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Emerging conservation initiatives for lampreys: Research challenges and opportunities

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ABSTRACT

Lampreys worldwide face multiple anthropogenic stressors. Several species are 'at-risk' listed, yet abundance data for most remain insufficient to adequately assess conservation status. Lamprey population declines are largely due to habitat degradation and fragmentation, pollution, and exploitation. Conservation priorities include: quantification of population trends and distribution; identification of Evolutionarily Significant Units; improved water quality and habitat; barrier removal or effective mitigation; ecologically-sensitive river flow management and hydropower planning; and mitigation of climate change impacts. There is urgent need for ecological and population demographics data for multiple species, particularly those in the Southern Hemisphere, Caspian Sea region, and Mexico. Irrigation and damming are already extensive, or rapidly expanding (e.g. Chile), while water-stressed regions (Mexico, California, Chile, Australia, Iberia) may be further impacted by climate change-induced flow alteration and increased temperatures. Barrier removal should benefit lampreys by increasing available habitat. However, fishways vary in effectiveness and are often inadequate, but present research opportunities encompassing ecohydraulics, biotelemetry and engineering. Environmental DNA permits rapid assessment of lamprey distribution within catchments, especially if improvements to distinguishing genetically similar groups are possible. Marine environments may play a critical role in population dynamics yet remain a "black box" in anadromous lamprey biology. Studying juvenile lamprey ecology is a substantial challenge but should be a priority. Some examples are monitoring of parasitic feeding-phase lamprey through trawl surveys and fisheries bycatch, telemetry of movements, or examining chemical tracers of marine habitat use. Knowledge transfer between the sea lamprey control programme and native-lamprey biologists worldwide remains crucial to developing effective lamprey management.

Introduction

We are in the midst of a conservation crisis for species reliant upon freshwater habitats (Duncan and Lockwood, 2001; WWF, 2018; IPBES, 2019) and over a quarter of lamprey (Petromyzontiformes) species are 'at risk' of disappearing from the wild (Maitland et al., 2015). Given that information on the distribution and population trends of most lamprey species is extremely fragmentary, or

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nearly non-existent (Renaud, 2011; Maitland et al., 2015), the true proportion of lamprey species at risk may be much higher. Lampreys are, to many people, non-charismatic organisms. In recent decades, the public perception and conservation needs of native lampreys have been overshadowed by the need to control invasive sea lamprey (*Petromyzon marinus* L. 1758) in the Laurentian Great Lakes (Marsden and Siefkes, 2019; Neave et al., 2021). The resulting misconception that lampreys, especially parasitic species, are harmful to natural systems has been severe and long-lasting (Lyons et al., 1994; Moser and Close, 2003). There have even been (unsuccessful) attempts to extirpate several populations of native parasitic species due to their predation of desirable yet non-native game fishes (Nuhfer, 1993; Lorion et al., 2000). There have also been unintended consequences, or 'collateral damage', to native lampreys and fishes through Great Lakes sea lamprey control (Marsden and Siefkes, 2019). Nevertheless, the conservation needs of native lampreys are now being increasingly communicated to society in terms of their ancient vertebrate evolutionary history, intriguing life history and ecology, ecological services and cultural importance (Close et al., 2002; Docker et al., 2015; Docker and Hume, 2019). The impacts of invasive predators on native lampreys are also apparent to conservationists, with recent evidence of the predatory impact of non-native wels catfish (*Silurus glanis* L. 1758) on adult sea lamprey in French rivers, in which up to 80% of migrating lamprey were recorded as predated within a month of release (Boulêtreau et al., 2020).

Today, native lampreys frequently offer media storylines under the 'weird nature' tag but provide a valuable alternative to 'cute and cuddly' species tags commonly adopted by the media. For aquatic animals that are often 'out of sight and out of mind', employing native lampreys as 'umbrella species' (Roberge and Angelstam, 2004) is a sensible and viable conservation approach. Native lampreys perform valuable ecosystem functions. They are ecosystem engineers of gravel and fine sediment (Hogg et al., 2014; Shirakawa et al., 2013), are food sources to predators (Close et al., 2002; Cochran, 2009) and adult migratory lampreys provide nutrient subsidies to stream and river habitats (Weaver et al., 2018). Further, populations of native lampreys are impacted by habitat degradation and fragmentation common to most of the world's river systems (Lucas et al., 2009; Maitland et al., 2015; Aronsuu et al., 2019), and several conservation initiatives and actions needed to restore lamprey populations (e.g., barrier removal or mitigation) are likely to benefit ecologically similar species and improve overall aquatic ecosystem health.

Despite great advances in our knowledge of the biology of lampreys during the 1960s to 1980s, exemplified by the multiple volumes edited by Martin Hardisty and Ian Potter (e.g. Hardisty and Potter, 1971), sufficient knowledge to develop effective conservation of lampreys was largely missing at that time. For several lamprey species, some of that information has been gained over the last 30 years, especially in western Europe and North America, and partly in response to conservation legislation frameworks (Maitland et al., 2015). Clemens et al. (2021) review the conservation needs and actions for native anadromous lampreys. The aim of this paper is to forecast challenges and opportunities in lamprey conservation, complementing themes addressed by Clemens et al. (2021), Moser et al. (2021) and Docker and Hume (2019). As such, we emphasize a select group of global issues that we consider important and, where possible, suggest initiatives or methodologies that have the potential to improve lamprey conservation. The reader is also reminded that research needs and conservation priorities have been discussed for lampreys generally (Mesa and Copeland, 2009; Maitland et al., 2015) and in detail for some species such as Pacific lamprey (*Entosphenus tridentatus* Richardson, 1836) (e.g. Clemens et al., 2017).

Lamprey conservation priorities

Lamprey population declines have been reported as being primarily attributable to pollution, habitat degradation, river barriers, and overexploitation (Maitland et al., 2015), although those declines have not always been well quantified because of inconsistent or semi-quantitative recording. The best-known examples of changes in lamprey abundance are for anadromous lamprey species, particularly where exploited by fisheries. Maitland et al. (2015) refer to extirpation of European river lamprey [*Lampetra fluviatilis* (L. 1758)] in the River Thames, England where from the 1700s until the late 1800s hundreds of thousands of individuals were captured each year, mainly for use as bait in the North Sea fishing industry (see Almeida et al., 2021, for a more detailed discussion). Nevertheless, the decline in catches of European river lamprey was primarily attributed to the intense organic pollution and damming of rivers, not exploitation *per se*. Although the Thames is cleaner now than it has been for over a hundred years, European river lamprey have not yet recolonised that river (M. Lucas, pers. obs.). Where multiple factors have contributed to the decline or extirpation of lamprey populations, it can be difficult to know which are the most important problems to solve. But ultimately all are due to anthropogenic activities. The following sections highlight lamprey conservation needs.

Basic biology

Most conservation biologists would argue that a focal species cannot be conserved effectively without a good understanding of its biology, in particular the ecological requirements of all life stages, conditions for reproduction and survival, and causes of population decline. All lamprey species use broadly similar physical habitats for spawning (gravel/cobble bed typically in flowing water [but see Johnson et al., 2015 for discussion of rare lentic spawning in lampreys]) and larval (silt-sand habitat, rich in organic material, in flowing, slow-moving or sometimes lentic water) life stages. Therefore, knowledge of those species we know most about can, arguably, be applied to those we know less about. Our biological knowledge is strongest for species such as sea, European river, European brook [*Lampetra planeri* (Bloch, 1784)], Pacific, silver (*Ichthyomyzon unicuspis* Hubbs & Trautman, 1937), chestnut (*I. castaneus* Girard, 1858), northern brook (*I. fossor* Reighard & Cummins, 1916), Arctic [*Lethenteron camtschaticum* (Tilesius, 1811)] and pouched lampreys (*Geotria australis* Gray, 1851). But even for several of these species, the context of our understanding is limited. For example, pouched lamprey biological knowledge has increased dramatically in the last 30 years, but mostly in cool, stony, New Zealand rivers (Jellyman and Glova, 2002; Jellyman et al., 2002; Kelso and Glova, 1993; Baker et al., 2017), very different habitat and climate to that of pouched lamprey in, for example, the 1,000,000 km^2 Murray-Darling Basin, Australia.

