Review

Population structure in anadromous lampreys: Patterns and processes ☆

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ABSTRACT

Population structure can reveal the diversity, gene flow, and dispersal of a species. This information can be used to make management decisions and reveal fundamental aspects of an organism's biology. Distinct intrinsic (e.g., biological characteristics) and extrinsic (e.g., geographical and historical events, environment, human pressures) factors can influence population structure, with significant differences among species. However, detection of population structure in migratory lamprey species can be difficult to detect due to their lack of natal homing; this is particularly the case for anadromous lampreys, with their potential for wide dispersal at sea during their parasitic feeding stage. We review phenotypic and genetic markers, as well as the methods that have been used to assess population structure in lampreys, and discuss the relative strengths and limitations of each. Structure has been detected in several anadromous species using some of these methods, even without homing in these species, but we briefly contrast the weak population structure observed in anadromous species with the stronger structure observed in freshwater-resident lamprey species (particularly non-migratory brook lampreys). We relate lamprey population structure to species-specific ecological traits, such as juvenile dispersal tendencies, and provide case studies of six species. Delineation of appropriate management units in migratory lamprey species is important for conservation and management.

Contents

Introduction

Population structure may exist in many distinct ways and be determined by multiple factors. In migratory species, structure is usually connected to a departure from panmixia (i.e., genetically homogenized populations). Population structure is here considered at various levels and representing different aspects of lamprey (Petromyzontiformes) life histories, as it can be determined by intrinsic biological characteristics (e.g., dispersal capacity of individuals; Spice et al., 2012) or by external environmental factors (e.g., geology; Mateus et al., 2011). All these factors shape population structure in lampreys, which is in turn confounded by the complexity of life histories present in this group of animals. Structure can be genetically determined or be a consequence of phenotypic plasticity in response to the environment experienced during certain life stages. Underlying genomic variation under selection or drift can drive evolutionary changes if environmental or anthropogenic pressures continue to act, especially in allopatric populations that are separated by a barrier (e.g., Docker and Potter, 2019). Regardless of its origin, recognizing structure is important to understand the connectivity and interactions (or lack thereof) of individuals and populations, and enables inference about, for instance, ongoing or ancestral migration patterns and the mechanisms that drive adaptation (e.g., Docker and Hume, 2019). In regard to conservation, population structure can highlight: stable units, stocks, population bottlenecks, range expansions or contraction, migration patterns and dispersal, evolutionary lineages, and potentially imperiled sub-populations (e.g., Lança et al., 2014; Mateus et al., 2011; Spice et al., 2012). The identification of population connectivity and dispersal is fundamental for conservation, fisheries management, and the management of imperiled species (e.g., Lança et al., 2014; Mateus et al., 2011). Structure also has implications for controlling invasive species, for example, through identification of priority habitats and reconstructing invasion pathways (e.g., Docker and Hume, 2019; Marsden and Siefkes, 2019).

How population structure is assessed has changed over time. As new tools become available, our understanding of the mechanisms that generate structure changes. For instance, genetic and genomic approaches using modern techniques, like high-resolution markers that allow better coverage across the genome (and thus better detection of allele frequency differences between populations), have allowed the identification of population structure, connectivity, and adaptive variation previously not detected using traditional approaches (e.g., Hess et al., 2013; Hume et al., 2018;

Mateus et al., 2013a; Rougemont et al., 2017). Similarly, advancements in chemical analyses (e.g., eye lens microchemistry and fatty acid profiles; Evans, 2017; Lança et al., 2014; see below) and telemetry (see Docker et al., 2021) have provided additional insights into lamprey population structure and dispersal.

Of the 44 extant lamprey species generally recognized, nine are anadromous and parasitic, and a further nine are freshwater resident and parasitic. A tenth anadromous parasitic species, Geotria macrostoma, has recently been revalidated by Riva-Rossi et al. (2020), but currently little is known about its biology. The remaining 26 species are non-parasitic "brook" lampreys that do not feed at all after metamorphosis and remain within natal streams throughout life (Maitland et al., 2015). Many anadromous lamprey species have at least some populations that are parasitic and complete their life cycle in fresh water (Docker and Potter, 2019). There is considerable intraspecific variation in the size of the anadromous species, from typically large-bodied, wide-ranging forms to others described as dwarf or "praecox" forms that feed at sea for a reduced period of time (Docker and Potter, 2019). The establishment of freshwater non-parasitic populations by anadromous parasitic forms creates the so-called paired species (Zanandrea, 1959).

Anadromous lampreys, unlike other anadromous fishes like salmonids, do not home to natal streams (e.g., Bracken et al., 2015; Spice et al., 2012; Waldman et al., 2008), resulting in more limited population structure across a widespread geographic range due to the high likelihood of gene flow among individuals from different locations. In the absence of homing, Waldman et al. (2008) suggested that lampreys use a strategy the authors called the 'suitable river strategy' to complete their life cycle. According to this strategy, instead of returning to natal streams, migratory lampreys use chemical cues produced by stream-resident larvae to locate suitable spawning and rearing habitat (Bjerselius et al., 2000). However, some isolation by distance and local adaptation has been described in sea lamprey (Petromyzon marinus) (Bryan et al., 2005; Lança et al., 2014; Rodríguez-Muñoz et al., 2004) and Pacific lamprey (Entosphenus tridentatus) (Hess et al., 2013; Spice et al., 2012), suggesting that limits to dispersal at sea preclude total panmixia. The absence of strong structure in wide-ranging anadromous lampreys contrasts with that of most freshwater-resident lampreys, whose migration is more constrained by the water bodies that they inhabit or, especially in the case of brook lampreys, as the result of limited dispersal due to small body size and life history (Docker and Potter, 2019; Spice et al., 2019). Invasive sea lamprey in the Laurentian Great Lakes might be an exception to this

Table 1
Strengths and limitations of different data used for assessing lamprey population structure with examples of published studies.

Trait	Data Type	Strengths	Weaknesses	References
Phenotype	Morphometric and meristic characters (e.g., body size and tooth counts, respectively)	- Data relatively easy to collect (fast, economic, not very technical). - Data relatively easy to access (e.g., from a database, from published literature). - Non-destructive (advantageous when studying small, vulnerable populations).	- Highly conserved morphology of lampreys makes it difficult to infer population structure. - Morphology may be plastic and change in response to environment.	Beaulaton et al. (2008); Berg (1931); Creaser and Hubbs (1922); Lança et al. (2014)
Microchemistry	Statoliths (calcified structures analogous to teleost otoliths) and eye lens	- Can reveal chemical characteristics of the natal stream environment.	- Statolith elemental signatures change during metamorphosis, making it difficult to infer an adult lamprey's stream of origin from statolith microchemistry. - Local stream-specific differences in geology may overwhelm basin-wide signatures. - Technically challenging to collect data from and to analyze/interpret. - Costly. - Destructive	Brothers and Thresher (2004); Evans (2017); Hand et al. (2008); Lochet et al. (2013)
Genotype	Allozymes	- Possibility of different loci may be active at different stages of the life cycle.	- Ontogenetic shifts may not be significant.	Brussard et al. (1981); Jacobson et al. (1984); Beamish and Withler (1986); Schreiber and Engelhorn (1998)
	Mitochondrial DNA (mtDNA)	- Many sequences available in databases. - Capable of resolving phylogenetic relationships among lampreys and intraspecific structuring. - Relatively inexpensive and not technically complex	- Resolution of weak population structure in anadromous lampreys is more complex (e.g., requires the use of more variable mtDNA regions or larger sample sizes). - Not capable of detecting structure in recently diverged species.	Boguski et al. (2012); Bracken et al. (2015); De Cahsan et al. (2020); Docker et al. (1999); Docker et al. (2007); Espanhol et al. (2007); Genner et al. (2012); Goodman et al. (2008), Lang et al. (2009); Mateus et al. (2013b); Nardi et al. (2020); Mateus et al. (2011); Rodríguez-Muñoz et al. (2004); Spice et al. (2019); Waldman et al. (2004), Waldman et al. (2006); Waldman et al. (2008); Waldman et al. (2009); Yamazaki et al. (2006)
	AFLP	- Can detect restriction site polymorphisms across the whole genome. - High resolution. - No requirement for prior sequence information. - Ability to detect polymorphisms in different genomic regions simultaneously.	- Low number of studies. - Calculation of allele frequencies more difficult because AFLPs are not scored as length polymorphisms per se, but rather as presence-absence polymorphisms.	Meudt and Clarke (2007)
	Microsatellite loci	- Highly polymorphic, well suited for resolving questions of intraspecific variation. - Use of multiple microsatellite loci increases resolution and decreases error compared to mtDNA analysis with one or a few genome segments. - Loci developed for several lamprey species; capable of detecting population structure and contemporary gene flow in several wide-ranging parasitic species and brook lampreys.	- Highly speciesor genus-specific; usually have to be developed separately for each species or group of species. - Difficult to standardize among labs. - Not informative for assessing adaptive (non-neutral) differentiation.	Bracken et al. (2015); Bryan et al. (2005); Gaigher et al. (2013); Luzier et al. (2010); Mateus (2016); Mateus et al. (2016); McFarlane and Docker (2009); Rougemont et al. (2015); Schedina et al. (2014); Selkoe and Toonen (2006); Spice et al. (2011); Spice et al. (2012), Spice et al. (2019); Takeshima et al. (2005); Yamazaki et al. (2011, 2014)
	Next Generation Sequencing (NGS)	- NGS (e.g., RAD-seq) allows genotyping of high numbers of individuals without prior sequence data. - Pool-seq (genome resequencing) can provide millions of SNPs, but requires a reference genome. - GT-seq allows genotyping of thousands of individuals at a few hundred targeted SNP loci for dramatically decreased costs relative to other NGS approaches, but requires primer design to target a select subset of SNP loci. - NGS can identify both neutral and adaptive differentiation.	- Costly for some methods: - RAD-seq – $50 USD per fish (1000s of SNPs). - Pool-seq – $60 USD per fish (millions of SNPs). - GT-seq – few $ per fish (100s of SNPs). - Complexity of data analysis (advanced bioinformatic knowledge).	Campbell et al. (2015); Hess et al. (2013); Hess et al. (2020); Hess et al. (2021); Rougemont et al. (2017); Mateus et al. (2013a); Sard et al. (2020)

