maitland et al., 2015). Species in more southerly areas may not survive warming temperatures and changes in precipitation and flow patterns, therefore, the community structure may be impacted more in these regions.

As juveniles, anadromous lampreys migrate to the ocean during winter and spring freshets and along their journey become a primary food source for fishes and birds (Arakawa and Lampman, 2020; Cochran, 2009). Lampreys comprise approximately 70% of the diet of some gulls and terns in the mainstem Columbia River ((Merrell, 1959)). Anadromous juveniles in the oceans are both prey and parasites. Lampreys parasitize a large variety of fish and mammal hosts (e.g., Clemens et al., 2019; Renaud and Cochran, 2019; (Silva et al., 2014)). Pacific lamprey have 32 documented hosts ranging from salmon and rockfish species to mackerel, herring and five species of whales (Clemens et al., 2019). Similarly, sea lamprey have wide dietary versatility ((Renaud and Cochran, 2019)). Sea lamprey invaded the Laurentian Great Lakes and became successful predators on freshwater hosts including non-native species, without a prolonged co-evolution period (Renaud and Cochran, 2019). A change in trophic interactions between European river lamprey and the whitefish (*Coregonus lavaretus*) has occurred since the introduction of non-native fish species to Loch Lomond in Ireland (Hume et al., 2013). Therefore, it is possible that anadromous lampreys in their native range will be able to adapt to new hosts if climate change shifts the range or distribution of their preferred hosts. The ability for species to become new hosts to native lampreys, without compromising their individual health or that of their stock however, remains to be seen. Lake trout and other species of host fish in the Great Lakes were severely impacted by the initiation of parasitism by sea lamprey though this occurred through invasion (Pearce et al., 1980; Schneider et al., 1996). Other examples of host shifting due to climate change could be occurring, resulting in changes in community composition, but these could be protracted and therefore are difficult to anticipate.

As the suitability for lamprey habitats change and move poleward, so do those of their hosts (Clemens et al., 2019; Lassalle et al., 2008; (Pinsky et al., 2013)). Pacific hake, a common host of Pacific lamprey, is already moving poleward (Auth et al., 2018; Cheung et al., 2015; Clemens et al., 2019). Juvenile sea lamprey forage over the continental shelf of the Atlantic Ocean and at depths of only 0 to 200 m (Mateus et al., 2021). The coastal marine environment has been increasing in water temperature faster than the global rate (MacKenzie and Schiedek, 2007; Hume at al., 2021), moving sea lamprey hosts northward and deeper and potentially out of the range of sea lamprey (Hume et al., 2021). An even more grave issue for native lampreys might be climate-induced changes to host abundance. Murauskas et al. (2013) found that marine survival and ultimate return specifically of Pacific lamprey into freshwater may be limited by environmental conditions and associated availability of hosts in the ocean. Maitland et al. (2015) found that parasitic lampreys are sensitive to climate-induced modifications to host abundance even if they are not affected by the changes in distribution of a particular host species. The abundance of Pacific salmonids (*Oncorhynchus* spp.), common hosts for parasitic lampreys (primarily Arctic lamprey and western river lamprey), in the North Pacific Ocean fluctuates with the ocean–atmosphere climate (Maitland et al., 2015). Cold phases of the Pacific Decadal Oscillation (PDO) are associated with greater marine survival and returns of Pacific salmon, whereas warm PDOs are associated with poor survival and returns (Clemens et al., 2019; (Murauskas et al., 2013)). Because Pacific salmonid abundance is associated with Pacific lamprey returns to the Columbia River, Clemens et al. (2019) hypothesized that the impact of the PDO on Pacific salmon could be similar for Pacific lamprey. Changes in ocean conditions from climate change impacts could directly affect the survival and spawning success of native anadromous lampreys and that of their hosts (Clemens et al., 2019; Murauskas et al., 2013) unless they both shift poleward as temperatures warm.