For the remaining Southern Hemisphere species and regional populations (Potter et al., 2015; Renaud, 2011) detailed biological knowledge is limited or absent. The same is true for the *Tetrapleurodon* species pair inhabiting the Mexican highlands (Lyons et al., 1994; Renaud, 2011). Also, large gaps in our understanding of the biology of Caspian lamprey [*Caspiomyzon wagneri* (Kessler, 1870)] are evident in a part of the world where damming and water diversion have dramatically changed the ecosystem (Holčík, 1986; Nazari and Abdoli, 2010; Abdoli et al., 2017) though Nazari et al. (2017) provide a good review of the current conservation status in the southern Caspian region. The biology of many brook lampreys across the *Entosphenus*, *Eudontomyzon*, *Ichthyomyzon*, *Lampetra*, and *Lethenteron* genera are sketchy at best (Renaud, 2011; Docker, 2019, 2015). Hence, a priority for effective conservation of most lamprey species is to fill knowledge gaps. Key knowledge can, in some cases, be gained relatively cheaply using grants from zoological, ichthyological, or geographical society support.

Better quantification of lamprey population trends and distribution

Measuring trends in abundance and distribution is crucial to conservation and management of populations, whether they are invasive Great Lakes sea lamprey or native species targeted for conservation. Much research resource has been put in to improving abundance estimates of Great Lakes sea lamprey (Christie and Goddard, 2003; Harper et al., 2018) for control purposes. For conservation of native lamprey species and populations, data of improved quality are needed for quantifying population changes (Moser et al., 2007). This requires long-term monitoring by standardised methods that are feasible to employ, in terms of cost and logistics, but as unbiased as possible. Yet these methods can be difficult to achieve. Historic data on the distribution and abundance of lampreys often rely on records of fishery catches, frequently without details of the fishery effort or location (Almeida et al., 2021) yet those fisheries may cease for reasons not linked to lamprey abundance, or fishing methods may change. One of the more prominent historical data sets underpinning a large-scale lamprey conservation initiative is derived from counts of adult Pacific lamprey passing observation windows at several dams in the Columbia River, U.S.A. (CRITFC, 2011). These data suggest high variability in population size, and a decline in adult abundance exceeding 50% over the period from the 1940s to the 2000s (Fig. 1), but these data are incomplete and potentially misleading (Moser and Close, 2003). Problems with these data include: major gaps in the timeline; recordings do not cover the entire migration period; counts taken during daylight for a mostly nocturnal life stage; passage counted at only one of several passage routes at each dam; and management and infrastructure changes that may have altered lamprey behaviour at recording sites.

For poorly researched species such as Chilean [*Mordacia lapicida* (Gray, 1851)], Mexican brook (*Tetrapleurodon geminis* Álvarez, 1964), and Alaskan brook lampreys (*Lethenteron alaskense* Vladykov & Kott, 1978), almost no population trend data nor contemporary status data exist, making it impossible to develop directed conservation plans. Even though Mexican brook lamprey and Mexican lamprey (*T. spadiceus*) are listed as Endangered and Critically Endangered respectively by the International Union for Nature Conservation (IUCN, 2019), the most recent surveys are over two decades old (Lyons et al., 1994), and no conservation plan has been generated (Daniels, 2019; Snoeks et al., 2019). Even for well-studied species, such as European river lamprey, the quality of some abundance data is dubious. The International Union for the Conservation of Nature (IUCN) listed European river lamprey as Least Concern, purportedly due to substantial recovery following pollution abatement in Central and Western Europe (Freyhof, 2011). Yet those data sources are not provided and are likely to be subject to the data quality problems highlighted above. In recent decades European river lamprey catches and probable population sizes have demonstrably fallen in areas of Sweden and Finland (Sjöberg, 2011; Aronsuu et al., 2019), Latvia (Birzaks and Abersons, 2011; Almeida et al., 2021) and in Poland (Kujawa et al., 2018).

Because of the difficulties in reliably catching or counting adult or post-metamorphic juvenile lampreys, especially where no fisheries or lamprey counting facilities occur, most abundance assessment schemes for lampreys rely on larval sampling (Moser et al., 2007). But in many cases larvae of closely-related species inhabit the same streams and cannot be distinguished before metamorphosis, either morphologically or genetically (Renaud, 2011; Potter et al., 2015; Docker and Hume, 2019). This is especially the case for so-called paired species (typically comprising a parasitic species and a closely related non-parasitic species) such as *Lampetra fluviatilis* and *L. planeri*, and *Tetrapleurodon spadiceus* and *T. geminis*. Genetic methods have facilitated quick identification of co-occurring larvae of some different taxa with wide distributional ranges (Docker et al., 2016). In other cases (Bracken et al., 2015) genome level DNA sequence data or consistently different single nucleotide polymorphisms must be used (Mateus et al., 2013b) [see Environmental DNA section below]. Lamprey larvae are also notoriously patchy in distribution (Torgersen and Close, 2004) making larval sampling (usually by electric-fishing in shallow habitats, but see Taverny et al., 2012) a poor choice for estimating population trends unless rigorous, large-scale, stratified sampling is carried out (Ferreira et al., 2013). However, research and development of new technologies such as eDNA, pheromone detection, genetic parentage analysis, and the ability to sample deep-water habitats all represent a significant opportunity to improve our knowledge of lamprey population trends and distribution (Docker and Hume, 2019).

To understand how lamprey population size may be affected by stochastic events (e.g. floods or droughts), conservation actions (e.g. habitat improvement, fishery restrictions), or an absence of rehabilitation measures, we need to develop recruitment models. These are available for Great Lakes sea lamprey (Jones, 2007) and could be extended to native species, but the complexities of reliable ageing and the plasticity in larval duration (Dawson et al., 2015), as well as difficulties in obtaining sound demographic input data are a challenge. Instead, most ecologists working on native lampreys have relied upon fragmented empirical data using multiple methods to best-guess recruitment patterns. Resources, funding in particular, are always a constraint for undertaking good-quality population and distribution assessments. However, greater effort is needed, nationally and internationally, to establish the current population and distribution status of over 70% of the lamprey species listed in Potter et al. (2015) that we regard as lacking robust, up-to-date data. Maitland et al. (2015) gave IUCN red-book listings for 25/41 (61%) of species and reported 'Data-deficient' for three species, Vancouver lamprey (*Entosphenus macrostomus*), Alaskan brook lamprey and Chilean lamprey. The IUCN (2019) red list gives population trend summaries for just 12/41 (29%) of the species listed in Potter et al. (2015), the most recent review of lamprey taxonomy and distribution.

