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Review

Management of anadromous lampreys: Common threats, different approaches

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ABSTRACT

Ten anadromous lamprey species (Petromyzontiformes) are recognized around the world, including four species in the Southern Hemisphere and six in the Northern Hemisphere. Eleven threats to these anadromous lampreys have been identified: climate change, shifting oceanographic regimes, artificial barriers, low water quantity/flow management, habitat degradation, poor water quality, reduced habitat availability, host and prey availability, predation, overharvest, and disease. Artificial barriers are a well-recognized threat to anadromous lampreys. Management strategies to improve access to spawning and larval rearing habitats have involved modifying these barriers, providing passage, and translocating adults around them. Habitat restoration targeting other fishes may also benefit some anadromous lampreys; however, research targeting lamprey responses to habitat restoration is lacking. The absence of recreational and commercial fisheries on many of the anadromous lampreys has created a paradigm where funding is unavailable to monitor and manage them. This has led to a general lack of awareness and scientific understanding for anadromous lampreys. We discuss management actions for each of the anadromous lampreys, and highlight key information gaps. Key information gaps include aspects of freshwater biology, distribution and abundance of anadromous lampreys, and the need to improve understanding of how to mitigate threats. In general, larger-bodied lampreys are the subject of more human interest (more harvest, research, and management).

Contents

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Introduction

Lampreys (Petromyzontiformes) are of significant ecological, cultural, economic, and scientific importance (Docker et al., 2015). A total of 41–44 lamprey species are recognized worldwide (Maitland et al., 2015; Potter et al., 2015). Of these, 23–26 are freshwater residents that do not exhibit a juvenile life stage, nine are freshwater residents that are parasitic as juveniles, and ten are anadromous and parasitic as juveniles (Maitland et al., 2015; Riva-Rossi et al., 2020). This paper focuses on the status, management, threats, research needs, and interest levels among nine anadromous lampreys. The tenth species, *Geotria macrostoma*, has only just been formally described (Riva-Rossi et al., 2020), and its biology is currently undocumented. The nine lampreys include three species in the Southern Hemisphere: the short-headed lamprey *Mordacia mordax*, the pouched lamprey *G. australis*, and the Chilean lamprey *M. lapicida*; and six in the Northern Hemisphere: the Caspian lamprey *Caspiomyzon wagneri*, sea lamprey *Petromyzon marinus*, Pacific lamprey *Entosphenus tridentatus*, western river lamprey *Lampetra ayresii*, European river lamprey *L. fluviatilis*, and the Arctic lamprey *Lethenteron camtschaticum*. Some of these anadromous lampreys also exhibit freshwater parasitic life histories, such as sea lamprey (Hume et al., 2021), European river lamprey (Tsimbalov et al., 2015), and Arctic lamprey (Kucheryavyy et al., 2016; Yamazaki et al., 2011), and this topic is covered in detail elsewhere (see Docker and Potter, 2019).

We begin with a brief description of the biology of anadromous lampreys. We then discuss the status of these fishes and identify current threats. We expand on the information presented by Maitland et al. (2015) by providing accounts on the status of each anadromous lamprey. These accounts are placed in order of distribution, from southern to northern latitudes. The status of each anadromous lamprey is provided at the international, national, and regional levels. Threats and management actions for each anadromous lamprey are also discussed within each species account. In addition, we discuss research needs, and provide a novel categorization of the social, management and research interest for each anadromous lamprey. We use "management" in a way that is synonymous with "conservation" to promote sustainable harvest of lampreys.

Biology

All anadromous lampreys feed as parasites on the blood of hosts or as predators on the flesh of prey in estuarine and marine environments for variable periods of time, ranging from a few months to two or more years (Quintella et al., 2021). After reaching their maximum body sizes (Fig. 1), anadromous lampreys stop feeding, enter freshwater, and migrate upstream to spawn (Johnson et al., 2015; Moser et al., 2015a). The entire freshwater migration has been described in terms of three to four stages: pre-spawning migration, holding, a shorter second migration that culminates in spawning (Clemens et al., 2010), and senescence (Johnson et al., 2015). The presence and duration of these periods are flexible both within and across anadromous lampreys. The migration and holding periods may take a few months or up to two or more years, with considerable variability occurring within and across anadromous lampreys, watersheds, and regions (Moser et al., 2015a). The cessation of feeding and use of body tissues to fuel the energy needed to migrate upstream and to sexually mature can result in anadromous lampreys shrinking up to 1/3 of their maximum body length (e.g., Docker et al., 2019; Glova, 1995; Moser et al., 2015a; Neira, 1984). Adult body size of anadromous lampreys can vary significantly within species. An example of this is provided for Pacific lamprey, with very large specimens being more common in large rivers such as the Columbia and smaller specimens occurring in coastal watersheds (Clemens et al., 2019). Hence body size is generally correlated with the maximum upstream migration distance, with larger lampreys migrating further than smaller ones, both within (Hess et al., 2014; Keefer et al., 2009) and across lamprey species (Potter, 1980a). Considerable variation in upstream migration distances occurs within species (Moser et al., 2015a). Lampreys are commonly attracted to increased river flows en route to spawning grounds; hence their presence upstream is correlated with river flow (Arakawa et al., 2019; Clemens et al., 2017a; Moser et al., 2015a).

Lampreys are also attracted to migratory pheromones released by larvae (Fine et al., 2004; Sorensen and Hoye, 2007) and to mating pheromones released by adults (Johnson et al., 2015; Moser et al., 2015a). Although most investigations on migratory and sex pheromone communication in lampreys have focused on the sea

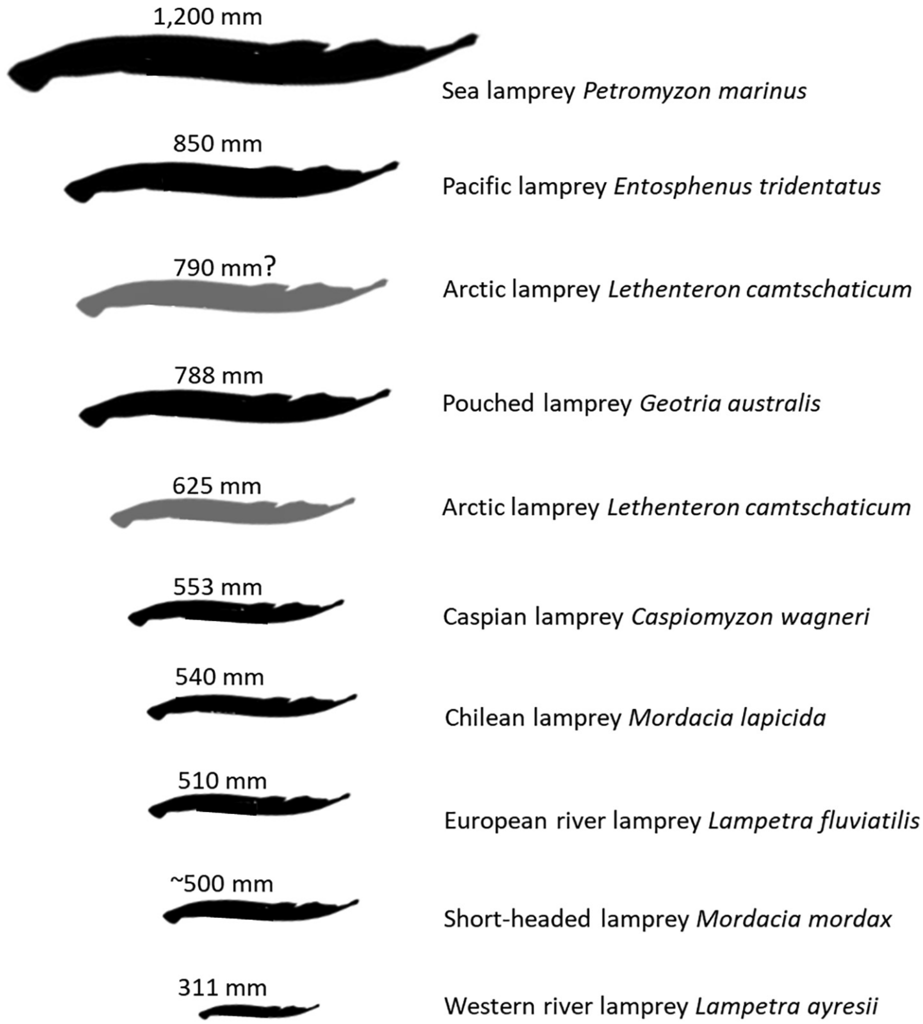

Fig. 1. Maximum body lengths of anadromous lampreys, shown in relative proportion to each other. This data is from Bartel et al. (2010), Berg (1948), and multiple references cited in Renaud and Cochran (2019). Although Orlov et al. (2014); cited in Renaud and Cochran, 2019) reported a 790 mm Arctic Lamprey, we suspect this may have been a mislabeled Pacific lamprey because it is far beyond what has been encountered for this species elsewhere. For example, the 625 mm body size is from Berg (1948), and the maximum body sizes of Arctic lamprey from both ocean and freshwater reported from Japan and Alaska are <600 mm (Kataoka et al., 1980; Mick Leach, Alaska Department of Fish and Game, pers. comm.; Jim Murphy, NOAA Fisheries, Alaska Fisheries Science Center, pers. comm.).

lamprey, our understanding of the role of pheromones as a migratory and mating cue for other lampreys remains limited. Given the length of divergence between Northern and Southern Hemisphere lampreys, *Geotria* and *Mordacia* spp. may have evolved different responses to the compounds attractive to migratory and mature sea lamprey. Post-spawning male pouched lamprey do not release high volumes of 3-keto petromyzonol sulphate (3kPZS; Buchinger et al., 2017). However, larval pouched lamprey have been shown to release petromyzonol sulphate (PZS), petromyzonamine disulfate (PADS; Baker et al., 2009; Stewart and Baker, 2012), allocholic acid, 3-keto allocholic acid and 3kPZS (authors' unpublished data). Therefore, the production of pheromone compounds has at least been partially retained in Southern Hemisphere lampreys.