Whether lampreys remain and parasitize new hosts in their existing distribution range or follow their current hosts as they shift poleward or a possible combination of the two scenarios, the resulting community composition will certainly change. Potentially, so will the reproductive and physical fitness of both lampreys and their hosts. Sea lamprey choose hosts that are large and muscular with large blood volume ((Cochran, 1994)) and will select the larger hosts if given an option (Schneider et al., 1996; Silva et al., 2014). Pacific lamprey choose larger hosts as they grow in size themselves (Clemens et al., 2019; (Orlov et al., 2009)). The availability of hosts in a range of sizes seems important for maintaining parasitic lampreys as they grow and mature. There is a connection between warming temperatures and the decrease in body sizes of fishes (Baudron et al., 2014; (Pauly and Cheung, 2018)). Baudron et al. (2014) found that the body sizes of six commercial fish species in the North Sea decreased over a 40-year period coinciding with a 1–2 °C increase in water temperature. The decrease in body size also decreased yield-per-recruit by an average of 23% (Baudron et al., 2014). Parasitic lampreys seeking larger hosts may have to look elsewhere, to other larger species who may not be accustomed to being parasitized. Alternatively, parasitic lampreys may suffer stunted growth due to the availability of only smaller hosts.

Like larval lampreys, adult anadromous lampreys migrating into freshwater to nest and spawn also act as physical and chemical 'ecosystem engineers' (e.g., Hogg et al., 2014; Lasne et al., 2015; Sousa et al., 2012). They create habitat while spawning and when they die provide marine-derived nutrients which create favorable conditions for other ecosystem inhabitants (Clemens et al., 2019; Dunkle et al., 2020). Lampreys are also known to inject nutrients into the environment through metabolic waste and gametes. Georgakakos et al. (Philip Georgakakos, University of California, Berkeley, personal communication) found that Pacific lamprey eggs and pro-larvae in the nest are an important source of nutrients for benthic invertebrates, drift-feeding fishes and even certain amphibians. Sea lamprey nests have been recently demonstrated to create heterogeneous microhabitat patches that last for several months and support greater macroinvertebrate abundance than adjacent reference areas due to both physical changes in the riverbed and the addition of nutrients with carcasses (Weaver et al., 2018). Spawning activities contribute to a change in mean sediment size at the center and edge of nests, also contributing to possible organic matter recycling (Sousa et al., 2012). Due to the great contribution of anadromous sea lamprey to Atlantic coast stream ecology and production of fish species important to fisheries, such as Atlantic salmon, *Salmo salar* (Nislow and Kynard, 2009; (Saunders et al., 2006)), all coastal states (USA) and provinces (Canada) with native anadromous sea lamprey are encouraged to implement restoration programs that benefit sea lamprey (Almeida et al., 2021). Potential consequences of changes in distribution and decreasing intensity of spawning events in rivers might lead to significant modifications of the riverbed sediment size and recycling of fine organic matter, and ecosystem productivity as a whole, with possible reverberating effects on other organisms from benthic organisms to valuable fish species.

Increasing temperatures, shifts in hydrologic regime and habitat disturbance caused by extreme events may make habitats currently occupied by lampreys uninhabitable and the ecosystem services they provide unavailable (Hughes, 2000; Wang et al., 2020).

Human communities

The impact of declining or shifting lamprey populations on humans has already been measured in some cases. Lampreys are important in human diet and culture and have been for centuries, and millennia (Almeida et al., 2002; Close et al., 2002; (Columbia River Inter-Tribal Fish Commission, 2011); (Peterson Lewis, 2009)). Since ancient times, lampreys have been considered as a gastronomic delicacy in Europe and Japan, encouraging the development of commercial fisheries for these species (Almeida et al., 2002; Docker, 2015). European river lamprey fisheries are now concentrated in the northern and eastern part of the Baltic Sea and are considered an important source of income for many fishermen in Sweden and Finland. Sea lamprey is a commercially important species in Spain and Portugal (e.g., Abersons and Birzaks, 2014; Almeida et al., 2002; Araujo et al., 2016; ICES, 2015). Gastronomy festivals and lamprey brotherhood meetings are still taking place annually in various places of Europe (e.g., Sainte-Terre in the south-west of France, Penacova in Portugal). Traditional recipes are passed down between generations such as ''lamproie à la bordelaise" in France where lampreys are cooked in red wine or ''lampreia de ovos", a lamprey-shaped cake in Portugal. The severe habitat degradation in Portugal, magnified by warming temperatures and intense fishing pressure, along with the shift in range northward of sea lamprey has already impacted the harvest of sea lamprey in Portugal making the lamprey meal more of a special occasion instead of a family meal as it once was (Pedro Almeida, University of Évora, personal communication). A three year research project started in 2019 is assessing how western European diadromous fishes are enhancing ecosystem services (Interreg Atlantic Area DiadES; http://www.diades.eu/). Both sea and European river lamprey are included in this initiative that will lead to the first comprehensive monetary valuation of ecosystem services provided by lampreys in this region of the world and how these services might change in a near future due to climate change.