Identification of evolutionarily significant units

Conservation is the act of preserving or protecting something of inherent value. In conservation biology this value is represented by a species' genetic legacy (its past) and its evolutionary potential (its future). From a utilitarian perspective it can be argued that species have socio-economic value; thus losing biodiversity can be harmful economically and ecologically (Edwards and Abivardi, 1998). In conservation biology, the goal is to protect a species; but in reality we manage only a portion of all populations that comprise that species. Given that conservation resources are limiting, how should we select those populations? The designation of Evolutionarily Significant Units (ESUs) or Designatable Units (DUs) is one promising approach to lamprey conservation because it can provide a framework for conserving diversity below the species level (Cassaci et al., 2014; Docker and Hume, 2019). Typically, ESUs are designated based on one, or some combination of two or more, of the following criteria:

- current geographic separation;

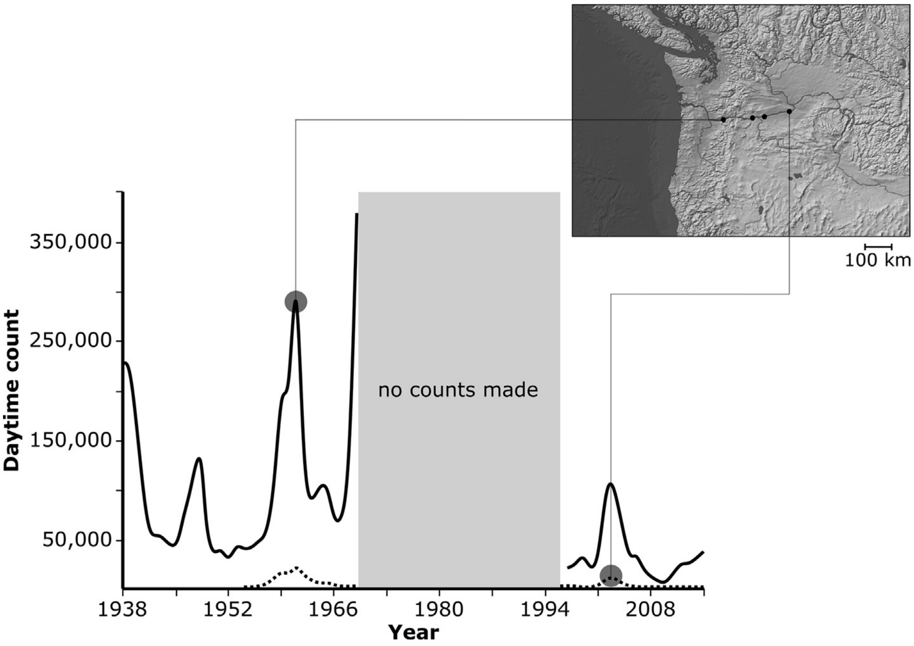

Fig. 1. Historical daytime observation window counts of Pacific lamprey at Bonneville Dam (black line) and McNary Dam (dashed line), separated by The Dalles and John Day dams on the Columbia River, Oregon and Washington. Limitations of interpreting trends of lamprey abundance from such data, including periods during which no data were collected, are outlined in the text.

- genetic differentiation at neutral markers caused by historic gene flow patterns;
- local adaptation of phenotypes.

Identification of an ESU therefore requires knowledge of an organism's evolutionary history (molecular genetics) and ecology. This necessitates input from a range of biological sub-disciplines and ensures that determinations are made only following acquisition of multiple lines of evidence. Candidate ESUs or DUs could be evaluated along two axes of diversity, molecular genetic and adaptive (de Guia and Saitoh, 2007). This can be achieved by analysis of neutral markers (reflecting historic isolation and gene flow), geographic distribution, life history, and phenotypic and genotypic data (reflecting current adaptation). Nevertheless, the goal is not to simply identify more conservation units, but to employ an objective process to evaluate across species and identify which units are the highest priority. In the U.S.A the Endangered Species Act of 1973 requires explicit designations of "distinct population segments" (=ESUs) to be protected by the law, but no lampreys are currently on that list. In Canada the Species At Risk Act currently recognizes several lamprey DUs; the western brook lamprey (*Lampetra richardsoni* Vladykov & Follett, 1965) of Morrison Creek, Vancouver lamprey throughout its range, and silver and northern brook lampreys in the Great Lakes-St. Lawrence (COSEWIC, 2010; Maitland et al., 2015; Docker and Hume, 2019). Similarly, in Europe currently only one lamprey ESU is recognized, a lake-feeding population of European river lamprey from the Endrick Water, Scotland (JNCC, 2017). In Portugal, four *L. planeri* ESUs and one *L. fluviatilis* ESU were proposed by Mateus et al. (2011), but three of these populations were subsequently described as separate species (Mateus et al., 2013a). Therefore, the precedent for application of ESUs already exists and could be readily extended to lampreys worldwide.

An example of the utility of ESUs in lamprey conservation is provided by the European river lamprey, a widely dispersed anadromous parasitic species, currently listed as Least Concern by the IUCN (Maitland et al., 2015). This species exhibits extensive genetic, phenotypic, and life history diversity. Based on neutral genetic markers, there were 1–2 post-glacial range expansions into northern Europe 8–12,000 years ago which can generally be considered to represent the species' "typical" form (=*L. fluviatilis* "sensu stricto", Mateus et al., 2016). After the northward range expansion, refuge populations in the Iberian Peninsula experienced reduced gene flow and are now genetically distinct from northern populations (Mateus et al., 2013a, b, 2011; Pereira et al., 2011, 2014, 2010). Similar to salmonids, some European river lamprey populations express diversity in terms of migration timing with discrete spring- and fall-runs (e.g., Witkowski and Kuszewski, 1995), and others have evolved novel trophic strategies such as feeding within large post-glacial lakes (Collett, 1905; Morris, 1989; Inger et al., 2010; Tsimbalov et al., 2015) or truncated periods of feeding in marine habitats (=*L. fluviatilis* "praecox", Berg, 1948; Abou-Seedo and Potter, 1979; Hume, 2013). Coincident with their expansion into de-glaciated regions, many *L. fluviatilis* populations abandoned parasitic feeding altogether and are currently recognized by some as *L. planeri*, the European brook lamprey. Pairs of European river and brook lampreys appear to be at different stages of the speciation process, with some populations exhibiting incomplete reproductive isolation and ongoing gene flow (Docker and Potter, 2019). Where genetic differences are evolutionarily significant, some populations of European river and brook lampreys could be recognized as ESUs or DUs.

European river lamprey is not unique in this regard (Docker and Potter, 2019). Worldwide, many lamprey populations will have a unique genetic legacy and evolutionary potential, and present as non-interchangeable ESUs. The vast majority of these unique populations are, in practice, unrecognized and unprotected by conservation legislation. Going forward, continuing to recognize lamprey diversity below the species level and expanding the approach will greatly benefit lamprey conservation. Docker and Hume (2019) recently called for a new, integrated taxonomic framework for lampreys, one that combines morphology and behavioral ecology as well as population genetic and molecular phylogenetic approaches. By collecting data such as these we may better recognize and systematically identify lamprey ESUs.

Water quality and habitat restoration

Lampreys are often thought to be moderately resilient to water quality insults although severe organic pollution caused, in part, the demise of lampreys, especially migratory stocks, in many industrialized European rivers (Maitland et al., 2015). Moreover, the egg and pro-larval development stage may be more sensitive than larval, juvenile (post-metamorphic but sexually immature) and adult (sexually mature) stages, as evidenced by reduced hatching success in environments with lower oxygen supply (Silva et al., 2015) and instances of recruitment failure at polluted sites (Dawson et al., 2015; Silva et al., b, 2016a). In the lowermost sections of many rivers entering the Finnish side of the Bothnian Bay, low larval densities are associated with poor water quality, especially low pH and high metal concentrations due to leaching from ditched acid sulphate soils. It has been shown that low pH and high metal concentrations increase mortality of eggs and newly hatched larvae (Myllynen et al., 1997) and impair the quality of eggs during the wintering period of adults (Mäenpää et al., 2001). Nevertheless, the effect of poor water quality on population levels is understudied and needs more attention.