The timing of spawning can vary within and across anadromous lampreys by latitude, flow, and migration distance, as noted for sea lamprey and Pacific lamprey (Clemens et al., 2010). Spawning of anadromous lampreys in the Northern Hemisphere generally occurs between 8 and 26 °C (Johnson et al., 2015). Spawning data for Southern Hemisphere lampreys is lacking for short-headed lamprey and Chilean lamprey, but is available for pouched lamprey. Daily mean temperature of spawning for pouched lamprey was 9–11 °C in the two streams where spawning was observed (Baker et al., 2017a and unpublished data) and approximately 14 °C within the laboratory (Paton et al., 2019). Fecundity is correlated with body size in lampreys (Docker et al., 2019; Docker and Potter, 2019). With the exception of pouched lamprey, that create nests in completely concealed cavities (Baker et al., 2017a), lampreys spawn in nests excavated in the cobble and gravel substrate of streams and lakes (Johnson et al., 2015). The spawning behaviour of the other Southern Hemisphere lampreys, short-headed lamprey and Chilean lamprey, is undocumented at this time. Baker et al. (2017a) hypothesized that the cryptic nesting habitats of pouched lamprey was primarily driven by reducing susceptibility to predation by endemic longfin eels, where New Zealand and Australia contain the largest freshwater eel species worldwide (*Anguilla dieffenbachii*, and *A. reinhardtii*, respectively). As eels from the family Anguillidae are not present in South America, the Chilean lamprey and Argentinian lamprey (*G. macrostoma*) may not display the same cryptic nesting behavior. Based on the hypothesis of Baker et al. (2017a), short-headed lamprey would be expected to display a similar reproductive ecology to the pouched lamprey.

The larvae hatch and emerge within a few weeks at a few millimetres in length and seek out soft, silty substrate to burrow into (Moser et al., 2019). The larvae feed off microscopic, particulate matter (detritus and algae), and with a few exceptions this stage typically lasts 3–8 years (Dawson et al., 2015). The larval stage of anadromous lampreys is usually the longest life stage of the entire life cycle (Dawson et al., 2015; Moser et al., 2015a; Quintella et al., 2021). Physiological and environmental cues stimulate transformation of the eyeless and toothless larvae into juveniles that have eyes and sharp teeth necessary for parasitic and predatory feeding (Manzon et al., 2015; Quintella et al., 2021). Transformation across species occurs at a median body length of 130 mm (range: 90–170 mm; Docker, 2009; Potter, 1980b). Juvenile lampreys can emigrate from freshwater throughout the year, although most emigrate from freshwater during annual peaks in river flows (Moser et al., 2015b). Similar to spawning timing, transformation and emigration timing can vary by latitude (Clemens et al., 2019; Manzon et al., 2015). Differences in the biological patterns described above are complex and are covered in one catalogue (Renaud, 2011), four volumes (Orlov and Beamish, 2016a; Orlov and Beamish, 2016b; Docker, 2015; Docker, 2019), and recent research articles. Despite this burgeoning literature on anadromous lampreys, key data gaps remain related to their biology and ecology (including temporal trends, population structure, and population dynamics). A detailed comparison of patterns and mechanisms for differences in the biology of anadromous lampreys is beyond the scope of this review.

Status

Confusion sometimes occurs among the terminology used to indicate status by different entities. We use "rank" to mean a general and somewhat informal status; "assess" to mean a formal status that is not legally binding, and "listing" to mean a legally-binding assessment. Some countries have regional assessments or listings and lack national assessments or listings (Table 1). The international statuses reported here are from assessments done by the International Union for the Conservation of Nature (IUCN, 2019) and NatureServe (2019), and other entities (e.g., Convention on the Conservation of Migratory Species of Wild Animals, 1979; HELCOM, 2013). International status was assessed for all anadromous lampreys with the exception of the short-headed lamprey in 2019. The status of these lampreys ranged from "data deficient" (pouched lamprey, Chilean lamprey) to "least concern" (sea lamprey, European river lamprey, Arctic lamprey), "apparently secure" (Pacific lamprey), "secure" (western river lamprey), and "near threatened" (Caspian lamprey; Table 1). These international assessments are nearly identical to those done in 2013 (Maitland et al., 2015). The most obvious difference between 2013 and 2019 was the change in status of western river lamprey from "apparently secure" (Maitland et al., 2015) to "secure" (Table 1).

Status assessments vary significantly within species, with some geographical areas exhibiting statuses that are significantly worse than the international status (Table 1). Disparities in status and nomenclature exist at the international, regional, and national levels (Table 1; Maitland et al., 2015).

Threats

Limiting factors are processes or activities that limit the biology and population growth of a species, but do not necessarily cause population declines and therefore changes in the status of a species (COSEWIC, 2018). By contrast, threats are processes or activities that can cause population declines that lower status (COSEWIC, 2018; IUCN, 2020). Threats are typically (but not always) attributed to human activities (COSEWIC, 2018). Acknowledging that different operational definitions have been used for limiting factors and threats (e.g., Clemens et al., 2019; ODFW, 2020), and that the processes that are limiting factors in some situations may become threats in others, we use the term "threats" here to include both limiting factors and threats.

Lampreys have lived through at least four global mass extinction events over the 360 million years of their existence (Barnosky et al., 2011; Docker et al., 2015; Gess et al., 2006), suggesting this group of ancient fishes has been resilient to environmental upheavals that extirpated many other species. Native lampreys are now facing many different threats related to human activities that have resulted in significant decreases in their populations over the last century (Jelks et al., 2008; Maitland et al., 2015; Renaud, 1997). A review of the literature suggests eleven threats to anadromous lampreys, including climate change, oceanographic regimes, interactions between climate change and oceanographic regimes (Clemens et al., 2019; Maitland et al., 2015; Wang et al., 2021), and four threats in each of two broad categories, land development and use and species interactions (Fig. 2). The following briefly describes each of these threats and effects on anadromous lampreys. We begin with discussion of climate change and oceanographic regimes, and then discuss threats within land use and within species interactions.

Climate change is an emerging threat to anadromous lampreys that is having, and will continue to have, complex interactions with other threats (Wang et al., 2021). For example, climate change will increase thermal and hydrologic variability including droughts and floods (Collins, 2018; Fernandez et al., 2015; Filipe et al., 2013) that will alter lamprey migration and metabolism, quality of in-stream habitat, and water quantity and quality (Wang et al., 2021). Climate change is predicted to drive extreme weather events, intensify industry and agriculture, and loosen environmental regulations — all of which may combine to escalate toxic runoff into watersheds that otherwise support anadromous lampreys (e.g., Lassalle et al., 2009; Meixler, 2018; Wang et al., 2020). Hence the ultimate impacts of climate change to anadromous lampreys are not completely understood at specific geographical locations and across life stages.

Oceanographic regimes and interactions between climate change and oceanographic regimes can limit the availability of host species (Maitland et al., 2015; Clemens et al., 2019). Additional threats to anadromous lampreys in marine environments include predation and fisheries bycatch, marine pollution, and host/prey contaminant loads (Clemens et al., 2019; Drevnick et al., 2006). Most of the life cycle of anadromous lampreys occurs in freshwater. In addition, management of lampreys occurs primarily in freshwaters and estuaries. Therefore discussions of threats to anadromous lampreys will focus on freshwater with some discussion of harvest management in estuaries.

Land use arguably poses the most significant direct threat to lampreys worldwide. Land use influences climate change, the availability of host and prey species for anadromous lampreys, and the abundance of predators on them. Land use includes human activities such as dredging of rivers, land excavation, and land development and use that leads to other threats. These threats include artificial barriers, water quantity/stream flow management, habitat degradation, and decreased water quality (Clemens et al., 2017b; Maitland et al., 2015; Mesa and Copeland, 2009; Moyle et al., 2009; USFWS, 2019a).

Artificial barriers include dams, culverts, weirs, and tidegates of various sizes and configurations. These barriers are a key threat for all anadromous lampreys, including adults attempting to migrate to upstream spawning habitat, and larvae and juveniles emigrating toward downstream rearing habitats (Mesa and Copeland, 2009; Moser and Mesa, 2009; Moser et al., 2021).