Table 1 (continued)

Trait	Data Type	Strengths	Weaknesses	References
	Parentage (PA) and sibling ship analysis (SA)	- Allows inference of the natal-origin of wide-ranging juveniles or returning adults by using assignments to a baseline of parents with known spawning sites or a baseline of full-siblings from known stream-rearing sites. - High efficiencies for cost effective genotyping of respective SNPs. - PA allow estimate total age and natal origin information. - Full sibship baseline can be used to identify natal origins of returning adults to sibling members of their family.	- Still logistical challenges to the successful implementation of these methods. - Successful implementation of PA requires a sufficient proportion of candidate parents from each target source and having a baseline of parents that spans the long lifetime of a lamprey. - PA and SA both require multi-year sampling.	Ackerman et al. (2017); Campbell et al. (2015); Hess et al. (2021); Steele et al. (2019)

rule—given both their large body size and the large lakes which they inhabit. Population structure of freshwater-resident sea lamprey is reviewed by Docker et al. (2021), although, for completeness here, discussion of the methods used to assess population structure include studies on Great Lakes sea lamprey.

In this review, we summarize different approaches used to assess lamprey population structure at various levels and over time, identify both patterns and processes and discuss how detecting structure is important for lamprey conservation and management. We focus on the nine anadromous species, most of which occupy relatively wide geographic ranges: six species from the Northern Hemisphere: Caspian lamprey (*Caspiomyzon wagneri*), sea lamprey, Pacific lamprey, western river lamprey (*Lampetra ayresii*), European river lamprey (*L. fluviatilis*), and Arctic lamprey (*Lethenteron camtschaticum*); and three species from the Southern Hemisphere: pouched lamprey (*Geotria australis*), short-headed lamprey (*Mordacia mordax*), and Chilean lamprey (*M. lapicida*). Of all lamprey species that feed in marine environments—with the exception of the recently revalidated *Geotria macrostoma*, which is not discussed here (Riva-Rossi et al., 2020)—we perhaps know the least about the Chilean lamprey. Based on larval collections, parasitic phase juvenile Chilean lamprey are likely restricted to the coast of Chile (Neira et al., 1988), but little else is known of their distribution at sea. We present as case studies specific examples of a few of the most well-studied lamprey species.

Assessing population structure in lampreys

Tagging studies were used as early as the 1950s to evaluate the dispersal abilities of juvenile sea lamprey in the Great Lakes (e.g., Applegate and Smith, 1951; Smith and Elliot, 1953; see "Dispersal tendencies at sea", below), but the degree to which a wide-ranging lamprey species forms a structured series of discrete populations has since been inferred by a number of additional methods. Methods showing genetic differentiation among locations imply barriers to or restricted gene flow among populations. In contrast, methods showing phenotypic variation (e.g., body size) among locations do not necessarily indicate genetic differentiation (e.g., if phenotype is environmentally determined), but they do suggest some restriction to dispersal of individuals among locations, or suggest that individuals disperse among locations in a non-random manner. Different phenotypic and genetic markers that have been used to assess population structure in lampreys are shown in Table 1, and the relative strengths and limitations of each are highlighted.

Phenotypic traits

Some of the earliest suggestions of population structure within wide-ranging lamprey species were derived from observations that body size varied considerably among locations (see Docker and Potter, 2019). For example, Berg (1931) reported that Arctic lamprey in the White Sea basin was smaller-bodied than elsewhere and suggested that this population should be considered a distinct subspecies. Although no longer recognized as a distinct subspecies (and other morphological and genetic differences have not been found), such size differences suggest that the smaller-bodied form does not disperse from the White Sea basin. Differences in sea lamprey body size among, and sometimes within, the Great Lakes likewise suggest population structure has a spatial component (Docker et al., 2021).

Size differences among upstream-migrating Pacific lamprey from different river systems have at times been used to suggest philopatry and local adaptation (i.e., population structure) in this wide-ranging species (Docker and Potter, 2019; Hess et al., 2013; Spice et al., 2012). However, recent studies show weak population

structure and instead habitat selection may be driving size-assortative mating and the differences recognized among locations even without reproductive isolation (see Pacific lamprey case study, below).

Given the highly conserved morphology of lampreys, it is not surprising that intraspecific differences in other morphometric (i.e., measurable) and meristic (i.e., countable) traits appear to be of little use in inferring population structure. For instance, at one time, number of myomeres (blocks of muscle tissue visible under the skin's surface) was used to separate Pacific lamprey into two subspecies (Creaser and Hubbs, 1922); however, this subdivision is no longer recognized. Nevertheless, Lança et al. (2014) found that morphological characters were able to partially differentiate sea lamprey from three regions of the western Iberian Peninsula (Portugal), which were consistent with cardiac muscle fatty acid signatures.

Microchemistry

Statoliths, calcified structures analogous to teleost otoliths ("ear bones"), are used by lampreys to maintain body orientation while swimming. Because statoliths are formed during development, they retain the chemical characteristics of the natal stream environment and have been explored in freshwater-resident sea lamprey as a means of identifying the stream of origin of adults, to provide insight into gross population structure of sea lamprey in the Great Lakes (Brothers and Thresher, 2004; Hand et al., 2008). Hand et al. (2008) were able to discriminate larvae from a small number of rivers reasonably well (e.g., with 82% classification success among streams in Lakes Michigan, Huron, and Superior), but several streams carried a common signature. Further, the ability to discriminate among lakes (when all streams within a lake basin were pooled) was only ~60%, presumably because local stream-specific differences in geology overwhelm basin-wide signatures (Hand et al., 2008). Perhaps most critically though, Lochet et al. (2013) found that statolith elemental signatures change during metamorphosis making it even more difficult to infer an adult lamprey's stream of origin from statolith microchemistry.

A pilot study by Evans (2017) investigated the use of the eye lens to identify sea lamprey natal origin. Using the concentration of 11 elements, classification success to individual streams and basins averaged 67% and 64%, respectively, but more research is required to determine the utility of this approach (e.g., regarding the effect of preservation and ontogeny on lamprey lens chemistry).

Genetic markers

Allozymes

Genetic population structure in lampreys was first studied using horizontal starch gel electrophoresis to characterize the spatial distribution of different allelic variants of enzymes (i.e., allozymes). It is believed that allozymes behave like neutral markers of gene flow, although it is possible that selection can maintain allelic differences even in the face of gene flow (Brussard et al., 1981). Several studies in the 1980 s used allelic frequency distribution of 4–6 polymorphic loci to examine genetic structure of sea lamprey in the Great Lakes (within and among lakes), and from the New York Finger Lakes, Lake Champlain, and Atlantic drainages (Brussard et al., 1981; Jacobson et al., 1984; Krueger and Spangler, 1981; Wright et al., 1985).

One potential concern regarding the use of allozymes, compared to DNA-based markers, is the possibility that different loci may be active at different stages of the life cycle, but Brussard et al. (1981) reported that ontogenetic shifts (i.e., between larval, metamorphosing, and adult life stages) were not significant. In contrast, concern regarding the use of larval samples (especially if only from one location within a drainage or region; Jacobson et al., 1984) is not specific to allozymes. Allozyme frequencies have been used in a similar manner in other lamprey species. For example, Beamish and Withler (1986) used allozymes to suggest genetic differentiation between Pacific lamprey from two rivers in British Columbia, and Schreiber and Engelhorn (1998) used the same approach to test for genetic differentiation among and between European river lamprey and European brook lamprey (*Lampetra planeri*) from different locations.