Although slight organic enrichment may favour larval lamprey populations (Dawson et al., 2015; Maitland et al., 2015), when this enrichment is moderate to high, lamprey abundance decreases (Maitland et al., 2015; Silva et al., 2016a). Lamprey population recovery from chemical pollution can be difficult even after the pollution stops, probably due to the persistence of pollutants in the sediment (Silva et al., 2016b). A chemical spill in the River Umia, Spain, in 2006 caused extirpation of the larval lamprey population in the affected section (Silva et al., 2016b). Larvae were available to recolonize the polluted section from upstream and downstream, but low larval densities persisted in the polluted zone for 4 years (Silva, 2014).

River regulation measures like dredging, channelization and embankment, degrade lamprey habitats (Streif, 2019; Maitland et al., 2015) and may also intensify the negative effects of other human activities such as hydropeaking. Therefore, habitat restoration is required to re-establish lamprey populations, especially in the regulated rivers. Several river restoration methods in northern latitudes inhabited by lampreys aim to restore habitats for salmonids (Silva et al., 2015; Moser et al., 2021). These restoration efforts increase heterogeneity of habitats within rivers, but important habitats for lamprey and other lotic biota are often ignored. For example, spawning gravels added into rivers in northern Europe and North America are often intended for salmonids and may be suboptimal for several lamprey species (e.g. European river lamprey, silver lamprey), as the gravel size may be too big and/or the finest fractions of gravel and sand have been removed by sieving before adding the gravel into the river (Smith and Marsden, 2009; Aronsuu and Tertsunen, 2015). In a Finnish river, lamprey-tailored methods of restoring fast-flowing areas increased larval densities in nearby reaches (Aronsuu et al., 2019). This was assumed to be mostly due to an increase in wintering and spawning habitats of mature lampreys. However, the effects of restoration of fast-flowing areas on lamprey populations are still speculative and more research is needed. In channelized rivers, larval habitats in slow-flowing areas are often deteriorated in condition, but restoration measures are mainly directed to fast-flowing areas. There have been attempts to restore depositional areas suitable for larval habitats in Finland, but results have not been very promising (Aronsuu et al., 2019).

Removal or effective mitigation of migration barriers

Barrier removal in rivers has accelerated rapidly in North America, and now Europe, over recent years, with the realisation that removal of redundant dams can re-institute natural hydrological, geomorphological, and ecological processes that are critical to the functioning of rivers (Poff and Hart, 2002; Birnie-Gauvin et al., 2017). This issue is contentious in the Great Lakes where barriers are a key method for restricting the distribution of non-native sea lamprey (Docker and Hume, 2019), but selective fish passage has become a research priority for the Great Lakes Fishery Commission in recent years and a dedicated research facility to test this approach is being constructed on the Boardman River, Michigan, U.S.A. (Marsden and Siefkes, 2019). Outside the Great Lakes region, barrier removal is a high priority conservation action to stimulate recovery of lamprey populations, especially migratory ones (Docker and Hume, 2019). Where dams have been removed, rapid upstream colonisation and increased abundance have been observed for native sea lamprey (Hogg et al., 2013; Lasne et al., 2014; Kynard and Horgan, 2019) and for Pacific lamprey (Moser and Paradis, 2017).

Worldwide, mitigation of barriers to fish movement, through incorporation or retrofitting of fishways, has increased markedly since the mid-20th Century (Silva et al., 2018). Concurrently, in many regions, there has been a shift from fishways that are designed predominantly for a few taxa such as salmonids (Clay, 1995) to those that cater for broader fish communities (Silva et al., 2018). Specific consideration of lamprey passage, however, is still in its infancy. Technical fishway designs may be inefficient at facilitating lamprey passage (Foulds and Lucas, 2013), and specific solutions for lamprey have been explored (Moser et al., 2011). Assessment of fishway effectiveness and the development of lamprey-specific fishway solutions have focused predominantly on Northern Hemisphere lamprey species, particularly Pacific, sea and European river lamprey (Goodman and Reid, 2017; Castro-Santos et al., 2017; Tummers et al., 2018). In contrast, research into the mitigation of migration barriers for other lamprey species, including pouched and short-headed lampreys [*Mordacia mordax* (Richardson, 1846)] in the Southern Hemisphere, has been lacking.

Since the 1920s, the River Murray in south-eastern Australia, has been regulated by tidal barrages adjacent to the river mouth, a series of 14 main channel weirs and two large headwater dams. Since 2000, a variety of fishways (e.g. vertical slot, Denil, fish-locks) have been incorporated into all mainstem migration barriers in the system, potentially facilitating fish passage along 2000 km of the river (Barrett and Mallen-Cooper, 2006). Pouched and short-headed lampreys are native to the River Murray; and whilst quantitative historical data on the abundance of these species is scant, lamprey were considered common in the system prior to river regulation (Potter and Strahan, 1968). However, after construction of barrages and weirs, the species have been seldom encountered.

Post construction of fishways at the River Murray tidal barrages, pouched and short-headed lamprey have become more prevalent (Bice et al., 2018). Using passive integrated transponder (PIT) tags and readers located in all mainstem fishways, it has recently been established that pouched lamprey are effectively utilising sequential vertical slot fishways and migrating large distances (>800 km) upstream in the River Murray, with migration rates of up to 40 km day^{-1} (Fig. 2; Bice et al., 2019). Small numbers (tens) of short-headed lamprey are now also passing through the tidal barrage fishways and have been detected as far as 400 km upstream (B. Zampatti, unpubl. data).

Restoration of migratory lampreys in catchments with depleted or extirpated populations

Although provision of longitudinal connectivity within river catchments is fundamental to achieving recovery of migratory lamprey populations (Docker and Hume, 2019; Moser et al., 2021), if migratory lampreys have been lost from a catchment,