Water quantity pertains to differences in the timing and extent of river flows that anadromous lampreys have adapted to, includ-

Table 1
Status of anadromous lampreys, organized by distribution (latitude), from Southern to Northern Hemispheres. Some countries have regional assessments or listings and lack national assessments or listings; in these cases, the listings are labelled accordingly. Most of this information presents results from status assessments. Legal status is indicated in **bold**; management actions are underlined. Note: The Argentinian lamprey *Geotria macrostoma* has not been assessed within Argentina or internationally.

Species	Status, Legal Listing or Management Plan
Short-headed lamprey *Mordacia mordax*	INTERNATIONAL -Not assessed (IUCN, 2019) AUSTRALIA: *Regional:* "Endangered" and "Vulnerable" in South Australia (Hammer and Wedderburn, 2009; Wilson and Bignall, 2009)
Pouched lamprey *Geotria australis*	INTERNATIONAL -"Data deficient" (IUCN, 2019) NEW ZEALAND: "Threatened – nationally vulnerable" (Dunn et al., 2018) AUSTRALIA: *Regional:* "Vulnerable" in South Australia (Wilson and Bignall, 2009); "Declining" and "Poorly-known species not under imminent threat" in Western Australia (Wildlife Conservation, 2018) SOUTH AMERICA: *Regional:* "**Not threatened**" and **insufficient data to assess** (Chile; Official Gazette of the Republic of Chile, 2008 — cited in Reyes et al., 2014)
Chilean lamprey *Mordacia lapicida*	INTERNATIONAL -"Data deficient" (IUCN, 2019)
Caspian lamprey *Caspiomyzon wagneri*	INTERNATIONAL -Not at risk globally (Maitland et al., 2015) -"Data deficient" and "highly threatened" (Nazari et al., 2017) -"**Near Threatened**" (Kiabi et al., 1999; IUCN, 2019) and close to meeting "vulnerable" (IUCN, 2019) RUSSIA: Protected in some nature reserves (Reshetnikov, 2010); **protected as decreasing sharply in number and/or distribution vulnerable species** (Russian Federation, 2020) IRAN: "**Near Threatened**" (Kiabi et al., 1999; IUCN, 2019); extirpated in some areas (Renaud, 1997), and declining in others (Nazari et al., 2017) AZERBAIJAN: "**Extinct**" (IUCN, 2019) KAZAKHSTAN: Decreasing in number and/or distribution (GRK, 2006); "**Vulnerable**" (Nazari et al., 2017; The Red List of Kazakhstan, 1996) TURKMENISTAN: "Data deficient" (Nazari et al., 2017) TURKEY: "**Extinct**" (IUCN, 2019; Fricke et al., 2007)
Sea lamprey *Petromyzon marinus*	INTERNATIONAL *Global*[a] -"Least concern" (IUCN, 2019) *Europe and Asia* -"Least concern" (NatureServe, 2019) -**Listed in Annex III of the Bern Convention** (Council of Europe, 1979) -**Listed in Annex B-II of the European Union Habitats Directive** (except in Sweden; Council of the European Communities, 1992) -**Listed in the OSPAR List of Threatened and/or Declining Species and Habitats** (OSPAR Commission, 2008) **of the OSPAR Convention** (Convention for the Protection of the Marine Environment of the North-East Atlantic) Listed in the Red List of Baltic Sea species "**in danger of becoming extinct**" (HELCOM, 2013) *North America* -"Secure" (NatureServe, 2019; Renaud et al., 2009) BELGIUM: "Endangered" (Verreycken et al., 2014) BOSNIA & HERZEGOVINA: "**Data deficient**" (Škrijelj et al., 2013; Tutman et al., 2020) CANADA: *Regional:* "Critically imperilled" in Newfoundland (NatureServe, 2019; Renaud et al., 2009) CZECH REPUBLIC: "**Regionally extinct**" (Lusk et al., 2004) DENMARK: "**Vulnerable**" (HELCOM, 2013) FRANCE: "**Endangered**" (IUCN French Committeeet al., 2019) GERMANY: "**Not threatened**" (Baltic Sea; HELCOM, 2013) IRELAND: "**Near threatened**" (King et al., 2011) ITALY: "**Critically endangered**" (Rondinini et al., 2013) NORWAY: "**Near threatened**" (Norwegian Biodiversity Information Centre, 2015) POLAND: "**Endangered**" (HELCOM, 2013) PORTUGAL: "Vulnerable" (Cabral et al., 2005); *Regional:* Tagus Estuary listed - site PTCON0009 Natura 2000 Site of Community Importance of the European Union's Habitats Directive (Council of the European Communities, 1992); Mid-season fishery interruption legislated since 2013 in river Mondego to facilitate upstream recolonization (Stratoudakis et al., 2016) SLOVENIA: "**Endangered**" (Povž, 2011) SPAIN: "Vulnerable" (Doadrio, 2001); *Regional:* "**Endangered**" in some river basins (BOE, 2011) SWEDEN: "**Near threatened**" (ArtDatabanken, 2015) RUSSIA: "Data deficient" (Russian Federation, 2020); included in protection list of the Kandalaksha Nature Reserve on seven islands (Reshetnikov, 2010) UNITED KINGDOM: "Vulnerable" (Maitland, 2000) UNITED STATES OF AMERICA: *Regional:* "Species of conservation need" (four states; Connecticut River Anadromous Sea Lamprey Management Plan, 2018)
Pacific lamprey *Entosphenus tridentatus*	INTERNATIONAL -"Vulnerable" (Jelks et al., 2008) -"Apparently secure" (NatureServe, 2019)

(*continued on next page*)

Table 1 (*continued*)

Species	Status, Legal Listing or Management Plan
	JAPAN: *Regional:* "**Critically endangered**" (Hokkaido Government, 2018; -Tochigi Prefecture, 2005) UNITED STATES OF AMERICA: "Species of concern"[b]; "High conservation risk" in most basins (Wang and Schaller, 2015) CANADA: "Apparently secure" (NatureServe, 2019; Renaud, 2009); "High priority" candidate wildlife species for status assessment (COSEWIC, 2019) MEXICO: "**Threatened**"[b] (Norma Oficial Mexicana — cited in Maitland et al., 2015)
Western river lamprey *Lampetra ayresii*	INTERNATIONAL -"Vulnerable" (Jelks et al., 2008) -"Secure" (NatureServe, 2019) UNITED STATES OF AMERICA: "Species of concern"[b]
European river lamprey *Lampetra fluviatilis*	INTERNATIONAL -"Least concern" (IUCN, 2019) -More stable in central and northern countries (e.g. Finland, Latvia, Estonia, Sweden, Russia; Lajus et al., 2013; Renaud, 2011; Sjöberg, 2011) -Highly threatened in some areas (Portugal and Italy), but relatively abundant in others (Mateus et al., 2019) -**Listed in Appendix III of the Bern Convention** (Convention on the Conservation of Migratory Species of Wild Animals, 1979) -**Listed in Annexes II and V of the European Union Habitats Directive** (except in Finland and Sweden; revised in Mateus et al., 2019) BELGIUM (FLANDERS): "Near threatened" (Verreycken et al., 2014) BELGIUM (WALLONIA): "**Regionally extinct**" (Kestemont, 2010; Philippart, 2007) BOSNIA & HERZEGOVINA: "**Endangered**" (Škrijelj et al., 2013; Tutman et al., 2020) CZECH REPUBLIC: "**Regionally extinct**" (Lusk et al., 2004) DENMARK: "**Data deficient**" (HELCOM, 2013) ESTONIA: "**Least concern**" (HELCOM, 2013) FINLAND: "**Near threatened**" (HELCOM, 2013) FRANCE: "**Vulnerable**" (IUCN French Committeeet al., 2019) GERMANY: "**Critically endangered**" (Baltic Sea; HELCOM, 2013) ITALY: "**Critically endangered**" (Rondinini et al., 2013) NORWAY: "**Least concern**" (Norwegian Biodiversity Information Centre, 2015) POLAND: "**Vulnerable**" (HELCOM, 2013) PORTUGAL: **"**Critically endangered" (Cabral et al., 2005); *Regional*: Tagus Estuary listed - site PTCON0009 Natura 2000 Site of Community Importance of the European Union's Habitats Directive (Council of the European Communities, 1992). SPAIN: "Regionally extinct" (Doadrio, 2001) SWEDEN: "**Least concern**" (ArtDatabanken, 2015) RUSSIA: Under protection in Nizhnesvirsky and Pechora-Ilych Nature Reserves (Reshetnikov, 2010) UNITED KINGDOM: Several Special Areas of Conservation established (King et al., 2011; Maitland et al., 2015)
Arctic lamprey *Lethenteron camtschaticum*	INTERNATIONAL *Global:* -"Least concern" (IUCN, 2019) *North America:* -"Apparently secure" (NatureServe, 2019) RUSSIA: under protection in Great Arctic State Nature Reserve, Kandalaksha, Nenets, Ussurisky, Sikhote-Alin, Kronotsky, and Dalnevostochny Morskoy Nature Reserves (Reshetnikov, 2010) JAPAN: "Vulnerable" (Ministry of the Environment, 2007); *Regional:* "Critical" in Akita, Toyama, Hyogo, Yamaguchi, "Vulnerable"; Yamagata, Niigata, Fukui, Kyoto, Shimane; "Near threatened" in Hokkaido, Aomori, "Data Deficient"; Miyagi, Fukushima, Ibaraki, Gunma, Saitama, Tottori (Association of Wildlife Research, EnVision Conservation Office, 2017; Hokkaido government, 2018; Yamagata Prefectural government, 2018; Yamaguchi Prefectural government, 2018)

[a] Informal term for species believed to need focused conservation efforts. Species of concern do not receive legal protection (USFWS, 2019b).
[b] Equivalent to "Vulnerable" status via the International Union for Conservation of Nature (IUCN).

ing somewhat predictable timing of peak flows and water availability throughout the year. Water quantity also pertains to the rapid dewatering of rivers from human causes at rates and extents that can decimate multiple age classes of larvae that are not able to escape (Maitland et al., 2015).