Mitochondrial DNA

Mitochondrial DNA (mtDNA) sequence variation has been extensively used to infer phylogenetic relationships and post-glacial movements or geological events that have shaped present structure (e.g., Mateus et al., 2013b). The conserved cytochrome *b* gene has been used to resolve relationships among lamprey species (e.g., Boguski et al., 2012; Lang et al., 2009), and mtDNA sequencing has even helped detect or suggest the existence of new lamprey species (e.g., Mateus et al., 2013b; Nardi et al., 2020). In many cases, mtDNA sequence variation has also been sufficient to resolve intraspecific structuring in non-migratory brook lampreys (e.g., De Cahsan et al., 2020; Mateus et al., 2011; Spice et al., 2019). However, it is difficult to detect recent speciation events with conserved mtDNA regions or intraspecific population structure when there is incomplete lineage sorting. Therefore, resolution of population structure in anadromous lampreys typically requires the use of more variable mtDNA regions (e.g., the control region), and, in the absence of fixed differences, larger sample sizes (several dozen to several thousand individuals) to detect differences in haplotype frequencies (see sea lamprey and Pacific lamprey case studies, below).

Amplified fragment length polymorphism (AFLP)

Only one study is known to have used amplified fragment length polymorphism (AFLP) variation to try to delineate population structure in lampreys; Lin et al. (2008) studied AFLP variation among Pacific lamprey from eight sites in Japan, Alaska, and the Pacific Northwest of North America. AFLPs, which can detect restriction site polymorphisms across the whole genome, have several advantages, including high reproducibility and resolution, no requirement for prior sequence information, and the ability to detect polymorphisms in different genomic regions simultaneously (Meudt and Clarke, 2007). However, AFLPs are not scored as length polymorphisms per se, but rather as presence-absence polymorphisms. As a result, they are not co-dominant (i.e., homozygous and heterozygous individuals appear identical), making accurate calculation of allele frequencies more difficult (Meudt and Clarke, 2007), and their use in lamprey population genetic studies was short-lived.

Microsatellite loci

Microsatellites have been the "marker of choice" for most recent lamprey population genetic studies. Microsatellites consist of repeating sequences of 1–6 nucleotides, and are presumed to be neutral markers. Because they have high mutation rates, usually involving changes in the number of repeats, microsatellites are highly polymorphic and are well suited for resolving questions of intraspecific variation (Selkoe and Toonen, 2006). Microsatellite loci can be amplified using polymerase chain reaction (PCR), and the number of repeats can be inferred from the size of the amplicon (Chistiakov et al., 2006). They are biparentally inherited (unlike mtDNA, which is maternally inherited) and co-dominant (unlike AFLPs), and use of multiple microsatellite loci (e.g., ~8–14 loci) increases resolution and decreases error compared to mtDNA analysis with one or a few genome segments (Selkoe and

Toonen, 2006). However, a disadvantage of using microsatellites is that they are highly species- or genus-specific and usually have to be developed separately for each species or group of species. Nevertheless, microsatellite loci have now been developed for several lamprey species (Bryan et al., 2005; Gaigher et al., 2013; Luzier et al., 2010; McFarlane and Docker, 2009; Schedina et al., 2014; Spice et al., 2011; Takeshima et al., 2005). Analysis of microsatellite variation has thus provided important insights into population structure in several wide-ranging parasitic species (e.g., Bracken et al., 2015; Bryan et al., 2005; Mateus, 2016; Mateus et al., 2016; Rougemont et al., 2015; Spice et al., 2012; Yamazaki et al., 2014), providing greater resolution in these species than was possible with mtDNA sequence variation (see case studies below). Microsatellite markers have also been used to assess population structure in brook lampreys (e.g., Mateus et al., 2016; Spice et al., 2019; Yamazaki et al., 2011), providing information on contemporary gene flow among sites that complements information from mtDNA sequencing regarding historical connectivity.

Genome-wide markers (e.g., RAD-seq markers)

More recently, next generation sequencing technologies have been used to generate large numbers of single nucleotide polymorphisms (SNPs) for use in lamprey population genomics studies. Such genome-scale population genetic studies were previously possible only in well-characterized model species (Davey and Blaxter, 2010). For example, restriction site associated DNA sequencing (RAD-seq), which sequences small segments (totalling ~0.1–10%) of the genome without requiring prior sequence data, allowed 518 Pacific lamprey to be genotyped at 4439 SNP loci, distributed across the target genome, at a reasonable cost (Hess et al., 2013). The majority of these SNPs (4068) were putatively neutral and thus valuable for examining genetic connectivity among locations, while 162 SNPs were identified as adaptive through outlier tests, and they permitted study of local adaptation. Sard et al. (2020) used RAD-seq to discover genetic variation in Great Lakes sea lamprey, and developed a RAD capture (RAPTURE) panel to genotype sea lamprey at 3446 RAD loci containing 11,970 SNPs. Capturing only the genomic regions of interest (i.e., targeted RAD tags) prior to next generation sequencing (Ali et al., 2016), Sard et al. (2020) rapidly and cost-effectively genotyped about 350 sea lamprey from five Great Lakes tributaries. RAD-seq has also been used to survey for genome-wide differences within and between European river and brook lampreys from different localities (Hume et al., 2018; Mateus et al., 2013a; Rougemont et al., 2017; see European river lamprey, case study).

Parentage and full-sibship analysis

The use of individual-level genotypic data to perform either parentage or full-sibship analysis to estimate migration rates between potential sources and sinks (e.g., Peery et al., 2008) is an emergent field in lamprey population genetics. These methods allow inference of the natal-origin of wide-ranging juveniles or returning adults by using assignments to a baseline of parents with known spawning sites or a baseline of full-siblings from known stream-rearing sites. The large number of markers required for accurate full pedigree reconstruction (i.e., >200 SNPs, Huisman, 2017) and high efficiencies for cost-effective genotyping of these SNPs (e.g., Campbell et al., 2015) have already been developed for Pacific lamprey (Parker et al., 2019) and sea lamprey (Sard et al., 2020). However, despite these technological hurdles having been overcome, there are still logistical challenges to the successful implementation of these methods in lampreys including Pacific lamprey (Electronic Supplementary Material (ESM) Appendix S1).

Parentage analysis (PA) has recently become a useful tool in species management. Implementation of PA has successfully been demonstrated in parentage-based tagging (PBT) applications across large geographic scales for salmonids (Steele et al., 2019) and on a smaller scale for Pacific lamprey (Hess et al., 2021). Parentage analysis requires genotypes of a set of candidate parents and offspring in order to identify the progeny of defined groups of spawners. The progeny identified in this way can be effectively aged and traced back to their precise natal origins, assuming the attributes of their parents (spawn year and location) are known. As an alternative to PA, the full sibship baseline can be used to identify natal origins of returning adults via full sibship assignment (SA) to sibling members of their family. This sibship baseline also requires a multi-year period to enable sampling of multiple years of out-migrating cohorts of juveniles from a set of major candidate natal-stream sources, as well sampling multiple years of returning adults that would be derived from the same families of sampled juveniles. We discuss these alternative methodologies through two similar scales of study designs that illustrate how logistical challenges can be weighed against the type of data gained (ESM Appendix S1).

Spatial and temporal distribution of anadromous lamprey populations

Dispersal tendencies at sea

Based on the distribution of spawning adults, juvenile anadromous lampreys likely forage in most of the temperate seas in both Northern and Southern hemispheres. Despite the vastness of oceanic basins, the heterogeneous nature of this environment—specifically bathymetry—concentrates life into much smaller areas based on the input of nutrients and subsequent plankton blooms supporting vast food webs. Planktonic blooms generally occur in the shallow margins of ocean basins, or in the vicinity of sea mounts. Elsewhere, oceans are sparsely populated and often referred to as "marine deserts" (Polovina et al., 2008; Ryther, 1969). As a consequence, lampreys foraging in marine habitats are unlikely to be randomly dispersed (see Quintella et al., 2021; Fig. 1). To ensure foraging is energetically efficient, juvenile lampreys probably associate closely with their hosts. The distribution of juvenile lampreys is, therefore, likely to be patchy and this non-random distribution could manifest as population structuring. The extent to which juvenile lampreys disperse at sea is still poorly understood; however, a better understanding of the feeding ecology of marine-phase anadromous lampreys is allowing for inferences regarding population structure. For example, Spice et al. (2012) suggested that sea lamprey, which are largely blood feeders, remain attached to their hosts for long periods of time. In contrast, Pacific lamprey, which are flesh feeders, switch to new hosts on a more frequent basis (Potter and Hilliard, 1987) and, as a result, are moved shorter distances at sea.