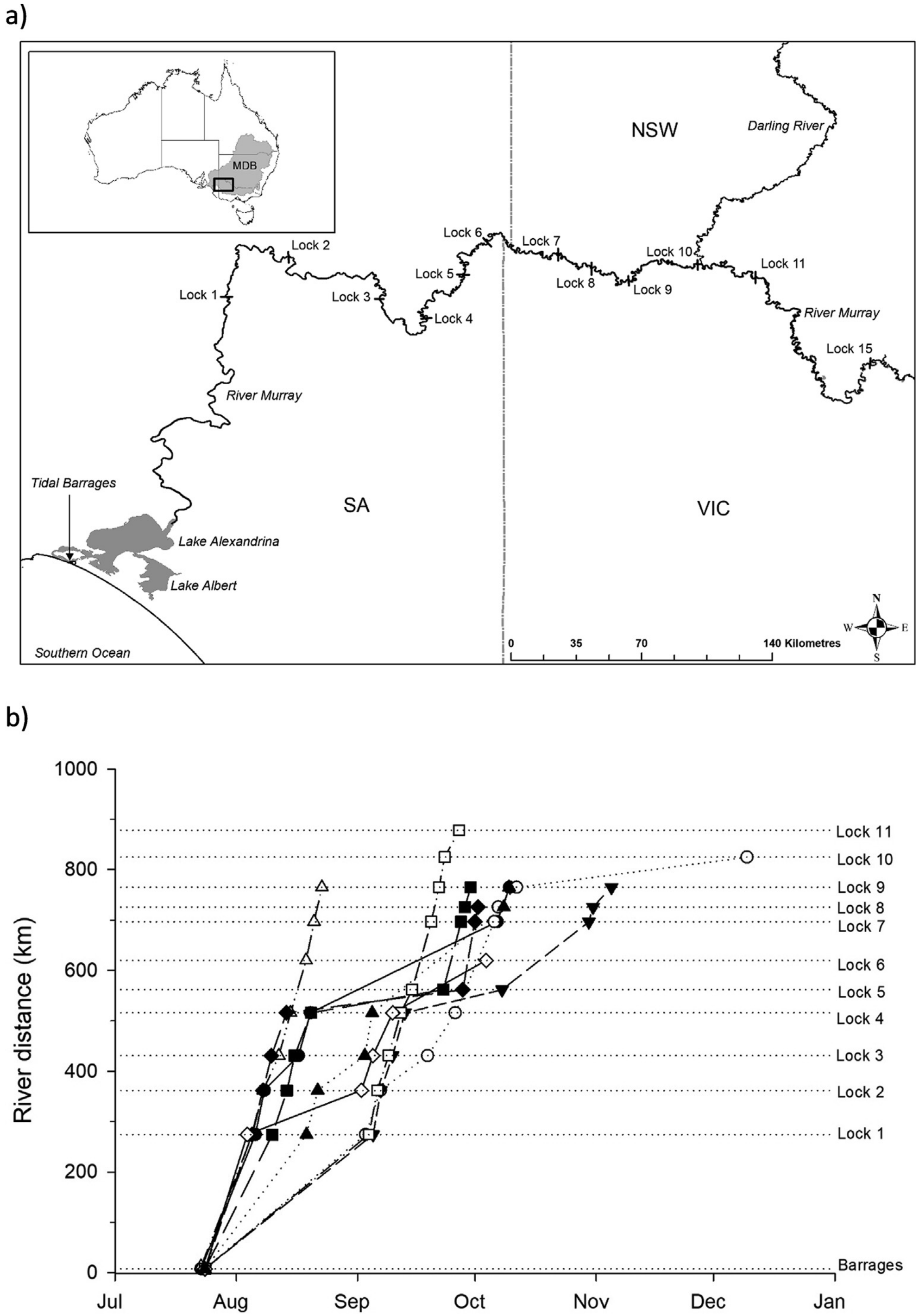

Fig. 2. Migration of pouched lamprey in the Murray-Darling Basin, Australia showing the location of tagging at the tidal barrages (a), the distribution of weirs and locks in the lower river (a) at which PIT-tagged lamprey were detected in fishways, and the rate of upstream progress by several tagged lamprey (b).

restoration relies upon natural or supported recolonization. In a review of the recolonization capacity by anadromous fishes, Pess et al. (2014) predicted that sea lamprey are quick to extend their range into suitable habitat upstream of dam(s) removed within a river they already occupy, but slow to colonise unoccupied neighbouring rivers. Their conceptual model for lamprey is based on the knowledge that, unlike salmon, sea lamprey do not home to natal streams (Bergstedt and Seelye, 1995; Waldman et al., 2008). Instead, adult sea lamprey enter rivers with larval odour (Sorensen et al., 2005; Moser et al., 2015a), and penetrate upstream into unoccupied reaches, making colonisation of uninhabited catchments a slow process. The effect of larval odour from non-migratory brook lampreys on recolonization by parasitic, migratory lampreys (e.g. sea lamprey) has not been adequately addressed in Pess et al.'s model, but has potential relevance to lamprey population restoration (Gaudron and Lucas, 2006; Hansen et al., 2016), as well as to pest sea lamprey control. Although the idea of releasing synthetic larval and/or sex pheromone has been suggested for lamprey conservation purposes (Hansen et al., 2016), it has not yet been attempted. Costs of doing so would be considerable and, to date, synthetic sea lamprey larval pheromone appears to be incomplete in composition, because upstream movement for Great Lakes sea lamprey in river habitats has not been demonstrated (Siefkes, 2017). Translocation of Pacific lamprey to subcatchments with depleted lamprey numbers has the potential to generate positive feedback to support natural repopulation through pheromone-based attraction, and seems promising but needs to be tested more thoroughly (Ward et al., 2012; CRITFC, 2018). However, lamprey migrating into or translocated to subcatchments with degraded habitat may be metapopulation sinks (Lucas et al., 2009; M. Moser, pers. comm.). The same is true of lamprey rearing and stocking if survival is poor and genotypes are not fitted to the local environment (Aronsuu et al., 2019).

Anadromous sea lamprey have an extraordinary capacity to recolonise river reaches that were historically used by the species, but which were unavailable for decades due to damming. Re-establishing river continuity either by barrier removal, or mitigation by the provision of an effective fishway has proven to be a good solution, at least in river basins where a residual population remained downstream from the first unpassable barrier (Pereira et al., 2019; Moser et al., 2021). This "pioneer" behaviour must have been very useful when lamprey encountered a natural barrier (e.g. small waterfalls) that were insurmountable in dry years, but occasionally became submerged during large floods, allowing lamprey to colonize productive upstream reaches. This is known in the southern Iberian Peninsula, where rivers have variable discharge regimes, as for the River Guadiana, where the Pulo do Lobo falls prevented upstream migration of anadromous fish in many years yet sea lamprey historically occurred upstream of the falls, hundreds of kilometres from the river mouth (Mateus et al., 2012). Intermittently flowing rivers are not high-quality environments for lampreys, and this is probably why such rivers on the southwest Iberian coast (i.e., Alentejo) and in the Algarve (except for the Guadiana, which is permanently flowing), both in Portugal, do not have lampreys (Mateus et al., 2012). Because all lamprey species are semelparous, for anadromous populations choice of river basin for spawning has extreme fitness consequences, because once maturing anadromous lamprey adopt freshwater osmoregulation, it appears this cannot be reversed (Ferreira-Martins et al., 2016). So there is no turning back to sea, to seek an alternative river basin. Attraction to larval odour plumes whilst still in coastal waters (Moser et al., 2015a) could explain why there are some gaps in sea lamprey distribution in Portugal (between rivers Tagus and Guadiana) and support Pess et al.'s (2014) hypothesis (see above) and the findings of Massiot-Granier et al. (2018), regarding lamprey colonization patterns.

Ecologically sensitive river flow management and hydropower planning

Damming, including for hydropower dams, has had dramatic impacts on migratory lamprey abundance (Maitland et al., 2015; Clemens et al., 2017). The magnitude of emerging hydropower developments in regions like Chile also threatens the sustainability of the riverine landscapes and the conservation of diadromous species (Habit et al., 2019). Fragmentation of river networks by one or multiple barriers, and the imposition of new hydrological regimes will impact lampreys. In Chile the exploitable hydropower potential is estimated at 11 GW, spread across about 1500 sites, mainly located in central Chile (Chilean Ministry of Energy, 2016). The projected 6.8-fold increase in barriers to fish movement will increase the already highly fragmented nature of rivers in central Chile (Díaz et al., 2019, Fig. 3).