Habitat degradation pertains to simplification of formerly complex river channels and the associated ecosystem processes, which has been associated with decreases in lamprey populations (Clemens et al., 2017b; Homel et al., 2019). Habitat degradation and decreased water quality can be especially problematic for lampreys due to the long periods of time these fishes spend in freshwater as larvae and as adults during their pre-spawning migrations (Maitland et al., 2015).

Water quality, including temperature, sedimentation, toxic pollutants, and other parameters (e.g., dissolved oxygen, pH, eutrophication, etc.) can affect lampreys in as-yet unknown ways (Clemens et al., 2017b; Maitland et al., 2015). With some exceptions for water temperature, significant unknowns remain on the effects of sedimentation, toxic pollutants, and other parameters on lampreys. The behavioural, physiological, and ecological effects of high water temperatures have been reviewed across the life cycle for Pacific lamprey (Clemens et al., 2016), and studied for larvae of the pouched lamprey (Macey and Potter, 1978), sea lamprey (Potter and Beamish, 1975), and European river lamprey (Golovanov et al., 2019). The migration of adult anadromous lampreys can occur at temperatures ≥25 °C. However, at >20 °C, a

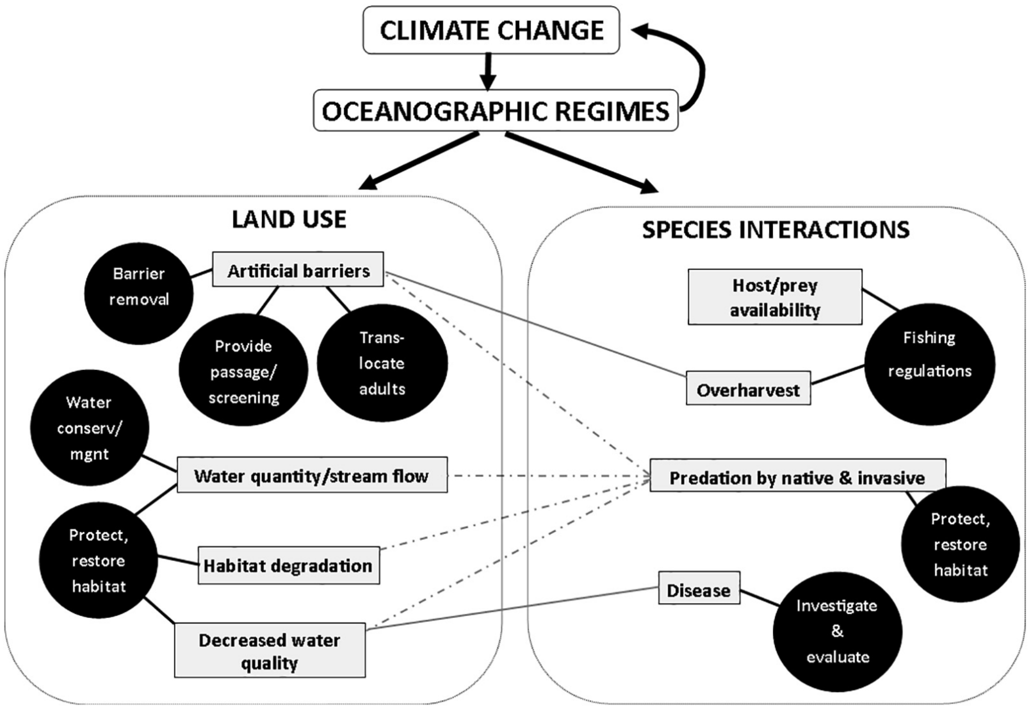

Fig. 2. Conceptual diagram of threats to anadromous lampreys, including climate change, oceanographic regimes, interactions between climate change and oceanographic regimes, land use, and species interactions. Arrows should be read as, "affects". Thus climate and ocean ecology influence the land use and species interactions threats on anadromous lampreys. Threats are indicated in grey rectangles within "land use" and "species interactions". Gray lines indicate interactions across land use and species interactions. The black circles indicate management strategies that are used in particular situations to offset the impacts of threats to anadromous lampreys.

number of physiological and life-threatening problems can be experienced by these fishes (Clemens et al., 2016). Thermal effects on anadromous lampreys include mortality of larval life stages at ≥28 °C (Golovanov et al., 2019; Macey and Potter, 1978; Potter and Beamish, 1975). Lampreys may be harmed by various toxic pollutants throughout their life cycles (Clemens et al., 2017b; Madenjian et al., 2021). However, two major unknowns remain about the effects of most toxic pollutants on lampreys: 1) the extent to which lampreys experience toxic pollutants throughout the landscape and across life stages, and 2) the ultimate effects of these pollutants on lamprey populations. Controls and practices to limit the adverse use, effects, and entry of toxic chemicals into rivers are improving in many areas of the world, but direct discharge (e.g., wastewater treatment overflow) and runoff (e.g., after pesticide and herbicide applications; from roads or urban areas) still occurs into rivers and streams. Larval lampreys can bioaccumulate mercury, flame retardants, and pesticides at levels that may be harmful to individuals and populations (Linley et al., 2016; Nilsen et al., 2015).

The four threats within species interactions include host/prey availability, predation by native and invasive species (mammals, birds, and fishes), overharvest, and disease (Cochran, 2009; Docker et al., 2015; Maitland et al., 2015). The lack of information and misinformation on anadromous lampreys, arising from perceptions of invasive sea lamprey or misunderstanding of their needs, while not a threat per se, impedes understanding and thus management of anadromous lampreys (Clemens, et al., 2017b; Close et al., 2002; Gephard, 2019).

Species accounts

The following species accounts detail the status, threats, and management actions of individual species of anadromous lampreys. We begin with discussions on the three species of Southern Hemisphere lampreys and then transition to accounts of the six Northern Hemisphere species. The species are presented by the latitudinal distributions, from south to north. The level of detail among species varies, depending on the amount of interest in them and research done on them. The general trend is that the knowledge of, and interest in, the Southern Hemisphere species is low in comparison with the Northern Hemisphere species (Table 2).

Southern Hemisphere lampreys

Short-headed lamprey

The short-headed lamprey is endemic to south-eastern regions of Australia and Tasmania (Potter et al., 2015). The upstream migration distance for short-headed lamprey is reported to be >1600 km (Renaud, 2011). Much of the information that is available is speculative or estimated from limited samples, including the effects of human impacts on the current population. The short-headed lamprey is a parasite that feeds on the blood of at least four different hosts over an estimated span of 23 months (Potter et al., 1968; Quintella et al., 2021; Renaud, 2011; Renaud and Cochran, 2019). The body size of adults is relatively small in comparison to the other anadromous lampreys (Fig. 1). Spawning has not been documented for the short-headed lamprey. Similarly, the environmental conditions that correspond with freshwater re-entry, upstream migration, and spawning of this species remain undocumented. Historically the short-headed lamprey was thought to be common in the far-upper tributaries of Australian rivers like the River Murray; however it is now considered rare (Bice and Zampatti, 2019).

Threats associated with short-headed lamprey include climate change, land development, dredging/excavation, pollution, artificial barriers, water quantity/stream flow management, water quality, predation, and disease (Bice and Zampatti, 2019; Hammer and

Table 2
Qualitative comparison of the anadromous lampreys of the world, ranked by the social, management, and research interest ("Interest"), defined as the relative intensity of human harvest ("C" = commercial; "S" = subsistence; "–" = none), management, and research ("H" = High, "M" = Medium, and "L" = Low).

Interest	Species (status)[a]	Harvest	Management intensity (and foci)	Research intensity
High	Sea lamprey *Petromyzon marinus* ("Least concern")	C	Europe: M – H (passage, harvest regulations); North America: L	Europe: H; North America: L – M
	Pacific lamprey *Entosphenus tridentatus* ("Apparently secure")	S	North America: H (passage, harvest regulations, hatchery production, translocation); Asia: L	North America: H; Asia: L
	European river lamprey *Lampetra fluviatilis* ("Least concern")	C	Europe: M (passage, harvest regulations, hatchery production, translocation)	Europe: H
	Arctic lamprey *Lethenteron camtschaticum* ("Least concern")	C, S	Japan: M (hatchery production, habitat restoration, translocation); Russia & North America: L – M	Japan: M – H; Russia & North America: L – M
Medium	Pouched lamprey *Geotria australis* ("Data deficient")	S	Australia & New Zealand: L	Australia & New Zealand: M
Low	Caspian lamprey *Caspiomyzon wagneri* ("Near threatened")	–	Europe & Asia: L	Europe & Asia: L – M
	western river lamprey *Lampetra ayresii* ("Secure")	–	North America: L	North America: L
	Short-headed lamprey *Mordacia mordax* ("Not assessed")	–	Australia: L	Australia: L
	Chilean lamprey *Mordacia lapicida* ("Data deficient")	–	South America: L	South America: L

[a]International status from Table 1.