Direct observation of attached lampreys and wounds have allowed for the identification of the hosts of many marine-phase lampreys (Renaud and Cochran, 2019), with inferences on their feeding habits (and, therefore, their feeding habitats) made using their dentition (Potter and Hilliard, 1987; Renaud and Cochran, 2019; Renaud et al., 2009). Previous research on flesh-feeding lampreys has also led to the observation of tissues, hard structures, eggs, and internal organs in the digestive tract (Beamish, 1980a; Beamish and Williams, 1976; Maitland et al., 1984; Renaud et al., 2009). In over half of the samples that were examined in these studies, gut contents were not identifiable. Recently, Shink et al. (2019) used both visual observation and DNA metabarcoding of Arctic lamprey intestinal contents collected during trawl surveys in the eastern Bering Sea (2014 and 2015). Similar to previous lamprey diet studies, various structures and tissues from unknown prey species were visually detected in the gut contents; however, ten different ray-finned fish taxa were identified using DNA metabarcoding. The most commonly identified taxa in Arctic lamprey gut contents were cape-
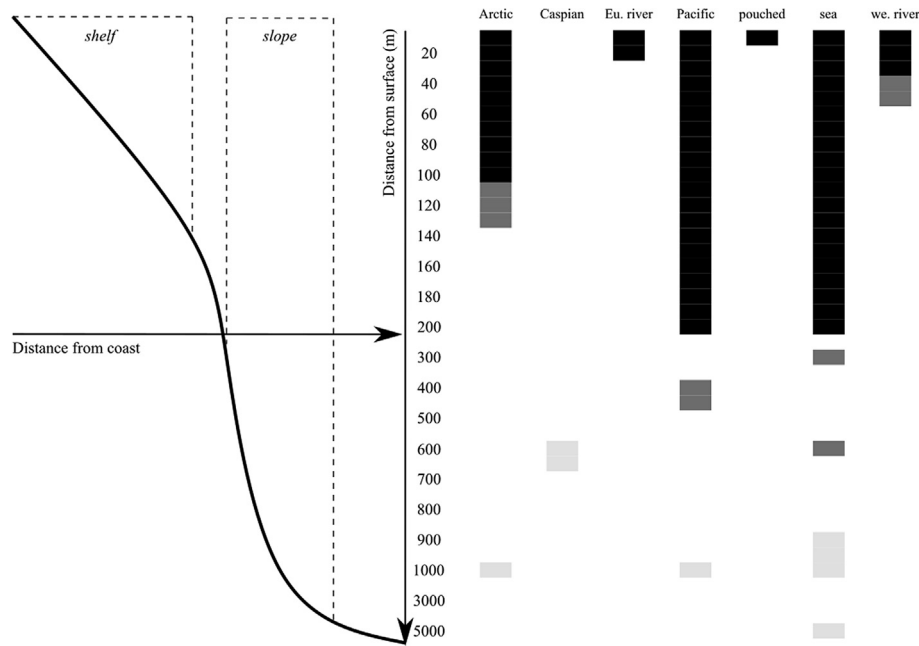
Fig. 1. Depth preferences of juvenile lampreys. Black bars show where the majority of specimens were recovered (>75%), grey where a few specimens were observed, and pale grey where only single specimens were observed. Note: Scale for the distance from the surface is not uniform.

lin (*Mallotus villosus*), Pacific sand lance (*Ammodytes hexapterus*), Pacific herring (*Clupea pallasii*), and various cods (*Gadus* spp.), and six of these taxa were reported as prey for the first time for this species. Pacific salmon (*Oncorhynchus* spp.) were only detected in 3.5% of Arctic lamprey samples. These results are in contrast to other lamprey studies, where predation on Pacific salmon was significantly higher (Beamish and Neville, 1995; Beamish and Youson, 1987; Novomodnyy and Belyaev, 2002; Shevlyakov and Parensky, 2010). These results corroborate previous research that has identified Arctic lamprey as a flesh-feeding lamprey, and also provide an example of using DNA metabarcoding as a means for characterizing lamprey food habits. A better understanding of the feeding mode and hosts of each lamprey species provide insights into the extent to which they will disperse at sea.

The co-evolution of phoresis (transport on a host), which permits at-sea dispersal, alongside adoption of a "suitable river strategy" (Waldman et al., 2008) to locate spawning tributaries using conspecific cuing of larval odor (Wagner et al., 2009), is in stark contrast to the regular migratory circuits and natal homing observed in other anadromous fish taxa (e.g., salmonids). However, this strategy enables juvenile lampreys to select from a wide range of hosts (Renaud and Cochran, 2019), whose own distributions shift in response to food availability, and establishes the suitability of spawning habitat on a contemporary timescale, avoiding entering rivers no longer suitable for reproduction. Both sets of information likely have ensured the evolutionary stability of this apparently haphazard dispersal strategy and enabled marine-feeding lampreys to colonize practically every ocean and sea basin. Available data concerning the dispersal of juvenile lampreys in marine environments is scant in comparison to other life stages, but fragmentary information on most species exists, with the exception of the Chilean lamprey (see case studies below).

The potential for local adaptation in the absence of homing in anadromous species

Local adaptation may be uncommon in anadromous lamprey species because high levels of gene flow among populations can counteract maintenance of a local optimum of genetic variation.

High gene flow can swiftly randomize genetic variation through recombination. Concentrated genomic architecture and the presence of inversions may be one way that highly dispersive species like anadromous lampreys can lock into place combinations of optimal genetic variants (genomic islands of divergence or supergenes; Hess et al., 2020). Inversion alleles can be maintained as polymorphisms in the population through forces of balancing and divergent selection (Faria et al., 2019). Whether the specific mechanism is understood or not there is evidence for local adaptation in Pacific lamprey and perhaps also in sea lamprey (see case studies below), despite a lack of natal homing. In the sea lamprey, morphological and physiological characters, which are apparently not genetically determined, reveal the existence of population structure possibly promoted by bathymetry during the juvenile life stage (Lança et al., 2014). Unlike local adaptation among anadromous species with high natal site fidelity, lampreys with particular behaviors, prey specializations, and body types may be passively sorted into spawning habitats where they are optimally suited, regardless if that is proximal to their natal origins.

Variable levels of gene flow and gene diversity related to geography and life history

There are differences related to the geographic distribution of populations that create structure within a species. The Quaternary climatic oscillations and geographic restrictions imposed by impassable glaciated areas are thought to have had major effects on the evolution and dispersal of numerous species (e.g., Lorenzini and Lovari, 2006; Taberlet et al., 1998). It is well-known that most fauna and flora presently distributed across Europe were isolated in southern refugia during glacial periods, many in the Mediterranean peninsulas of Iberia, Italy, and the Balkans (Hewitt, 1999). After the glaciers retreated and the climate warmed, founder populations retained in southern refugia expanded rapidly northwards, into newly available habitats, leading to a reduction from southern to northern Europe in the number of species, sub-specific divisions, and allelic variation (Hewitt, 1999). While most northern expansions were extirpated during subsequent ice ages, populations in southern areas could survive
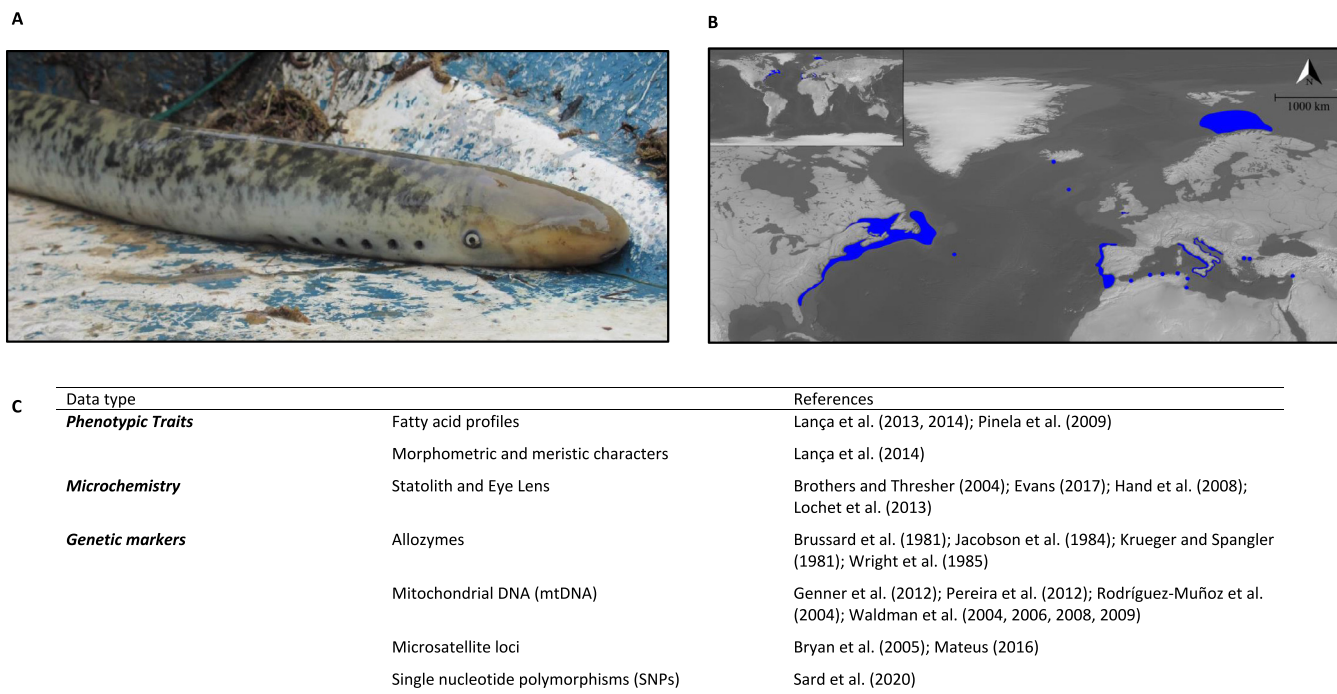
A