Even though Chilean dam projects undergo an environmental impact assessment, none have been built yet with fishways. As a result, migratory species like pouched lamprey and diadromous populations of the native galaxiid [*Galaxias maculatus* (Jenyns, 1842)] have significantly reduced their distribution ranges in Chile (Habit et al., 2010). Both species are either absent or in very low abundance in highly fragmented river networks from central Chile (Díaz, 2019), where they were previously present and abundant (Neira, 1984; Dyer, 2000; Habit et al., 2006). It is estimated that the distribution range of pouched lamprey has been reduced by at least 380 km from North to South in Chile (Reyes et al., 2017). In rivers like the Biobío, the river with the highest species richness of aquatic vertebrates in Chile, pouched lamprey remains present only in lower tributaries of the Coastal mountain range. It was extirpated from the upper Biobío ("Alto Biobío") following construction of three large dams in the main river (Pangue in 1996; Ralco in 2002 and Angostura in 2014). These dams have blocked the migratory routes of pouched lamprey to several tributaries of the upper catchment where it was historically abundant (Campos et al., 1993). Although some local Chilean people might support fishways to benefit salmonids, given that non-native salmonid fisheries support tourism there, to do so would also encourage the spread of non-native fishes; the cost-benefit is, as yet, unclear.

Much less information is available for Chilean lamprey, endemic to Chile. Currently there are few reports of this lamprey, and its biology is still largely unknown. It was frequently reported for the Andalién River, a small basin of the coastal mountain range located in Central Chile (Ruiz, 1993; Habit and Victoriano, 2005), which has been increasingly channelized since 2007 (Ortiz-Sandoval et al., 2009). There are no new records of Chilean lamprey in that river since 2007.

In dryland rivers, including in the Iberian Peninsula, Australia and California, river regulation can severely alter the magnitude and temporal patterns of natural flow regimes (Kingsford, 2006). Better implementation of ecological flows is needed but can be difficult to achieve in these water-scare regions. For example, in Australia's Murray-Darling Basin (MDB), flow storage and abstraction have reduced total end-of-system discharge by ~65%, and in conjunction with rainfall drought, the Basin may now cease flowing to the sea for years at a time (Walker, 2006; Zampatti et al., 2010). In its natural state, the River Murray was perennial, with persistent end-of-system discharge (Mallen-Cooper and Zampatti, 2018). Post-regulation, it has been common for the tidal barrages to be closed, and for freshwater flow to the estuary/sea to cease through autumn and winter, the latter being a key period for the upstream migration of pouched lamprey. It is likely that this practice, along with the physical impediments of regulating structures, has contributed to the decline of lamprey in the MDB.

In recognition of these impacts, the movement and recruitment of diadromous fishes now form specific objectives under environmental watering strategies in the MDB (Murray-Darling Basin Authority, 2014). As such, since 2015, specific allocations of environmental water have been provided to facilitate the year-round discharge of fresh water through the tidal barrages, including fishways, to facilitate the spawning and juvenile migrations of catadromous and anadromous species (Bice et al., 2018). This improved hydrological and physical connectivity aims to rehabilitate the spatial distribution and abundance of lamprey in the MDB (Murray-Darling Basin Authority, 2014).

Climate change

Understanding how climate change can impact lamprey species is imperative to their conservation. Temperatures on earth have increased over the last three decades, precipitation patterns are changing and snow and ice are melting, affecting hydrologic systems worldwide (IPCC, 2014). How lamprey species react and potentially adapt to a changing climate is dependent on their life history strategies, native range and vulnerability to rising temperatures and changing hydrologic regimes. Thermal tolerance of lampreys is quite well known for some species and life stages (Dawson et al., 2015;

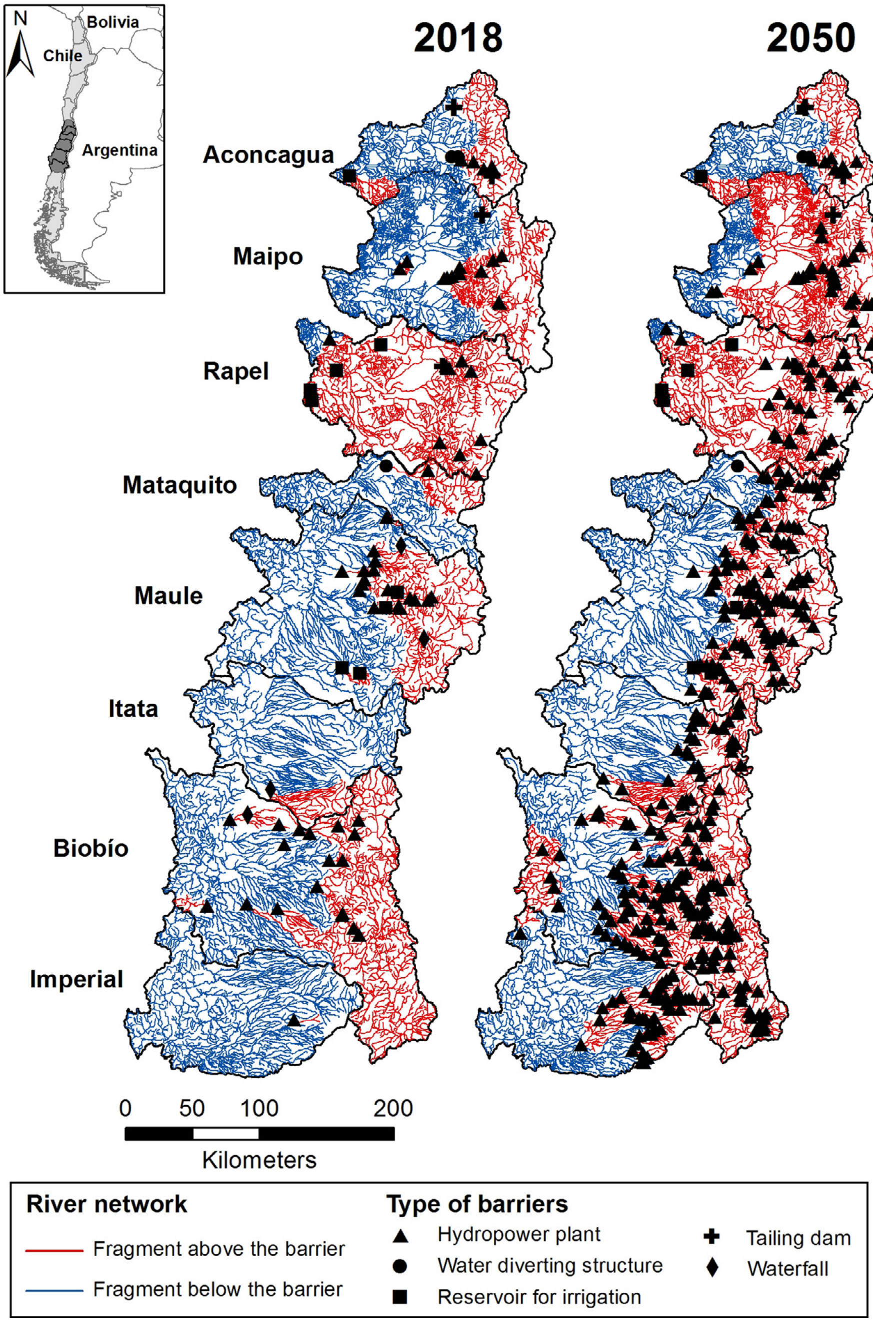

Fig. 3. Current (2018) and future (2050) fragmentation scenarios in river basins of central Chile in relation to planned water infrastructure development. Fragmentation will reduce river connectivity for migratory fish species including lampreys, especially in the Aconcagua, Maipel and Rapel, and alter hydrological conditions, impacting fluvial habitats for native species.