Wedderburn, 2009; Wilson and Bignall, 2009; Fig. 2). Most recently, the species was threatened by major fish mortalities in the Murray–Darling Basin — likely caused by drought and prevailing weather conditions (MDBA, 2019). Events such as these and other events related to climate change are the most significant threats to short-headed lamprey (Wilson and Bignall, 2009).

The status of short-headed lamprey remains unassessed at the international level. However, status has been assessed at the regional level in Australia (Table 1). Management policies do not currently exist for short-headed lamprey in Australia, and the species will likely remain unmanaged until key knowledge gaps are addressed. Management actions that affect a "vulnerable" resident lamprey species that co-occurs with the short-headed lamprey, the Australian brook lamprey *M. praecox* (Wager, 1996), may also benefit the short-headed lamprey.

Pouched lamprey

The pouched lamprey has a wide southern temperate distribution occurring in western and eastern Australia, Tasmania, New Zealand (including Stewart and Chatham Islands), Chile, Argentina, Uruguay, Falkland Islands and South Georgia Island (McDowall, 1990). Recent investigations provided genetic and morphological evidence for a second *Geotria* species in South America (Nardi et al., 2020; Riva-Rossi et al., 2020). The Argentinian lamprey *G. macrostoma,* is distributed along the southeast coast of South America (presently from 40°S to 55°S; Riva-Rossi et al., 2020).

The upstream migration distance for pouched lamprey has been reported to be over several hundred kilometers (Moser et al., 2015a). Maximum upstream migration has been recorded in the low gradient Murray Darling Basin, Australia where pouched lamprey historically penetrated up to 2000 km inland, but now due to flow alterations and migration barriers they are rarely encountered past 800 km (Bice et al., 2019). The pouched lamprey is a predator, feeding on the flesh of marine animals (the number of species of which has not been documented) over an estimated period of 15 or more months (Quintella et al., 2021; Renaud and Cochran, 2019). The adult body size of pouched lamprey is intermediate to relatively large in comparison with other anadromous lampreys (Fig. 1).

Threats associated with the pouched lamprey include climate change, land development, dredging and excavation, pollution, artificial barriers, water quantity/stream flow management, habitat floodplain degradation, water quality, overharvest, predation, and disease (Maitland et al., 2015; Williams et al., 2017; Wilson and Bignall, 2009; Fig. 2). Climate change is anticipated to be a key threat across the distribution of pouched lamprey (Maitland et al., 2015; Williams et al., 2017; Wilson and Bignall, 2009).

Loss of access to habitat through artificial barriers, particularly high-head dams, is thought to be a primary threat causing the decline in pouched lamprey in New Zealand (James, 2008; Williams et al., 2017). In South America continued hydropower developments present a key threat to pouched lamprey (Wilkes et al., 2018). Harvest is an insignificant threat to pouched lamprey in Australia (Wilson and Bignall, 2009) and New Zealand (Williams et al., 2017). Within Chile, the Donguil River, Gorbea, supports a culturally and commercially important pouched lamprey fishery that is believed to be threatened by overharvesting, as well as point source and diffuse pollution from wastewater discharges, pesticides, and fertilizers from ongoing land development (Reyes et al., 2014). The disease, Lamprey Reddening Syndrome (LRS), has resulted in mass deaths of pre-spawning pouched lamprey from the lower South Island of New Zealand (Brosnahan et al., 2019; Williams et al., 2017). A similar condition to LRS has been reported as "haemorrhagic septicaemia" in pouched lamprey in Australia (Hilliard et al., 1979).

The status of pouched lamprey has been deemed "data deficient" at the international level (Table 1). However, the status of pouched lamprey varies throughout its range. Nationally, pouched lamprey has been assessed as "threatened — nationally vulnerable" in New Zealand, and regionally it has been assessed as "vulnerable" in South Australia, and as "declining" and a "poorly-known species not under imminent threat" in Western Australia. The status of pouched lamprey is unknown nationally and regionally within South America.

The lack of knowledge on the ecology of pouched lamprey inhibits the implementation of management across its range. Formal management plans have not been developed in Australia or South America. In New Zealand, statutes guide the management of indigenous fisheries, including the Fisheries Act (1996), Freshwater Fisheries Regulations (1983), and Conservation Act (1987). However, the mechanisms for management are not well-coordinated among legislative agencies, and no government agency actively manages or monitors populations of pouched lamprey. A number of national strategy documents were recently developed to help guide management actions. For example, in 2017, the Department of Conservation released a draft Threatened Species Strategy with pouched lamprey listed as one of the 150 priority threatened species. In 2018, the Biodiversity Collaborative Group released a draft National Policy Statement (NPS) on Indigenous Biodiversity and in 2019 an updated NPS for Freshwater Management (draft for discussion) was released by the Ministry for the Environment. Both of these NPSs aim to improve protection for threatened indigenous species and their habitats in New Zealand. Although these strategy documents now require development of plans to ensure land and water management enables threatened species to thrive, these documents have not yet led to the implementation of management actions.

Management of pouched lamprey in New Zealand has been led by Māori through tribal bylaws with a focus on harvesting (see Almeida et al., 2021). To improve management practices for pouched lamprey and support Māori in exercising their customary rights, Te Wai Māori Trust led the establishment of a collective of representatives from both Māori and government agencies in 2017. The collective developed a restoration strategy in 2018 to promote research to improve the ecological and cultural knowledge required to manage pouched lamprey populations.

Chilean lamprey

The Chilean lamprey occurs in Chile and in the estuarine and nearshore ocean environments of Chile (Pequeño and Sáez, 2016). Similar to the other *Mordacia* species, short-headed lamprey, information regarding the abundance, diet, migration, spawning, and marine phase is lacking for the species. The Chilean lamprey is a parasite, feeding on the blood of an undocumented number of marine animals for an unknown period of time (Quintella et al., 2021; Renaud and Cochran, 2019). The adult body size of the Chilean lamprey is small relative to other anadromous lampreys (Fig. 1).

Although direct evidence is lacking, we used our best professional judgement to identify threats associated with Chilean lamprey. These include land development, dredging and excavations, pollution, artificial barriers, water quantity/stream flow management, habitat degradation, decreased water quality, and predation (Fig. 2). Chilean lamprey has not been considered for fish passage at barriers. The status of the Chilean lamprey is not known, and it has been deemed "data deficient" (Table 1). The lack of knowledge on the ecology of Chilean lamprey inhibits management throughout its range. Formal management plans have not been developed.

Northern Hemisphere lampreys

Caspian lamprey

The Caspian lamprey occurs in the Caspian Sea and freshwater rivers draining into this basin. The Caspian lamprey is the only anadromous lamprey in this region (Holčík, 1986; Nazari et al., 2017). This species migrates into rivers in its northern, western, and southern watershed (Holčík, 1986; Nazari et al., 2017) in Iran, Kazakhstan, Russia, Azerbaijan and Turkmenistan (Nazari et al., 2017). The maximum upstream migration distance for Caspian lamprey has been reported as $\leq$1500 km (Moser et al., 2015a); however, historically it was $\leq$2631 km (Berg, 1948). The distance of upstream migration by the Caspian lamprey has since been significantly truncated by artificial barriers. Caspian lamprey feed on invertebrates, demersal fish eggs, and dead fishes, and is therefore considered a scavenger in the Caspian Sea, where it feeds for an unknown period of time (Nazari et al., 2017; Quintella et al., 2021; Renaud, 2011; Renaud and Cochran, 2019). The adult body size of the Caspian lamprey is medium relative to other anadromous lampreys (Fig. 1).