Arctic lamprey has been an important fishery and diet staple to local communities in Japan (Arakawa et al., 2021)). The northward shift in their southern limit distribution by six degrees in latitude has had a significant influence on the fishing community and culture. In Alaska, USA, in the Yukon River Basin, Arctic lamprey are a major commercial fishery for the Yup'ik people via the Kwik'pak Fishery. The Yukon River Basin has experienced rapid rates of warming in the last three decades (Hinzman et al., 2005; (Toohey et al., 2016)). A result of the rapid warming has been the thawing of permafrost layers beneath the Yukon which is contributing to geochemical and flowpath changes which could have significant impacts to aquatic ecosystems in the Yukon River Basin (Toohey et al., 2016).

In Western North America, Native American tribes have depended on Pacific lamprey for food, medicine and traditional purposes for millennia (Close et al., 2002; CRITFC, 2011; Peterson Lewis, 2009). Elmer Crow, Jr., a Nez Perce tribal elder once said, "The lamprey is our elder, without him the circle of life is broken." Ron Suppah, an elder of the Confederated Tribes of the Warm Springs has stated, ''The Creator told the people that the eels [Native American tribes often refer to lampreys as eels] would always return as long as the people took care of them, but if the people failed to take care of them, they would disappear." These are just two of the many examples that directly illustrate the importance of Pacific lamprey for Native American cultures. Declines in Pacific lamprey have occurred due to a variety of threats (ODFW, 2020; USFWS, 2019), and climate change induced impacts to water temperature and stream flow is a primary threat identified by the Columbia Plateau member tribes and coastal Oregon tribes, to the persistence of Pacific lamprey (CRITFC, 2011; Wang et al., 2020).

Vulnerability of lampreys to climate change

Due to the identification of climate change as a primary threat to Pacific lamprey populations, Columbia Plateau and Coastal Oregon (USA) tribes along with federal agencies conducted climate change vulnerability assessments for Pacific lamprey (Sharma et al., 2016; Wang et al., 2020). One assessment categorized the vulnerability of Pacific lamprey occupying 15 rivers in the western USA using downscaled projected changes to stream temperature and hydrologic regime for two time periods (mid-century 2040–2069 and end-century 2070–2099) under Representative Concentration Pathways (RCP) 4.5 and 8.5 (Wang et al., 2020). The vulnerability generally increased in all basins when going from RCP 4.5 to RCP 8.5 for three Global Circulation Models from mid- to end-century. Additionally, the vulnerability increased in basins that are highly altered or under significant stress from other threats.

The Columbia River Inter-Tribal Fish Commission conducted a climate change study investigating freshwater and ocean effects on Pacific lamprey within the Columbia River Basin (Sharma et al., 2016). The study concluded that Pacific lamprey will be adversely affected under climate change projections by poor ocean conditions impacting growth; higher peak flows during winter months causing scouring and premature movement; seasonal flows and warmer tributary water temperatures will affect spawning and rearing habitat availability and limit upstream migration to areas already limited by passage impediments.

Moyle et al. (2013) conducted a climate change vulnerability assessment of 121 native and 43 invasive fish species to California, USA, including seven species of native lampreys. The authors compared the baseline risk of extirpation to the risk of extirpation with climate change at the species and family taxonomic levels. The assessment found that by family (Petromyzontidae), under baseline conditions, four species of lamprey were highly vulnerable to extirpation and three species were less vulnerable. Under climate change conditions, two species were categorized as critically vulnerable and five species were highly vulnerable to extirpation. They concluded that predicted climate change impacts on freshwater habitats will drastically change the fish communities in California because no native fishes will benefit from climate change and native anadromous fishes are at particularly high risk to extirpation from the predicted climate change (Moyle et al., 2013).