Lennox et al., 2020). Due to the importance of soft-sediment habitat and gravel for larval and adult spawner life stages respectively, changes in the availability and distribution of appropriate sediment size fractions resulting from altered catchment hydrology and hydrogeomorphology could be important in determining lamprey population responses (Lennox et al., 2020). Hughes (2000) proposed that climate change could have major impacts on species and the communities to which they belong. The IPCC (2014) reported that many freshwater and marine species have already shifted their ranges and migration patterns, seasonal activities and species interactions in response to ongoing climate change.

Increasing temperatures are impacting physiological processes in lampreys, for example, the survival rate of Pacific lamprey embryos (Meeuwig et al., 2005) and growth rates of Arctic lamprey larvae (Arakawa, 2018) decrease when temperatures rise. Phenological changes resulting from increasing temperatures, changes in precipitation patterns and shifts in the hydrograph are impacting lamprey species worldwide (McCann et al., 2018). Record setting high temperatures induced early spawning in American brook lamprey [*Lethenteron appendix* (DeKay, 1842)] (Cochran et al., 2012). Spawning was delayed and potentially precluded altogether in chestnut lamprey due to unseasonably high flows (Cochran, 2014) indicating that shifts in the hydrograph due to climate change could have an impact on lampreys. The distribution of native sea lamprey is shifting northward due to a decrease in habitat suitability at the southern extent of its range, including Italian basins and the Iberian Peninsula, and an opening of favourable basins in Iceland and Sweden (Lassalle et al., 2008; Lassalle and

Rochard, 2009), although to date, sea lamprey in Iceland have not been recorded spawning (Pereira et al., 2012). Two species of anadromous lampreys, pouched lamprey and short-headed lamprey, are among the freshwater fish species in southeastern Australia whose occurrences are projected to decline substantially due to climate change (Bond et al., 2011). Dramatic decreases in precipitation in Iran have led to severe drought, compounded by the long-term effects of dams and weirs. The Caspian lamprey has consequently lost one of its major spawning grounds in the southern Caspian Sea basin (Nazari et al., 2017). Loss of Arctic lamprey in southern parts of Japan, due to shifts in distribution, has forced changes to the fishing culture there (Wang et al., 2021).

What research and conservation actions should be prioritized to mitigate potential climate change impacts to lampreys? Conducting species-specific vulnerability assessments to learn how lampreys and their habitats will respond to climate change is critical. Lampreys are inherently resilient which has allowed them to inhabit the earth for hundreds of millions of years. Some lampreys, such as Laurentian Great Lakes sea lamprey, may benefit from a warming climate (Lennox et al., 2020), but many others will suffer from loss of habitat and range contraction. Surveys and modelling for detecting shifts in distribution should be increased. Distribution and abundance surveys of host populations should be conducted. It is critical to implement restoration actions such as barrier removal and habitat rehabilitation to restore stream complexity, as this will likely increase population resilience and effective population size. Finally, recognizing lampreys and the potential impacts from climate change in conservation and restoration plans worldwide will help protect vulnerable populations of lampreys and their habitats.

Emerging research opportunities and challenges

Lamprey passage solutions

Barrier removal is undoubtedly the preferred solution for improving habitat connectivity and quality for lampreys (Birnie-Gauvin et al., 2017). Nevertheless, it is often not feasible, and provision of fishways suitable for lampreys, or specific to lampreys, is a more common mitigation. Designing effective lamprey passes is still an evolving field and needs improved understanding of the behavioural, kinematic and physiological attributes of lamprey movement towards, and passage past, obstacles/fishways (Silva et al., 2018; Moser et al., 2021) through experimental studies. Whilst consideration of lamprey passage at migration barriers has increased substantially in the Northern Hemisphere (Moser et al., 2011; Tummers et al., 2018; Ackerman et al., 2019; Pereira et al., 2019), studies concerning Southern Hemisphere lamprey are scarce, with just one published study investigating the utility of a rock-ramp fishway for pouched lamprey passage in southwestern Australia (Beatty et al., 2007). The effectiveness of alternative fishway designs or approaches to barrier mitigation, remain relatively unexplored for Southern Hemisphere lampreys, although laboratory tests of lamprey-specific ramps are underway in New Zealand (C. Baker, pers. comm.).

Following construction of a series of low-gradient (1:23 and 1:32 slope) vertical-slot fishways at sequential weirs along the River Murray, Australia, biological assessment demonstrated that the fishways facilitated the passage of a wide range of fish species and sizes (Baumgartner et al., 2014). Lamprey, however, were absent at the time of assessment. More recently, fish sampling at the River Murray tidal barrages has enabled the tagging of pouched lamprey with PIT tags and subsequent assessment of lamprey passage through the vertical slot fishways further upstream (Bice et al., 2019). Passage efficiency was 71–100% and 78–100% for the 1:23 and 1:32 slope vertical slot fishways, respectively, and ascent rates varied with fishway slope and length, with longer and steeper fishways characterised by longer ascent times. The physiological implications of longer ascents in steeper (more turbulent) vertical-slot fishways remain to be explored. Nevertheless, both fishway designs effectively facilitate the passage of pouched lamprey and may also be suitable for other lamprey species.

A glaring knowledge gap remains the migratory behaviour and mitigation of barriers to the downstream movement of post-metamorphic juveniles of almost all migratory lamprey species. Potential impacts include behavioural responses to altered flow regimes (e.g. timing or seasonality of flow), and the physical and hydraulic impacts of dams and weirs, and their attendant reservoirs (Moursund et al., 2003; Moser et al., 2015b). Although screening may be applied at hydropower facilities and other water offtakes, many are designed for salmonid juveniles and the water approach velocities, and bar spacings often result in high levels of impingement (Moser et al., 2015b). Finely-pored travelling screens have been found to be much more successful than louvers for downstream-migrating juvenile lamprey but more research is needed (Goodman et al., 2017). Consideration of bidirectional connectivity and the effects of barriers on upstream and downstream migrating life stages, is essential to the conservation of diadromous fishes (Calles and Greenberg, 2009), and these data are urgently required for many lamprey species.

Environmental DNA

Sampling lampreys is a time and labour-intensive process (Moser et al., 2007), yet meaningful conservation actions will require more effective monitoring of the distribution and abundance of lampreys. Conventional larval sampling is limited by difficulties in identification to species level, especially in the field. Therefore, the recent development of environmental DNA (eDNA) assays for several lamprey species has strong potential for use in routine sampling of lamprey distribution on a wider scale than is possible by physical collection (Docker and Hume, 2019). In some cases, it may also have the potential to infer abundance and quantitative DNA sampling is likely to improve dramatically in the next decade. Species-specific eDNA rather than eDNA metabarcoding is likely to be most valuable for lamprey conservation criteria due to the greater sensitivity of the former (Gustavson et al., 2015; Gingera et al., 2016; Schloesser et al., 2018).

Currently several species-specific eDNA assays are available including for sea lamprey (Gustavson et al., 2015; Gingera et al., 2016; Schloesser et al., 2018), as well as other assays that work for genera, such as *Entosphenus*, but do not distinguish between species (Ostberg et al., 2018). Calibration of qPCR with field observation or manipulation is beginning to demonstrate that spatial and temporal peaks in eDNA can reveal biologically meaningful patterns of lamprey biomass within rivers, as shown for sea lamprey in Irish catchments (Bracken et al., 2019). Given the problems of conventional sampling and lack of morphological distinction between larvae of closely related species, such as European river and brook lampreys, a major opportunity and challenge for eDNA is to improve upon that limitation. Currently this is not possible but could be solved by using an assay based upon species-specific or, more likely, population-specific, single nucleotide polymorphisms (SNPs). Several research groups (e.g. Zancolli et al., 2018) are developing these methods and routine monitoring may be achievable within the next decade or so.