The Caspian lamprey is scarce throughout its range, and there is a need to enhance protection of this species (Mitrofanov and Mamilov, 2015). Currently, few spawning sites remain in rivers draining from the eastern part of the Caucasus Mountains in Russia and Azerbaijan, the Volga River Basin in Russia, and some rivers in Iran, where it may have stabilized at a minimum level (IUCN, 2019; Nazari et al., 2017). Threats associated with the Caspian lamprey include climate change and drought, dredging and excavation, pollution, artificial barriers, water quantity/stream flow management, habitat degradation, decreased water quality, predation, disease, and overharvest (Abdoli et al., 2017; Coad, 2016; Nazari et al., 2017; Fig. 2). Climate change is a key threat which has led to recent and dramatic declines in precipitation, resulting in severe droughts and loss of spawning grounds in the southern Caspian Sea Basin (Nazari et al., 2017). The loss of spawning grounds and decreased water quality from pollution are two major causes of the decrease of this species (Kiabi et al., 1999; Maitland et al., 2015; Nazari and Abdoli, 2010; Nazari et al., 2017). Dam construction in the Volga River (Russia) has blocked the Caspian lamprey from reaching productive spawning grounds (Holčík, 1986), and this species appears to have been extirpated above dams in the Sura River (Docker and Potter, 2019). Caspian lamprey currently use spawning grounds below dams, where this fish is at risk from drought (Nazari et al., 2017). In Kazakhstan, the Caspian lamprey has always been considered rare (Mitrofanov and Mamilov, 2015) as the result of decreasing habitat and substantial alterations in spawning habitat caused by hydroelectric projects (Nazari et al., 2017). The Caspian lamprey has apparently been extirpated from the Kuma, Terek and Kura (IUCN, 2019). The Caspian lamprey has disappeared in the Sefid River, is rare in the Anzali Lagoon and tributaries in Iran (Nazari et al., 2017), and extirpated from the Turkish Aras River Basin (Fricke et al., 2007; Nazari et al., 2017; Table 1). The reproductive success of the Caspian lamprey may also be negatively affected by increasing concentrations of heavy metals in rivers (Eagderi et al., 2017; Nasrolah Pourmoghadam et al., 2015). Overharvest is a threat to the Caspian lamprey because many fishermen in Iran kill or leave this species to die on the river bank in the unsubstantiated belief that it parasitizes other commercially-important fishes (Nazari et al., 2017).

Although the status of the Caspian lamprey varies considerably across its range (depending on the authority, Table 1), three themes are apparent: 1) this species is not listed or protected in some countries; and internationally it is 2) "highly threatened"; and 3) "data deficient". As in other parts of the world, most of the conservation efforts in Iran focus on commercially important fishes. In Iran, the Caspian lamprey receives no legal protection and management plans are lacking (Nazari et al., 2017). The Caspian lamprey is protected in Russia, where two governmental agencies are responsible at the state level. Conservation actions identified for other anadromous lampreys, such as barrier removals, fishway construction, and restoring and managing river habitats (e.g., Clemens et al., 2017b) could also be considered for the Caspian lamprey, in addition to managing pollutants (e.g., municipal sewage, pesticides, and heavy metals) of Iranian rivers (Nazari et al., 2017). Raising public awareness can also play an important role in management.

Sea lamprey

Sea lamprey are endemic to the North Atlantic Ocean. This distribution includes freshwater drainages in North America and Europe (including northern Scandinavia). The species occurs south and east to the Mediterranean Sea and south and west to the Gulf of Mexico and freshwater drainages into these marine waters (Potter et al., 2015; Renaud, 2011). The maximum upstream migration distances reported for sea lamprey in Europe and North America are 850 and 320 km, respectively, but artificial barriers throughout its distribution now generally limit spawning to within 100–200 km of the estuary (Moser et al., 2015a). The sea lamprey is parasitic, feeding on the blood of over 50 different species of animals for an estimated time period of 10–28 months (Quintella et al., 2021; Renaud and Cochran, 2019; Silva et al., 2014). The adult body size of the sea lamprey is the largest of all anadromous lampreys (Fig. 1). The biology of anadromous sea lamprey is well-studied in Europe, and less so in North America (Clemens et al., 2010; also see below).

Threats associated with sea lamprey include climate change, land development, artificial barriers, pollution (Gephard, 2019; Limburg and Waldman, 2009; Mateus et al., 2012), and overharvest (Europe; Almeida et al., 2018; Araújo et al., 2016; Mateus et al., 2012; Fig. 2). Climate change has been projected to reduce the abundance and distribution of sea lamprey in Europe (Almeida et al., 2018). By the end of the 21st century, it has been projected that sea lamprey will disappear from river basins bordering the east coast of the Adriatic Sea, in most of the Italian river basins, and in the majority of the river basins in the Iberian Peninsula (Lassalle et al., 2008).

Internationally, the status of sea lamprey is of "least concern"; however, status varies widely across its geographic range (Table 1). European populations are the most imperilled, and therefore receive the most protection. The sea lamprey is protected at the European Union level, and at the local level in some countries. Even though assessed as "least concern" at the global and European levels, it is listed as regionally threatened and nationally listed in some countries. For instance, the sea lamprey is "vulnerable" in Portugal and Spain. By contrast, status assessments and management plans for sea lamprey in North America are lacking (but see the Connecticut River Anadromous Sea Lamprey Management Plan, 2018; Table 1).

In Europe, efforts have been made to understand and rehabilitate sea lamprey and their habitats, with a focus on fisheries management and habitat restoration. For example, habitat restoration in the heavily-impounded Mondego River Basin (Portugal) included the construction of several fish passes to provide passage for fishes including lamprey (Almeida et al., 2018; Pereira et al., 2017; Pereira et al., 2019). A complementary set of conservation and management actions engaged local commercial fishermen and promoted dialogue among fishermen, scientists, and managers. For the first time in Portugal, a mid-season fishery interruption was legislated in 2013 to facilitate recolonization of sea lamprey upstream (Almeida et al., 2018; Mateus et al., 2015; Stratoudakis et al., 2016). This integrated approach to restoring connectivity of river habitats in the River Mondego is currently being replicated in other Portuguese watersheds.

In North America, the non-game status of sea lamprey translates to a lack of direct management among most federal, state, and provincial agencies. Few management efforts focus specifically on anadromous sea lamprey. Dam removals, fishway construction, and habitat improvements targeting other highly-valued anadromous fishes probably also benefit sea lamprey by addressing threats (Watson et al., 2018; Fig. 2). For example, removal of smaller dams has led directly to rapid recolonization by sea lamprey (e.g., Hogg et al., 2013). Examples of the few entities that directly manage for sea lamprey in the USA include the Connecticut River Department of Energy and Environmental Protection and their partners (Gephard, 2019), the Maine Department of Marine Resources (grants permits for take), and the Penobscot Indian Nation (may grant harvest permits in tribal waters). Groups like Downeast Salmon Federation and Project SHARE in Maine use a holistic approach to species management by restoring ecological in-stream processes, improving connectivity, and rehabilitating anadromous fish communities (Pess et al., 2014; Saunders et al., 2006), with sea lamprey as one beneficiary. Similar efforts exist in other large watersheds like the Connecticut River, where initial focus on charismatic Atlantic salmon *Salmo salar* and American shad *Alosa sapidissima* expanded to include sea lamprey as public perceptions and management philosophies evolved (Gephard, 2019). A combination of dam removal, improved passage through fishways, and translocations of pre-spawn adult sea lamprey into vacant habitat has been successful in restoring populations to the Connecticut River watershed (Gephard, 2019).

Pacific lamprey

Pacific lamprey is distributed in the North Pacific Ocean, including the Bering and Chukchi seas, and freshwater drainages in North America and Japan. This species is not known to enter freshwater drainages in Russia. The latitudinal range of this species is the greatest of all lampreys at > 50° (Renaud, 2008). The maximum upstream migration distance for Pacific lamprey had been reported to be up to 800 km (Renaud, 2011) and ~1200 km (Clemens et al., 2017b). Although Renaud (2011) reported, "spawning migrations of 800 km up to Kettle Falls, Washington (USA)...", he likely meant 800 *miles* (=1200 km). Further migration distances may occur (but remain unreported) in Canada. Further investigation suggests that Pacific lamprey was documented to migrate upstream to Kinbasket Lake in the Upper Columbia River, a distance of 1615 km (Allan Schultz, pers. comm. 2020). Pacific lamprey are predators and parasites that feed on the flesh and blood of nearly 30 different species of marine animals over an estimated time period of 20–42 months (Clemens et al., 2019; Quintella et al., 2021; Renaud and Cochran, 2019). The adult body size of the Pacific lamprey is large relative to other anadromous lampreys (Fig. 1).

Threats associated with Pacific lamprey include climate change (Wang et al., 2020), oceanographic regimes, interactions between climate change and oceanographic regimes (Clemens et al., 2019), land use, artificial barriers, water quantity/stream flow management, habitat degradation, decreased water quality, host/prey availability, predation, overharvest, and disease (Arakawa and Lampman, 2020; Clemens et al., 2019; ODFW, 2020; Clemens et al., 2017b; CRITFC, 2011; Moyle et al., 2009; USFWS, 2019a; Fig. 2). However, evidence for overharvest and disease as threats is lacking (Clemens et al., 2017b; Jackson et al., 2019; USFWS, 2019a). Barriers to both upstream and downstream passage are a key threat (Clemens et al., 2017b; CRITFC, 2011; ODFW, 2020; USFWS, 2019a), as are water quantity/quality and habitat (Clemens et al., 2017b; ODFW, 2020). Commercial harvest used to occur for Pacific lamprey but has been banned (Close et al., 2002; Kostow, 2002).

Across the United States and Canada, the most recent international status assessment for Pacific lamprey is "apparently secure"; sub-assessments include "secure" in British Columbia to "critically imperilled" in the states of Washington, Idaho, and Oregon (the states of Alaska and California were assessed "apparently secure"; NatureServe, 2019). Within the United States, the U.S. Fish and Wildlife Service ranks Pacific lamprey as a "species of concern," (USFWS, 2019b), and it is recognized as being of "high conservation risk" in most basins in the USA (Wang and Schaller, 2015). The national status in other countries varies from no assessment in Russia and Japan to "threatened" in Mexico (Table 1).