B

C

Data type		References
Phenotypic Traits	Fatty acid profiles	Lança et al. (2013, 2014); Pinela et al. (2009)
	Morphometric and meristic characters	Lança et al. (2014)
Microchemistry	Statolith and Eye Lens	Brothers and Thresher (2004); Evans (2017); Hand et al. (2008); Lochet et al. (2013)
Genetic markers	Allozymes	Brussard et al. (1981); Jacobson et al. (1984); Krueger and Spangler (1981); Wright et al. (1985)
	Mitochondrial DNA (mtDNA)	Genner et al. (2012); Pereira et al. (2012); Rodríguez-Muñoz et al. (2004); Waldman et al. (2004, 2006, 2008, 2009)
	Microsatellite loci	Bryan et al. (2005); Mateus (2016)
	Single nucleotide polymorphisms (SNPs)	Sard et al. (2020)

Fig. 2. A) Sea lamprey, *Petromyzon marinus* (photo ©Esmeralda Pereira); B) Distribution of sea lamprey juveniles in marine waters (Beamish, 1980b; Bird et al., 1994; Çevik et al., 2010; Clavero et al., 2014; Economidis et al., 1999; Haedrich, 1977; Halliday, 1991; Holčík et al., 2004; Lança et al., 2014; Nichols and Hamilton, 2004; Nichols and Tscherter, 2011; Novikov and Kharlamova, 2018; Pereira et al., 2012; Pinela et al., 2009; Potter et al., 2015; Silva et al., 2014; Tutman et al., 2020; Waldman et al., 2008; Zanandrea, 1961). Note: The absence of data on some locations (e.g., the French coast) is more likely due to a lack of study than a real absence; C) Methods used to access population structure in sea lamprey.

several of these glacial periods throughout the climatic cycles, and it is expected that bursts of speciation events at northern latitudes must have occurred in recent evolutionary times (Bernatchez and Wilson, 1998; Hewitt, 1999). Freshwater fishes tend to show particularly deep phylogeographic structure as they do not disperse between presently unconnected river basins, and thus the distribution of their lineages tends to reflect more the history of river drainages than contemporary dispersal (Gómez and Lunt, 2006). Recently deglaciated regions were relatively inaccessible to freshwater fishes but easily reached by anadromous fishes. Because anadromous fish reproduce in fresh water, they have ample opportunity to colonize unexploited post-glacial systems and establish freshwater isolates (Bell and Andrews, 1997). Many species inhabiting northern latitudes typically have larger geographic ranges than species from non-glaciated areas, which is largely due to post-glacial dispersal opportunities provided by proglacial lakes (Bernatchez and Wilson, 1998).

A well-known example of northern expansion following glacial retreat can be seen in European river and brook lampreys (*L. fluviatilis/L. planeri*), where the anadromous European river lamprey presumably gave rise to the freshwater-resident non-parasitic species. It is likely that previously glaciated areas in northern Europe may have been colonized by lamprey expanding out of Iberian refugia (Mateus et al., 2016). Permanence in more stable climates during ice ages promoted long periods of isolation and allopatric differentiation in the Iberian refugia (Espanhol et al., 2007, Mateus et al., 2011, 2013b, 2016), especially for freshwater-resident derivatives. In this region, there are non-parasitic resident lamprey species (*Lampetra alavariensis*, *L. auremensis* and *L. lusitanica*) that derived from a presumably extinct *L. fluviatilis*-like ancestor, as their lineage derived before that of present-day *L. fluviatilis* (Mateus et al., 2011, 2013b). The *L. fluviatilis/L. planeri* pair is apparently at different stages of speciation in different locations; there is evidence of high reproductive isolation in the southern

refugium, and low differentiation in the north (Mateus et al., 2016). In the Italian Peninsula, recent work has revealed high genetic differentiation of European brook lamprey from southern Italy compared to populations from northern Europe (De Cahsan et al., 2020), corroborating the pattern of glacial refugia in southern regions for lampreys.

Case studies

In this section, we present case studies relevant to understand the dynamics and complexity of life histories and population structure encountered in lampreys. We detail some aspects of dispersal tendencies, intraspecific differentiation, some peculiarities of paired species, and geographic variation in genotypic and phenotypic traits. The six species discussed (sea lamprey, Pacific lamprey, Arctic lamprey, pouched lamprey, European river lamprey, and western river lamprey) are presented from the largest in body size to the smallest (see Clemens et al., 2021, for body size variation across anadromous species).

Sea lamprey (Petromyzon marinus)

The anadromous sea lamprey is the largest of all extant lamprey species, with a body size at maturity typically ranging from ~600 to 900 mm total length (TL) (reviewed in Docker and Potter, 2019). The species is found along the eastern and western seaboards of the North Atlantic Ocean into the Mediterranean Sea (Potter et al., 2015). In some areas of its distribution, it has established parasitic freshwater resident populations, namely in the Laurentian Great Lakes, Lake Champlain, the Finger Lakes (Cayuga and Seneca lakes), and Oneida Lake (Docker and Potter, 2019; Docker et al., 2021). Juveniles can be encountered along most of the Atlantic coast of Europe and North America. In the western Atlantic basin, juveniles disperse along the coast from Newfound-

land, Canada, to as far south as Florida (Potter et al., 2015). In northern Europe, they appear sporadic and perhaps are rare (Holčík et al., 2004), although they have been captured in both fisheries-dependent and fisheries-independent surveys throughout the Greater North Sea (Elliott et al., 2021), and they can be found as far north as the Barents Sea (Novikov and Kharlamova, 2018) (Fig. 2). Sea lamprey are relatively scarce in the U.K. compared to France or Portugal, where the species is commercially harvested (Almeida et al., 2021; Beaulaton et al., 2008). However, juveniles have been recovered from the Severn Estuary, which drains into the Celtic Sea in southwest England (Bird et al., 1994). Sea lamprey juveniles have also been captured in the north Atlantic, off the south coast of Iceland (Pereira et al., 2012) although spawning has not been documented in Icelandic streams.

Juveniles also occur in the Mediterranean Sea, although less abundantly than in the Atlantic. Larval sea lamprey are rarely recorded from Balkan coast streams (Tutman et al., 2020), but perhaps the species has become scarce only in the last few decades (Holčík et al., 2004). Holčík et al. (2004) reported that Italian fishermen frequently encounter the species at sea, whereas it is virtually unknown by Balkan fishermen.

In the Adriatic Sea, juveniles appear most commonly in waters <100 m deep along both the Italian and Balkan coasts (Holčík et al., 2004; Fig. 1). This is consistent with captures of juveniles in the northwest Atlantic Ocean, off the coast of Nova Scotia and in the Gulf of Maine (Halliday, 1991). In recent reports of juvenile sea lamprey from the Barents Sea, specimens were captured in pelagic trawls 15–50 m deep, and in bottom trawls set at 128–159 m deep (Novikov and Kharlamova, 2018). Reports of sea lamprey from the bathypelagic (700–1000 m below surface) zone (Beamish, 1980b), or from the abyssopelagic zone (>4000 m below surface) are very rare occurrences (Haedrich, 1977). In such cases, capture may in fact have taken place at any point nets began fishing or during retrieval, not necessarily the deepest point. Regardless, given the distance from the nearest spawning habitat, such individuals may be vagrants that do not survive to reproduce. Juvenile sea lamprey may move into deeper waters as they grow, but too few data are available to establish this, and it appears all sizes largely remain on the continental shelf and slope while foraging (Beamish, 1980b; Halliday, 1991).

The variety of methods used to assess population structure in sea lamprey are shown in Fig. 2C. Together with Pacific lamprey, it is one of the best studied anadromous lamprey species. From the early 1980s, several studies used allozymes to examine genetic structure of sea lamprey in the Great Lakes and from the New York Finger Lakes, Lake Champlain, and Atlantic drainages (Brussard et al., 1981; Jacobson et al., 1984; Krueger and Spangler, 1981; Wright et al., 1985). Only Brussard et al. (1981) and Wright et al. (1985) included anadromous populations in their studies. They found that genetic distances among the three collection locations in the western Atlantic were small (Hudson River, Connecticut River, and Delaware River), but all North American populations (anadromous and freshwater) were genetically distinct from sea lamprey from the U.K. Later, studies using mtDNA analysis to investigate the demographic history and population structure of freshwater-resident and anadromous sea lamprey examined sequence variation in the hypervariable control region (~500 base pairs, bp) in several dozen to several hundred individuals (Genner et al., 2012; Rodríguez-Muñoz et al., 2004; Waldman et al., 2009, 2008, 2006, 2004). Although fixed differences were detected between North American and European sea lamprey populations (Rodríguez-Muñoz et al., 2004), resolution of population structure among locations on either side of the Atlantic Ocean relied on detection of more subtle differences in haplotype frequencies among population segments or, as with allozymes, the presence or absence of rare haplotypes (Waldman et al., 2004, 2006, 2008,

2009). The same pattern was observed by Mateus (2016) using microsatellite markers. The apparent within-region panmixia over several hundred miles along the North American coast (Waldman et al., 2004, 2006, 2008), and even greater distances in European waters (Genner et al., 2012; Mateus, 2016; Rodríguez-Muñoz et al., 2004), suggests juveniles mix in coastal areas before returning to spawn but do not stray across the Atlantic. In Table 2, we present a synthesis of published population genetic parameters across anadromous lamprey species.