A primary factor in determining the vulnerability of lamprey species to climate change is the degree to which their habitats are altered. Climate vulnerability assessments for lampreys found increased vulnerability for lampreys and their habitats in rivers which are highly affected by anthropogenic impacts such as dams and other passage impediments and stream and floodplain degradation (Sharma et al., 2016; Wang et al., 2020). While uncertainty exists around how climate change impacts such as changing temperatures and shifting hydrologic regimes will specifically impact lampreys and their communities, the assessments show that those impacts will likely be magnified on altered river systems. These assessments suggest restoring passage and habitat degradation now might lessen the impact of climate change impacts into the future.

Resiliency of lampreys to climate change

It seems certain that climate change, and associated impacts to water temperature and flow, will influence lampreys. Although the examples were not intended to be comprehensive, the preceding discussion supports the likelihood that climate change will affect the physiology and phenology of lampreys as well as their distribution and contributions to communities and ecosystems. However, lampreys have existed for hundreds of millions of years (Gess et al., 2006; Xu et al., 2016) and within that time period, there is evidence that lampreys likely experienced global temperature increases in the range of 5–8 °C (McInerney and Wing, 2011). This would have been similar, at least in some regards, to current climate change projections. Numerous examples of how lampreys did or may cope with, or be resilient to, changes in temperature and flow were discussed previously. Several characteristics may be particularly important to illustrate the potential for resiliency. For the larvae of many species (often the lengthiest developmental stage), the Ultimate Upper Incipient Lethal Temperature appears to be in the range of 28–31 °C (e.g., Arakawa and Yanai, 2021) and the Critical Thermal Maximum often exceeds 31 °C in laboratory setting (e.g., Potter and Beamish, 1975). These values appear to be fairly consistent, and possibly conserved, across species. These values are also well above most of the maximum temperatures that are predicted to result from climate change (see previous discussion). Thus, predicted changes in water temperature may not exceed lethal or critical limits for lamprey. In addition, studies on Arctic and Pacific lamprey concluded that the habitat in which larvae burrow can be significantly cooler than the adjacent water column, potentially providing a thermal refugia (Hiroaki Arakawa, Ishikawa Prefectural University, personal communication; Ralph Lampman, Yakama Nation Fisheries, personal communication; Paul Sankovich, USFWS, personal communication). Furthermore, observations in the field revealed that lamprey larvae of a nonparasitic brook lamprey (*Lampetra* sp.) survived in the water-saturated sub-surface interstices of an intermittent stream in the absence of surface water for at least 22 days (Rodríguez-Lozano et al., 2019). This behavior previously reported for just a few fish species has potential key implications for the adaptive capacity of lampreys to climate change when considering that the frequency of droughts will very likely increase in a near future.

The impact that climate change will have on lamprey populations is difficult to predict. It is possible that climate change may produce sublethal effects to individuals, such as the impaired burrowing behavior observed in Pacific lamprey (Christina Uh, USFWS, personal communication) or the reduced affinity for oxygen in the blood of pouched lamprey (Macey and Potter, 1982). It is unknown whether these sublethal effects will have significant overall impacts on lamprey populations. It seems clear, however, that there may be effects from climate change that we have not yet anticipated or described (e.g., warmer winter temperatures, reduced food resources, human responses to climate change) that may also have significant impacts on lamprey populations. Furthermore, effects from climate change discussed in this paper may act synergistically to cause severe reductions or extinctions of lamprey species. It may be most important to consider not whether such changes will occur but how soon (see Hughes, 2000).

At the very least, it seems certain that the physiological and phenological responses of any organism, including lampreys, to climate change will be complex and difficult to predict (DeLeo et al., 2019). This is especially true when considering the poor conservation status and declining trend of lampreys in some locations and highly altered nature of river systems globally (e.g., Legrand et al., 2020; USFWS, 2019; Wang et al., 2020). However, when considering their length of time on the planet, evolutionary history, multitude of life history expressions and range of distribution, it is worth considering whether lampreys may be relatively resilient to climate change.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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