Parasitic feeding-phase lampreys in marine and large lake environments

For native lampreys, the ecology and behaviour of juveniles at sea or in large lakes remains a 'black box' for which scarce information is currently available (Silva et al., 2014; Hansen et al., 2016; Clemens et al., 2019). As a result, we do not currently know how important this life stage is for lamprey species conservation, irrespective of the difficulty of making conservation interventions for lampreys at sea. Anadromous lampreys can attain up to 99% of total growth in weight during this stage so it is crucial to their reproductive potential (Silva et al., 2016a). Missing information includes: how lampreys disperse at sea, their distribution at sea, and the degree of exchange of individuals between river basins (due to a lack of natal homing) including from a source-sink perspective (but see Mateus et al., 2021, for hypotheses). How parasitic lampreys select and move between prey items is poorly known, as are feeding rates (Renaud and Cochran, 2019). Although Kitchell and Breck (1980) developed a bioenergetics model for Great Lakes sea lamprey, issues such as its applicability to anadromous sea lamprey, other parasitic lamprey species, and the effects of different environments remain to be tested. Survival rates of lampreys at sea are also largely absent (Hume et al., 2021 - a), impacts of overfishing on prey populations and exploitation rates are sparse, and return movement to inshore waters and transition back to rivers is currently only investigated in the Great Lakes (Meckley et al., 2014, 2017).

To help solve these knowledge gaps, better use needs to be made of systematic and opportunistic sampling at sea and in lakes (Hume et al., 2021 - b). For some species, such as European river lamprey, water intakes from coastal power stations have provided valuable year-round sampling mechanisms (Maitland et al., 1984), but these only provide point-sample locations, close to shore. Data from oceanographic expeditions and fisheries can provide relevant information on the biology and ecology of lamprey species at sea (Beamish, 1980; Halliday, 1991; Orlov et al., 2009, 2014, 2008; Murauskas et al., 2013; Silva et al., 2016a, 2014). Combination of oceanic capture, tagging with PIT tags and automated telemetry in the Columbia River demonstrated transoceanic migration in a Pacific lamprey from the Bering Sea to the Columbia River (Murauskas et al., 2019). In general, however, lamprey captures are rare at sea. For example, despite intensive, standardised research vessel fish surveys in the North Sea, Celtic Sea and Baltic Sea (1977–2013), sea lamprey and European river lamprey records are scarce, usually with just a few records per year (Heesen et al., 2015).

In almost all marine fisheries surveys, lamprey samples are obtained as non-target bycatch, recording may be incomplete, and raw capture data are not readily accessible to many lamprey biologists. Normally lamprey detach from their host during the capture and landing process and may be susceptible to escaping through most larger-meshed net gears. Further research is needed to explore patterns of lamprey records at sea. For example, in the North Sea, the two most important producers of European river lamprey are likely the Humber (England) river basin on the west coast and the Elbe (Germany) river basin on the south east coast, and although European river lamprey records are spread in coastal waters around the Elbe outflow, they are rare around the Humber (Heesen et al., 2015). Whether this reflects different dispersal patterns from these estuaries or spatial bias in capture probability by differing gears remains to be determined. Besides lamprey captures, analysis of wounds made by lampreys to their prey is also a useful source of data concerning distribution and the timing of occurrence of parasitic feeding phase lampreys in particular localities (Lantry et al., 2015; Silva et al., 2014; Weitkamp et al., 2015). Therefore, in addition to information from scientific surveys, better communication with, and education of, commercial fisheries is needed to enable them to supply more and better records of incidental lamprey captures, or prey with fresh sucker wounds, during their fishing.

Molecular tools are also expected to play an important role in lamprey studies at sea. Thus, population genetics has been used to advance this field, and future studies will better identify stocks and exchange of lampreys between river basins (Mateus et al., 2021). Otolith microchemistry has proved to be a useful tool for diadromous teleost species to determine natal origin and movements between habitats (Walther and Limburg, 2012; Martin et al., 2015; Nachón et al., 2020). In lampreys, attempts to use statolith microchemistry to reconstruct movements between habitats have not been so successful, because the elements in statoliths appear more labile (Howe et al., 2013; Lochet et al., 2014, 2013). DNA metabarcoding has also been suggested as a promising tool to characterize the diet of juvenile lampreys (Shink et al., 2019), as well as stable isotope analyses (Adams et al., 2008; Harvey et al., 2008; Inger et al., 2010; Miles et al., 2014). Analyses of fatty acid profiles have also been used to advance knowledge of the parasitic phase of sea lamprey (Happel et al., 2017; Lança et al., 2014). Therefore, molecular techniques will likely underpin future advances in knowledge regarding the trophic phase of anadromous lampreys.

Telemetry will be a key methodology in improving our understanding of lamprey distribution during the growth phase at sea or in large lakes and, in particular, the outmigration phase of juvenile lampreys. The small size of emigrating juvenile lampreys has made it a challenge to tag them. PIT tags as small as 8 mm in length (and hence, PIT tagged lamprey) can be detected at sea post-capture, or with specialised trawls fitted with antennas (Cooke et al., 2012), or upon re-entry to a stream or fishway fitted with a PIT station, but such methods give a low probability of detection (hence requiring large sample size) and crude spatial information. Detection of PIT tags in coastal seabird colonies, as at the mouth of the Columbia River (Evans et al., 2012), could be a useful method of recording predation mortality during the estuarine and coastal outmigration of lampreys. Until recently, battery-powered tags have been too large to tag juvenile lampreys, but new micro-acoustic tags (12 × 2 mm, 0.08 g, 30-day life) for juvenile eels and lampreys (Mueller et al., 2019), using the 416 KHz JSATS system, make tracking of outmigrating lampreys in the marine environment a future possibility. Estuaries and the coastal marine zone are noisy environments (Cooke et al., 2012), and it is likely that omnidirectional receivers would have to be positioned 50–200 m from one another to maximise detection probability. Consequently, estuarine and coastal tracking of outmigrating juvenile lamprey would require a substantial array of receivers. Currently, tracking is concentrating on understanding the behaviour of juvenile lamprey at large dam forebays for Pacific lamprey (M. Moser, pers. comm.) and in the outlet regions of Great Lakes streams for invasive sea lamprey (M. Wagner, pers. comm.), both much quieter environments than in estuaries or at sea. Nevertheless, building on experiences from those studies and with a substantial budget it will be possible, within the next decade, to track juvenile anadromous lampreys at sea.

Conclusions

It is an exciting, but worrying, time to be conserving and researching lampreys. On the one hand, we have an outstanding model taxon that presents a host of intriguing questions across fields of evolution, physiology, behaviour, ecology and development to name a few. Native lampreys are less misunderstood and more appreciated by stakeholders now than they were for decades; and we have new methods becoming available that can provide key information needed to inform conservation of these lampreys. There is a surge of interest in river restoration with barrier removals, habitat reinstatement, ecological flow provision and better pollution control, often using protected species legislation for lampreys as leverage in support of these. On the other hand, there is a strong risk that some lamprey species and habitats may be lost before we can characterise and understand them. Consequently, there is an urgency in lamprey conservation to prioritize information exchange and the establishment of best practises. An international lamprey meeting on a regular 2–4 year cycle might be one way of facilitating this. It has been said that control and conservation are two sides of the same coin in lamprey biology applications (Docker and Hume, 2019), and there is no doubt that knowledge transfer with the invasive sea lamprey control programme remains a key element to developing effective lamprey conservation initiatives.

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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