Despite admixture occurring in European waters, there is some population sub-structuring among sea lamprey juveniles that could be influenced by diet in the coastal areas of Portugal. Lança et al. (2013), Lança et al. (2014) were able to distinguish two groups of juveniles based on their heart fatty acid profiles, which may have been feeding on either mesopelagic or benthic hosts in two or three contiguous regions of the continental shelf and slope. Differences in body composition imply that juvenile sea lamprey feed on regionally divergent prey types and suggest there is a lack of mixing among some groups. Lança et al. (2014) speculated that the observed heart fatty acid variation between southern and northern populations in Portugal reflects host availability, where the scarcity of pelagic hosts off the southern coast results in demersal host selection by southern population, while northern populations can select from both pelagic and demersal fishes. The authors also found that morphometric characters (particularly eye length, length of the second dorsal fin, and branchial length) were more useful than meristic characters (i.e., tooth counts) to differentiate groups. The existence of groups of sea lamprey along the Portuguese coast differentiated at the morphological and physiological levels (Lança et al., 2014), but not the genetic level (Mateus, 2016), may suggest localized variation as a result of ecological factors lampreys were exposed to during the oceanic trophic phase. The authors hypothesize that, following a dispersal and mixing period of out-migrating juveniles, foraging juveniles have a less mobile behavior associated with the isolated abyssal plains (and/or nearby continental slopes) off the western Iberian Peninsula, which would restrict the mixture of sea lamprey from different geographical groups (Lança et al., 2014).

The identification of stocks is essential for both fisheries and endangered species management and conservation, as is the case of sea lamprey in Portugal, where it is classified as Vulnerable (Cabral et al., 2005) and exploited by commercial fisheries. For instance, the probable existence of a common stock in northwestern Iberia, as detected by Lança et al. (2014), reinforced the need for international joint efforts to manage this resource, commercially exploited both in Portuguese and Spanish watersheds. The authors also detected that Tagus and Guadiana stocks (the southernmost populations) are a priority in conservation terms, as the number of lamprey entering these basins, particularly in the southern Guadiana River basin, is very scarce. The hydric stress known to occur in this basin, which is exacerbated by the potential effects of climate change, makes this stock especially prone to extinction.

Structuring has also been reported in Great Lakes sea lamprey. Sard et al. (2020) used RAD-seq to genotype sea lamprey from five Great Lakes tributaries (see Table 2 for details on genetic parameters). The greatest genetic differentiation was between the Lake Ontario basin and four tributaries to the upper Great Lakes (Superior, Michigan, and Huron), and differentiation at finer spatial scales and among cohorts was also possible (see Docker et al., 2021). Harvey et al. (2008) used stable isotope analysis to suggest that sea lamprey from the Black Bay region of Lake Superior, given their primary reliance on lower-trophic level fishes, are isolated from sea lamprey from other regions of the lake where they predominantly prey on mid-trophic level fishes. A better understanding of sea lamprey population structure has important implications

Table 2

Synthesis of published population genetic parameters (marker type and number, general location, number of sites and individuals (range per site or total) sampled, F_{ST} or equivalent, gene diversity (H_e), and allelic richness) in anadromous lamprey species.

| Species	Marker (N)	Location	N sites (min–max per site or total)	Genetic differentiation	H_e (min–max)	Allelic richness (min–max)	Reference
P. marinus	Allozymes (4)	Lake Superior basin	18 sites (15–81)	F_{ST} = 0.02–0.06	–	–	Krueger & Spangler (1981)
P. marinus	Allozymes (4)	Northeastern North America and British Isles	53 sites (3253)	F_{ST} = 0.009–0.071	–	–	Wright et al. (1985)
P. marinus	Microsatellite (8)	Great Lakes	20 sites (23–48)	Θp =0.01–0.48	0.329–0.606	1.88–5.13	Bryan et al. (2005)
P. marinus	Mitochondrial control region (~600 bp)	Europe	16 sites (9–61)	Φ_{ST}= −0.071–0.853	–	–	Genner et al. (2012)
P. marinus	Microsatellite (12)	West Atlantic North American coast, Northern Europe and Iberian Peninsula	20 sites (8–50)	F_{ST} = −0.0109–0.287	0.10–0.64	1.25–4.19	Mateus (2016)
P. marinus	RAD-seq (11,818 SNPs)	Great Lakes	5 sites (1–162)	(Neutral loci) F_{ST} = −0.001–0.018 (Non-neutral loci) F_{ST} = 0.116–0.233	–	–	Sard et al. (2020)
E. tridentatus	AFLP	North America and Asia	8 sites (218)	F_{ST} = 0.042–0.182	0.066–0.111	–	Lin et al. (2008)
E. tridentatus	RFLP	British Columbia to California	81 sites (1246)	Φ_{ST} = 0.0143	–	–	Goodman et al. (2008)
E. tridentatus	Microsatellite (9) + RFLP	British Columbia to California	20 sites (965) 20 sites (530)	F_{ST} = −0.0032–0.0584 F_{ST} = −0.0494–0.3123	0.169–0.689 -	2.46–8.22	Spice et al. (2012)
E. tridentatus	RAD-seq (4439 SNPs)	British Columbia to California	21 sites (4–39)	(Neutral loci) F_{ST} = 0.000–0.057 (Non-neutral loci) F_{ST} = −0.003–0.818	–	–	Hess et al. (2013)
La. fluviatilis	Allozymes (24)	Central Europe	4 sites (11–35)	Gst = 0.0537	0.049–0.090	–	Schreiber & Engelhorn (1998)
La. fluviatilis	Mitochondrial Cytb (1173 bp), ATPase 6/8 (828 bp)	Europe	9 sites (1–3)	Φ_{ST} = 0.718	–	–	Espanhol et al. (2007)
La. fluviatilis	Mitochondrial non-coding region I (644 bp)	Rivers draining to North and Baltic seas	2 sites (24–28)	F_{ST} = 0.083	–	–	Pereira et al. (2010)
La. fluviatilis	Mitochondrial Cytb (1173 bp), ATPase 6/8 (829 bp)	Portugal	3 sites (1–13)	F_{ST} = 0.214	–	–	Mateus et al. (2011)
La. fluviatilis	Microsatellite (13) +Mitochondrial ATPase 6/8 (829 bp)	British Isles	11 sites (24–43) 4 sites (25–35)	F_{ST} = −0.000–0.0935 F_{ST} = 0.002–0.008	0.000–0.938 -	1.000–14.325 -	Bracken et al. (2015)
La. fluviatilis	Microsatellite (13)	France	17 sites (15–40)	F_{ST} = 0.000–0.120	0.480–0.542	3.068–3.769	Rougemont et al. (2015)
La. fluviatilis	Microsatellite (10) + Mitochondrial Cytb (1173 bp) ATPase 6/8 (829 bp)	Europe	3 sites (29–46)	F_{ST} = 0.011–0.146	0.000–0.678 -	1.000–3.667 -	Mateus et al. (2016)
La. fluviatilis	RAD-seq (14,199–17,330 SNP)	France	9 sites (14–26)	F_{ST} = 0.000–0.024	0.294–0.305	–	Rougemont et al. (2017)
La. fluviatilis	RAD-seq (7678 SNPs)	Scotland, U.K.	2 sites (36)	F_{ST} = 0.154	0.020–0.040	–	Hume et al. (2018)
La. ayresii	Mitochondrial Cytb (1191 bp)	British Columbia to California	5 sites (1–4)	–	–	–	Boguski et al. (2012)
Lethenteron spp.	Microsatellite (8)	Yukon River drainage, Alaska	3 sites (30–33)	F_{ST} = 0.048–0.057	0.364–0.515	2.696–2.958	Shink et al. (2018)
Le. camtschaticum	Microsatellite (7)	Far East, along Japan and Russia	12 sites (10–30)	F_{ST} = −0.049–0.171	–	2.714–3.714	Yamazaki et al. (2014)

to sea lamprey control, including delineation of management units within the Great Lakes, which could increase program effectiveness. For example, if sea lamprey disperse freely throughout a lake but not among lakes, lake-specific control programs may be more appropriate than a program operating at the scale of the entire Great Lakes basin (see Docker et al., 2021).