Native American tribes were the first to raise awareness of the plight of Pacific lamprey and to promote the need for passage improvements at dams and other conservation measures. Pacific lamprey was petitioned to be listed under the federal Endangered Species Act, but the petition was declined based on lack of biological information and listable population units (USFWS, 2004). Several plans in the Pacific Northwest of North America exist for Pacific lamprey, including a Tribal Restoration Plan for the Columbia River Basin (CRITFC, 2011), the Pacific Lamprey Conservation Initiative (PLCI; USFWS, 2019a; Wang and Schaller, 2015), and several other regional plans by the U.S. Army Corps of Engineers and public utility districts (Clemens et al., 2017b). In addition, management plans specific to the state of Oregon have recently been completed (see ODFW, 2020). Best management practices have been developed (Crandall and Wittenbach, 2015; USFWS, 2010), and an update to these has recently been completed (LTWG, 2020a). Some tribal agencies are conducting translocation of adults (Ward et al., 2012) and hatchery production (CRITFC et al., 2018; Lampman et al., 2021). In the USA, harvest of Pacific lamprey is regulated in the states of California, Oregon, Washington, and Idaho (as revealed by an internet search of fishing regulations, by state agency).

Pacific lamprey have been extirpated in reservoirs following impoundment and subsequently restored following dam removal (reviewed in Docker and Potter, 2019; Maitland et al., 2015; but see Larson et al., 2020). This underscores the importance of providing passage (Moser et al., 2021). Provision of passage for all life stages has increased (e.g., Moser et al., 2011; Moser et al., 2015b), and detailed passage guidelines for adults are available (LTWG, 2017; LTWG, 2020b). Agencies are working collaboratively on mitigating the impacts of larval and juvenile entrainment into water diversions (Clemens et al., 2017b; Lampman and Beals, 2020). Although habitat restoration for salmonids (*Oncorhynchus* spp.) is thought to also benefit Pacific lamprey (Streif, 2009), habitat restoration specific to Pacific lamprey is also now being considered (Gonzalez et al., 2017; Homel et al., 2019). Finally, the PLCI has created Regional Implementation Plans (RIPs) to address threats specific to particular regions, and attempts to find funding for prioritized research and restoration projects that address threats within these regions. These RIPs have increased interagency collaboration for restoration and research on Pacific lamprey.

Western river lamprey

Western river lamprey is endemic to the nearshore ocean and estuaries of the eastern portion of the North Pacific Ocean. This distribution includes freshwater drainages in North America, from British Columbia south into California (Potter et al., 2015; Renaud, 2011). Western river lamprey occurs in estuaries and the nearshore ocean (Bond et al., 1983; Vladykov and Follett, 1958; Weitkamp et al., 2015). Although information is sparse on the maximum upstream migration distance for western river lamprey, juveniles were recently found 348 km (Jolley et al., 2016) and 608 km (Lampman et al., 2014) upstream from the ocean. However, western river lamprey is a paired species with the western brook lamprey (*L. richardsoni*, a resident species; Docker, 2009), and western brook lamprey is present in these upper freshwater reaches. Therefore, the aforementioned juveniles of western river lamprey may have originated from offspring of western brook lamprey (Jolley et al., 2016; Lampman et al., 2014). Western river lamprey prey on the flesh of at least 16 different marine and estuarine animal species over an estimated time period of 3–4 months (Quintella et al., 2021; Renaud and Cochran, 2019). The adult body size of western river lamprey is the smallest of all anadromous lampreys (Fig. 1).

Threats associated with the understudied western river lamprey include climate change, oceanographic regimes, interactions between climate change and oceanographic regimes, land use, artificial barriers, water quantity/stream flow management, habitat degradation, decreased water quality, predation, and host/prey availability (Maitland et al., 2015; Mesa and Copeland, 2009; Moyle et al., 2009; ODFW, 2020; Fig. 2).

The status of western river lamprey in North America had been assessed as "vulnerable" (Table 1). More recently the status of western river lamprey overall was assessed as "least concern" (Maitland et al., 2015) and "secure" (Table 1), ranging from "apparently secure" in British Columbia and "vulnerable" in Oregon and California, to "imperilled" in Alaska and Washington (NatureServe, 2019). Within the United States, the U.S. Fish and Wildlife Service ranks western river lamprey as a "species of concern". Western river lamprey was petitioned to be listed under the federal Endangered Species Act, but the petition was declined based on lack of biological information and listable population units (USFWS, 2004). Best management guidelines have been created for Pacific lamprey with applications to western river lamprey and other, less understood lampreys in North America (LTWG, 2020a). With the exception of a conservation plan in Oregon (ODFW, 2020), no known management actions specific to western river lamprey have been instituted in particular localities or throughout their range. In the USA, harvest of western river lamprey is regulated in the states of California, Oregon, and Washington.

European river lamprey

The European river lamprey is distributed in the Northeast Atlantic Ocean and associated freshwater drainages in Europe as far north as Scandinavia and as far south as Portugal and Italy (Potter et al., 2015; Renaud, 2011). The maximum upstream migration distance for European river lamprey is >3000 km (Gdovka, Museum of Zoological Institute RAS, ZISP 25430-25432); however, artificial barriers have truncated upstream migration distances, in some cases down an order of magnitude. European river lamprey preys on the flesh of at least 12 different marine and estuarine species over an estimated time period of 3–24 months (Quintella et al., 2021; Renaud and Cochran, 2019). The adult body size of the European river lamprey is relatively small (Fig. 1).

The international status of the European river lamprey is classified as "least concern" (Table 1). However, the status of this species varies greatly among countries, with status concerns in the southern distribution ("critically endangered" in Portugal and "regionally extinct" in Spain) and more stable status in central and northern countries. Threats to the European river lamprey include climate change, land use, artificial barriers, water quantity/stream flow management, habitat degradation, decreased water quality, host/prey availability, predation, harvest, and disease (Fig. 2; Aronsuu et al., 2015; Foulds and Lucas, 2014; Lucas et al., 2009; Mateus et al., 2012; Mateus et al., 2019; Thiel et al., 2009). Climate change may modify migration behaviour of the European river lamprey (Aronsuu et al., 2015). However, two threats, artificial barriers and overharvest, are thought to be the most significant.

Artificial barriers to spawning grounds are the primary threat to European river lamprey throughout Europe (Aronsuu et al., 2015; Lucas et al., 2009; Mateus et al., 2012; Mateus et al., 2019). Mitigation of these barriers occurs through translocation of adults past the barriers or provision of upstream passage for adults at the barriers. Translocation of lampreys above migration barriers has been employed in several rivers in Finland and in Sweden (Sjöberg, 2011). Fish ladders in Finland have been modified to enable passage of adult European river lamprey using brushes (Sjöberg, 2011). The upstream passage performance of adult European river lamprey has been tested with studded plastic tiles (Tummers et al., 2016; Tummers et al., 2018; Vowles et al., 2017).

Historically, the European river lamprey was harvested extensively in several British rivers (Almeida et al., 2021; Docker et al., 2015; Foulds and Lucas, 2014; Masters et al., 2006). Currently the largest commercial harvest for European river lamprey occurs in rivers that flow into the Baltic Sea. River lamprey fishing exists in Sweden, Finland, Estonia, Latvia, Lithuania, Poland, Russia; Almeida et al., 2021; Lajus et al., 2013; Renaud, 2011; Sjöberg, 2011). Fishing for European river lamprey in Latvia and Estonia is restricted during the later part of the spawning run, and fishing gear and season is regulated in Finland and Russia. Harvest of European river lamprey in Sweden is regulated according to the Bern Convention (Convention on the Conservation of Migratory Species of Wild Animals, 1979). Because the European river lamprey is protected by a number of European directives (Table 1), several management measures are under way (reviewed in Mateus et al., 2019).

Arctic lamprey

Arctic lamprey is distributed in the Arctic Ocean, North Pacific, and associated freshwater drainages in Canada, the United States (Alaska), Japan, and Russia (Potter et al., 2015; Renaud, 2011). The maximum upstream migration distance for Arctic lamprey has been reported to be >2100 km (Moser et al., 2015a), and this species has been observed spawning >2036 km from the sea in North America. Historical distribution of Arctic lamprey may have been as high as 4200 km (near Omsk city in Russia) in the Amur river — up to China, but is now greatly truncated by artificial barriers in many areas throughout its range. Arctic lamprey preys on the flesh of at least 9 different marine and estuarine species over an estimated time period of 24–48 months (Quintella et al., 2021; Renaud and Cochran, 2019). The body size of this species is approximately medium, relative to other anadromous lampreys (see Fig. 1 for further details).