Pacific lamprey (Entosphenus tridentatus)

The Pacific lamprey is the largest and sole anadromous species in the genus *Entosphenus*; it is widespread in the North Pacific Ocean and occurs in drainages of western Canada, USA, Mexico, and Japan (Potter et al., 2015; Fig. 3). This species is typically a large-bodied anadromous lamprey, but considerable geographic variation in body size has been reported, with adults ranging from 130 to 850 mm TL. The wide variation in body size among rivers may be the most visually apparent evidence of local adaptation. In some locations, this species also exhibits variation in migration timing (Docker and Potter, 2019). Loci correlating with both body size and migration timing have been identified, indicating that there is a genetic basis for these different ecotypes (Hess et al., 2014, 2013; Parker et al., 2019). More recently, "ocean-maturing and stream-maturing" life history types, described by Clemens et al. (2013, 2016), have also been shown to have a genetic basis in two portions of the species' range (Klamath River and Willamette River; Hess et al., 2020; Parker et al., 2019). This latest life history type or ecotype with evidence of a genetic basis is related to the sexual maturation process (Clemens et al., 2016). Specifically, the ocean-maturing ecotype is most readily distinguished from the stream-maturing ecotype in females by the presence of large, ripe gonads at the time of freshwater entry of their adult migrations prior to spawning (Parker et al., 2019). The stream-maturing ecotype is presumed to require a freshwater overwintering period to mature prior to spawning the following spring; this ecotype is hypothesized to be adapted to cooler stream temperatures with faster flowing water (Clemens et al., 2016). The distribution of these body size, migration timing, and maturation traits may be largely influenced by the genetic diversity that has been described for portions of the species' range across the eastern Pacific Ocean.

Recognizing the role of natural selection and its influence on genetic markers has been key to synthesizing the various population genetic studies that have been conducted on Pacific lamprey over time (Fig. 3 C). Genetic studies that have employed mtDNA and microsatellite markers (Goodman et al., 2008; Spice et al., 2012), which appear to have had minimal influence from natural selection (i.e., being putatively neutral markers), have indicated a general lack of population structure or weak (but statistically significant) structure (Spice et al., 2012). However, genetic studies with AFLP and SNP markers (Hess et al., 2013; Lin et al., 2008; Parker et al., 2019), which may be influenced by natural selection (i.e., putatively adaptive markers), have shown higher levels of structuring within populations. According to a set of several thousand SNP markers that were determined to be neutral based on F_{ST} outlier tests, the Pacific lamprey range in North America may represent at least three different populations: 1) northern British Columbia; 2) Vancouver Island, British Columbia, and Puget Sound, Washington; and 3) the West Coast of the United States and the Columbia River basin (Hess et al., 2013). However, under the lens of adaptive variation (i.e., using putatively adaptive SNPs), these populations can be further resolved into large-bodied and small-bodied (Hess et al., 2014) and ocean-maturing and stream-maturing (Parker et al., 2019) ecotypes. The diversity of ecotypes and the genes that underlie these phenotypes is present within populations. Therefore, despite neutral variation being relatively homogenized in each of the broadly distributed populations, the adaptive variation is highly heterogenous and associated with ecotypes (Hess et al., 2014; Parker et al., 2019).

A

B

C
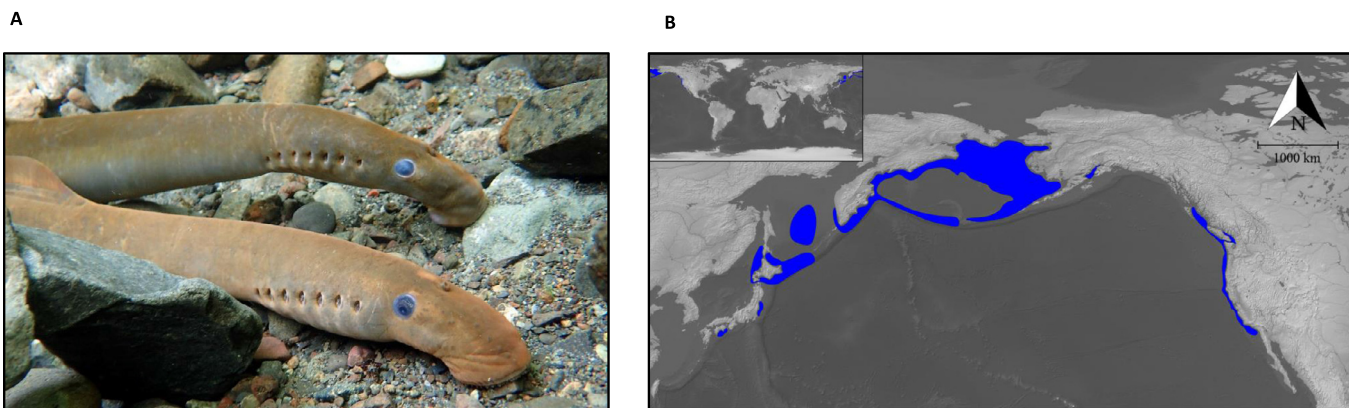
Data type		References
Phenotypic Traits	Morphometric and meristic characters	Creaser and Hubbs (1922); Docker and Potter (2019); Hess et al. (2013); Spice et al. (2012);
Genetic markers	Allozymes	Beamish and Withler (1986)
	Mitochondrial DNA (mtDNA)	Goodman et al. (2008); Spice et al. (2012)
	Amplified fragment length polymorphism (AFLP)	Lin et al. (2008)
	Microsatellite loci	Clemens et al. (2017); Howard and Close (2003); Spice et al. (2011; 2012)
	Single nucleotide polymorphisms (SNPs)	Hess et al. (2012, 2013, 2014, 2015); Parker et al. (2019)

Fig. 3. A) Pacific lamprey, *Entosphenus tridentatus* (photo ©Amanda Anderson); B) Distribution of Pacific lamprey juveniles in marine waters (Goodman et al., 2008; Lin et al., 2008; Morita et al., 2009; Orlov et al., 2008; Potter et al., 2015; Shevlyakov and Parensky, 2010; Spice et al., 2012; Wade and Beamish, 2016; Yamazaki et al., 2005); C) Methods used to access population structure in Pacific lamprey.

Despite evidence for associations of adaptive genetic variation with various ecotypes of Pacific lamprey, the traits that are the true targets of natural selection remain unclear. For example, differences in body size can manifest in a number of ways, including through differences in ocean duration and prey preference (Hess et al., 2014). Similarly, female gonad characteristics used to identify ocean-maturing and stream-maturing ecotypes could be correlated with traits such as spawn timing that are more difficult to measure but that could reveal the true target of selection (Hess et al., 2020). Further study examining a greater level of detail that spans physiological, behavioral, and morphometric differences is clearly needed for a better understanding of the population genetic structure of Pacific lamprey.

Pacific lamprey juveniles have been recorded from the coastal regions of the Japanese Archipelago where the species appears to spawn regularly, mainly on Shikoku, Hokkaido, and Honshu Islands (Yamazaki et al., 2005). Juvenile Pacific lamprey are especially abundant in the north Pacific, near the eastern Aleutian Islands (Orlov et al., 2008), the southern Sea of Okhotsk (Morita et al., 2009), and the east coast of the Kamchatka Peninsula (Shevlyakov and Parensky, 2010) (Fig. 3). Pacific lamprey foraging off the coast of Kamchatka may have travelled significant distances as they do not reproduce on this peninsula, and this may explain the low frequency of their wounds observed on Pacific salmonids here compared to Arctic lamprey (Shevlyakov and Parensky, 2010). Opportunistic physical tagging of juvenile Pacific lamprey has provided the first evidence that individuals are capable of migrating transoceanic distances, moving from the Bering Sea to the Columbia River (>5000 km, Murauskas et al., 2019). The species also spawns widely in rivers from British Columbia to southern California on the west coast of North America (Goodman et al., 2008), so they are presumably dispersed broadly along this coast.

Similar to sea lamprey, Pacific lamprey appear to forage along the continental shelf where they target pelagic and demersal fishes (Orlov et al., 2008; Fig. 1). Although juveniles may be captured at depths >1400 m, Orlov et al. (2008) report that >80% of juveniles captured in the Bering Sea, either in benthic or pelagic trawls, were foraging in water <200 m deep. This is consistent with juvenile Pacific lamprey feeding in the Strait of Georgia, which were most frequently captured between 30 and 100 m below the surface (Wade and Beamish, 2016). There does not appear to be a change in depth preference as juveniles grow, with Pacific lamprey up to 650 mm TL captured while feeding in water 5 m deep (Orlov et al., 2008). There is some evidence that Pacific lamprey juveniles perform diel vertical migrations in the water column, being captured more frequently in pelagic zones than benthic zones between the hours of 12:00 and 06:00, possibly as a result of tracking planktivorous prey species such as Alaska pollock (*Gadus chalcogrammus*) (Orlov et al., 2008).