Threats to Arctic lamprey are not well understood, but likely include climate change, oceanographic regimes, interactions between climate change and oceanographic regimes, artificial barriers, water quantity/quality, habitat degradation, decreased water quality, host/prey availability, overharvest, and predation (Fig. 2; Arakawa et al., 2018; Brown et al., 2005; Hayes et al., 2008). Climate change is a key threat that is projected to occur rapidly at the high latitudes that Arctic lamprey inhabit, yet the cumulative impact from this threat is still unclear (Arakawa et al., 2018; Brown et al., 2005; Hayes et al., 2008). Declines in host fishes may contribute to recent low numbers in adult Arctic lamprey (Siwicke and Seitz, 2015). Overharvest may be a key threat to this species because it is harvested both commercially and for subsistence by Indigenous and local people throughout its range (e.g. Yukon and Kuskokwim rivers, Alaska, and many rivers on Hokkaido and Honshu islands, Japan; Arakawa et al., 2018; Brown et al., 2005; Hayes et al., 2008). With the exception of the Amur River in Russia, the population dynamics of Arctic lamprey are unknown (Almeida et al., 2021). Therefore sustainable harvest rates for Arctic lamprey are unknown in all but the Amur River. In Japan, key threats include adult passage barriers, freshwater habitat degradation, and overharvest (Arakawa and Yanai, 2017; Fukushima et al., 2007; Hokkaido Government Ishikari Sub-prefectural Bureau, 2007; Shirakawa et al., 2009). Concern over pesticides and wastewater pollutants on water quality has recently increased (Arakawa et al., 2018; Hokkaido Government Ishikari Sub-prefectural Bureau, 2007).

The international status of Arctic lamprey is "least concern"; however, status varies considerably across its range, with medium to high concern in Asia and unknown conservation status in North America (Table 1). The Arctic lamprey is under protection in some areas in Russia, and is recognized as "vulnerable" nationally in Japan and "critical" in some of its prefectural governments. By contrast, the status of Arctic lamprey across the United States and Canada is "apparently secure" (Table 1).

Arctic lamprey is harvested commercially in Alaska, Japan, Russia (Almeida et al., 2021; Brown et al., 2005; Hayes et al., 2008). In Japan, management actions have included artificial propagation, adult translocation, larval habitat restoration, and outreach (Hokkaido Government Ishikari Sub-prefectural Bureau, 2007; Kataoka, 1985; Kataoka and Hoshino, 1983; Takeuchi et al., 2007). Although some prefectural governments regulate harvest, resource management for Arctic lamprey, in general, is still lacking in Japan. Best management guidelines have been created for Pacific lamprey with applications to other, less understood lampreys like Arctic lamprey in North America (LTWG, 2020a). Although Arctic lamprey is not formally protected in Alaska, subsistence and commercial harvest for this species is regulated by the Alaska Department of Fish and Game (ADFG, 2006) and are restricted to the lower and middle reaches of the Yukon River.

Research needed to inform management

Research needs have been identified many times in previous publications. Specifically, calls have been made for more research in each of three different categories: 1) for better taxonomic resolution and an improved ability to identify lamprey species in the field; 2) for acquisition of more data on the distribution and abundance of anadromous lampreys in freshwater; and 3) the need to improve the understanding of the freshwater biology, ecology, threats, and threat mitigation for anadromous lampreys (Kucheryavyy et al., 2017; Maitland et al., 2015; Mesa and Copeland, 2009; Moser and Mesa, 2009; Nazarov et al., 2016; Renaud et al., 2009). Artificial barriers are a primary threat to anadromous lampreys (see also Moser et al., 2021); therefore, research to inform passage requirements is important (e.g., Mesa and Copeland, 2009; Nazari et al., 2017; Pavlov et al., 2017; Zvezdin et al., 2019).

Recent advances in research and management of lampreys are encouraging. These include taxonomy, genomics, genetic species identification, genetic stock structure, and tools for monitoring various life stages (Docker and Hume, 2019). However, new or extended research often requires more time and funding, and includes competition and trade-offs with the needs of humans and other animals (Stephen and Wade, 2018). Ironically, in some cases, the alternative — more research, more time, and more funds — may prohibit management progress by waiting to take management actions that may not require comprehensive data. Without management actions, lamprey declines may outpace research and management and research progress in some geographical areas. Management action in the absence of more data may not work for all species or in all situations. Consideration of risks, uncertainties, and application of the precautionary principle can help establish the best course of adaptive management for lampreys (e.g., see work on natural resource issues in Dovers and Handmer, 1995; Falcy, 2016; Nichols and Williams, 2006).

The four anadromous Southern Hemisphere lampreys are the least understood with respect to their distributions, biology, and ecology. For example, the spawning behavior and reproductive ecology of all *Mordacia* species remains unknown, with knowledge of *Geotria* spawning ecology limited to pouched lamprey and only recently documented in New Zealand (Baker et al., 2017a) and within the laboratory (Paton et al., 2019). Knowledge of the biology of Southern Hemisphere lampreys lags behind that of Northern Hemisphere species. The biology of pouched lamprey and short-headed lamprey poses unique challenges to researchers. Adults entering freshwater have limited space in the body cavity to implant radio transmitters (Baker et al., 2017b; Bice et al., 2019). Externally mounted radio tags are also problematic as both pouched lamprey and short-headed lamprey bury themselves in large substrates, and as shown for pouched lamprey, they can quickly shed the tag (Jellyman et al., 2002). In addition, the weight of adult pouched lamprey (75–200 g) precludes using active radio tags that last the 16 month period from stream entry to spawning, a concern that may also hold for the Argentinian lamprey and other, smaller anadromous lampreys (Fig. 1). The pouched lamprey is the only known lamprey species to spawn exclusively in completely concealed substrate cavities (Baker et al., 2017a).

Relative interest levels in anadromous lampreys

The current state of management of anadromous lampreys and future needs for each species can be understood within the context of social interest (human harvest), and the level of management and research intensity. We qualitatively categorized anadromous lampreys into three levels of interest: high, medium, and low (Table 2). The first category, "high", corresponds with the occurrence of harvest, status assessments, research and biological understanding (Docker et al., 2015). Species in this category are subjected to relatively high levels of management and research intensity in parts of their range. This includes sea lamprey in Europe, Pacific lamprey in the USA, European river lamprey, and Arctic lamprey in Japan. These species have international statuses ranging from "least concern" to "apparently secure" (Table 2). The second category is "medium" and corresponds with the occurrence of harvest, limited status assessments, and limited research that is nevertheless increasing rapidly. This research is being led by Indigenous peoples in collaboration with researchers. However, this species lacks formal management plans. The pouched lamprey is the sole species in this category, and it has an international status of "data deficient". The third category is "low" because of the absence of harvest, status assessments, and research and management plans. The species in this category include the short-headed lamprey, Caspian lamprey, Chilean lamprey, and western river lamprey. These species have international statuses that are quite varied, including "not assessed", "data deficient", "secure", and "near threatened".

We note an interesting correlation between the maximum body size of anadromous lampreys, their distributions, and the level of interest in them. The general pattern is that the largest anadromous lampreys exhibit the widest distributions, and generally receive the greatest human interest (sea lamprey, Pacific lamprey); whereas, smaller species are less-widely distributed, less well-understood, and receive less human interest (e.g., Caspian lamprey, Chilean lamprey, short-headed lamprey, and western river lamprey; Fig. 1; Table 2). The pouched lamprey is approximately in the middle of the relative body sizes of anadromous lampreys, exhibits a fairly wide distribution, and experiences a medium level of human interest. A notable exception is the relatively small European lamprey, for which human interest is high. However, it is interesting that this species exhibits the ability to migrate upstream thousands of kilometers, which may have made it more accessible to fishers historically.

The reasons for the degree of human interest in each of the anadromous lampreys are undoubtedly complex, and may pertain to geographic differences in ecosystems and human ecology (e.g., culture, sociology, anthropology). That being said, we hypothesize that the general correlation between body size and distribution of anadromous lampreys and human interest may be related to the accessibility of these lampreys to fishers, relative conspicuousness (large animals are generally more noticeable), and relative nutrition, all factors relating to optimal foraging by humans on lampreys. This may partly explain why Northern Hemisphere lampreys tend to be of more interest to humans relative to Southern Hemisphere lampreys as the Northern Hemisphere exhibits higher human population density than the Southern Hemisphere and has many more entities in charge of managing them. This suggests that for at least some smaller-bodied lampreys for which little human interest currently exists (Caspian lamprey, short-headed lamprey, Chilean lamprey, and western river lamprey), concerted education and outreach, management, and research may be especially important.

Conclusions

The international assessments of anadromous lampreys that were done in 2019 are nearly identical to those done in 2013 (Maitland et al., 2015). For current status assessments within particular lamprey species, some geographical areas exhibited a significantly worse status than the international status (Table 1). Disparities in status (and nomenclature) at the international, regional, and national levels had been identified previously (Maitland et al., 2015). Improved coordination within and among governments could promote communication and collaboration on management actions for anadromous lampreys (Maitland et al., 2015).

Several threats are common to anadromous lampreys, and different approaches have been taken to address them (Fig. 2). We compared anadromous lampreys based on the relative amount of human interest they receive (Table 2). The extent of management actions towards anadromous lampreys varied as much across species as across geographical ranges within species (Table 1). The absence of recreational and commercial fisheries on many of the anadromous lampreys of the world creates a paradigm where funding is unavailable to monitor and manage them, thus perpetuating lack of awareness and scientific understanding. This lack of awareness, along with key information gaps, different levels of human interest, and common threats pose challenges to managing anadromous lampreys.

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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