Low levels of mtDNA variation have been observed among 81 Pacific lamprey populations ranging from British Columbia to southern California, a distance of ~2250 km (Goodman et al., 2008), using five restriction fragment length polymorphism (RFLP) assays to interrogate sequence differences at 18 polymorphic sites in >2600 bp of the ND5 and ND6 genes in 1246 Pacific lamprey (Docker et al., 2007). From the 29 composite haplotypes, three haplotypes were common throughout this region, and <1.5% of haplotype variation can be explained by variation among drainages within this area. Similar to the observed mtDNA variation in sea lamprey populations of the Atlantic, juvenile Pacific lamprey likely mix broadly in coastal waters and exhibit substantial rates of straying. However, although Lin et al. (2008) found evidence for high levels of historic gene flow, they also suggest genetic isolation by distance based on variation in AFLP loci in Pacific lamprey from Japan, Alaska, and British Columbia (see Table 2 for details on genetic parameters). These data suggest that panmixia between Asia and North America is constrained, but not as strongly as it is for sea lamprey on both sides of the Atlantic. However, Spice et al. (2012), using microsatellites, found higher genetic differentiation within North American west coast populations than would be expected should complete panmixia be occurring. Based on the narrow width of the continental shelf of the North American west coast (average 32 km), limited Pacific lamprey dispersal ability might be the cause, with individuals straying for short to moderate distances in a north–south direction as they track prey, and gene flow occurring in a "leap frog" fashion (Lin et al., 2008). Individuals that get transported off the shelf area may suffer higher rates of mortality as a consequence of failure to locate suitable hosts (Murauskas et al., 2013), from direct predation, or failure to relocate suitable spawning rivers (cf. Meckley et al., 2017). This is in stark contrast to the coastal shelf of the eastern coast of North America, which can extend up to 120 km, perhaps imposing less severe penalties on dispersing sea lamprey juveniles there and enabling greater degrees of gene flow north–south.

Efforts to improve our understanding of population structure of Pacific lamprey have implications for conservation and management. Pacific lamprey numbers in many rivers in the US have declined by orders of magnitude since the 1960s, but, until recently, conservation had been impeded by a lack of understanding regarding appropriate management units (see Spice et al., 2012). Although Pacific lamprey along the west coast of North America do not show strong population structure, new knowledge of weak isolation by distance and local adaptation even in the face of high gene flow (Hess et al., 2013) can help inform management decisions. For example, special attention may be required for management of sites exhibiting distinct genetically based ecotypes (Hess et al., 2013, 2014; Parker et al., 2019). Knowledge of the geography of population structure is also important during ongoing efforts to re-establish Pacific lamprey populations in the Columbia River basin through translocation (Hess, 2016; Maitland et al., 2015; Ward et al., 2012). In the absence of strong genetic population structure, translocations among regions may still be successful, but survival and fitness might be greatest when lamprey come from geographically proximal sites or from regions with similar ecotypes.

Arctic lamprey (Lethenteron camtschaticum)

The Arctic lamprey occurs as both anadromous and freshwater-resident forms, although anadromous populations are more common and widespread (see Docker and Potter, 2019). This species is found further north than any other lamprey species, being present to the northern tip of Alaska at about 72 °N. It has a wide distribution in the Arctic Ocean, being present from the White Sea in Russia to the Beaufort Sea in Canada and southwards to Japan in the western North Pacific Ocean (Potter et al., 2015; Fig. 4). Freshwater-resident populations of Arctic lamprey have been reported in Asia and North America, but they are not known from Europe (Docker and Potter, 2019). Like in the Pacific lamprey, the size at maturity in anadromous Arctic lamprey varies widely (ranging from <170 mm to >600 mm TL), and there appear to be geographical differences suggesting spatial structure (reviewed in Docker and Potter, 2019; see below).

Like other anadromous lamprey species, Arctic lamprey exhibit weak genetic differentiation across large geographic distances, but some signatures of isolation by distance are evident. Yamazaki et al. (2014) using microsatellite loci found that Arctic lamprey from the western Bering Sea were genetically divergent from specimens captured from Sakhalin in the Sea of Okhotsk, and both were somewhat divergent from other specimens captured from the Sea of Japan (see Table 2 for details on genetic parameters). These patterns appear consistent with limited movement of juveniles from
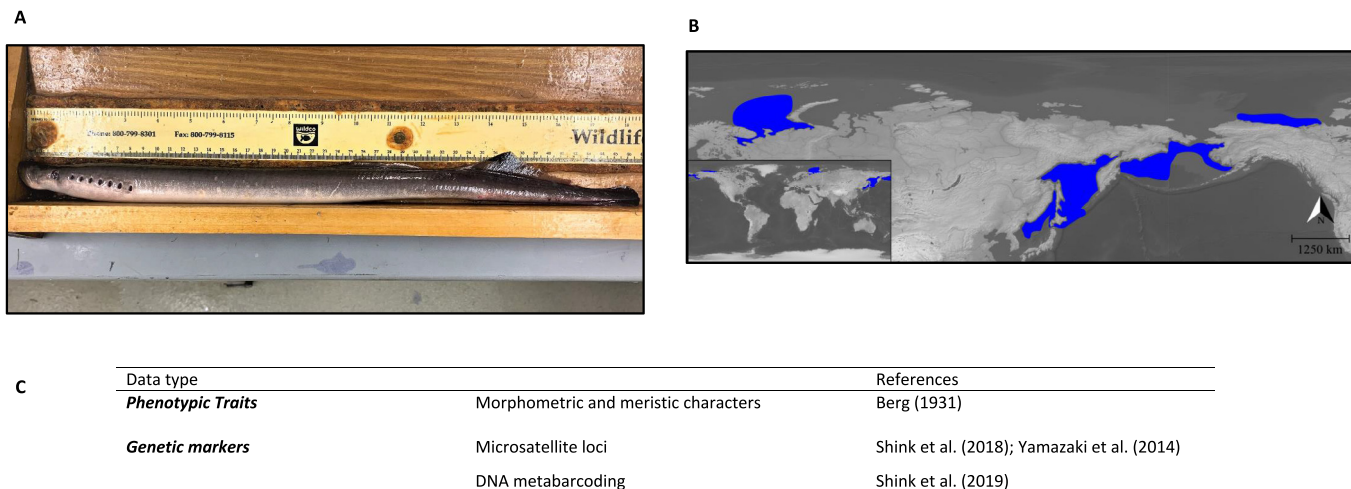
A

B

C

Data type		References
Phenotypic Traits	Morphometric and meristic characters	Berg (1931)
Genetic markers	Microsatellite loci	Shink et al. (2018); Yamazaki et al. (2014)
	DNA metabarcoding	Shink et al. (2019)

Fig. 4. A) Arctic lamprey, *Lethenteron camtschaticum* (photo ©Trent Sutton); B) Distribution of Arctic lamprey juveniles in marine waters (Makhrov et al., 2013; Morita et al., 2009; Novikov and Kharlamova, 2018; Orlov and Baitaliuk, 2016; Orlov et al., 2014; Shevlyakov and Parensky, 2010; Siwicke and Seitz, 2015; Yamazaki et al., 2014); C) Methods used to access population structure in Arctic lamprey.

the Bering Sea south around the Kamchatka Peninsula, and perhaps a larger aggregation of juveniles that remain near the mouth of the Amur River draining into the Strait of Tartar west of Sakhalin.

Although the ecological and/or environmental mechanisms leading to variable levels of gene flow among Arctic lamprey populations remain unresolved, Yamazaki et al. (2014) hypothesized that populations of this species are panmictic likely due to the lack of homing to their river of origin. In the eastern extent of their geographic range (i.e., North America), few studies have focused on the genetic structure of Arctic lamprey (ADF&G, 2006; Thorsteinsen and Love, 2016). As a result, there is a need to characterize the relatedness of Arctic lamprey in Alaska and Canada to allow comparisons of population-level genetic structure throughout their geographic distribution.

In Alaska, little is known about the population structure of Arctic lamprey and its closely related paired species, the Alaskan brook lamprey *Lethenteron alaskense* (Sutton, 2017). To increase the understanding of *Lethenteron* spp. in Alaska, Shink et al. (2018) examined larval genetic diversity among three Yukon River tributaries using microsatellite loci. Using a Bayesian clustering analysis approach, a single ancestral population, suggestive of panmixia, was identified, along with three genetic clusters. Within-river population structure detected panmixia within the two lower Yukon River populations, and levels of admixture that were reduced in the upper Yukon River. Contemporary gene flow estimates suggested reciprocal migration, albeit at reduced levels, among sites. Migration was symmetrical among populations, but with the highest migration rates occurring in a downstream direction. The values of F_{ST} (0.048–0.057) were indicative of restricted, but continuous gene flow among sampled tributaries. Shink et al. (2018) hypothesized that the resident, non-parasitic Alaskan brook lamprey may have contributed to the relatively high values of F_{ST} reported, in accordance with the current understanding of genetic differentiation among populations of non-parasitic lamprey species (Blank et al., 2008; Boguski et al., 2012; Bracken et al., 2015; Docker et al., 2012; Espanhol et al., 2007; Mateus et al., 2011; Rougemont et al., 2015). As noted above, contemporary estimates of migration were symmetric among sampling locations and non-migrant proportions were greater in the lower Yukon River. Reduced levels of heterozygosity and admixture suggested that dispersal was reduced, which is typical of resident life-history forms. As a result, gene flow among populations occurs at low

levels, preventing the formation of a single panmictic population. Additional analyses, including on adults that can be identified to species, are necessary for a more comprehensive assessment of gene flow and divergence between Arctic and Alaskan brook lampreys in the Yukon River drainage.

Regarding dispersal at sea, Arctic lamprey juveniles have been recovered in the northern Pacific Ocean, overlapping somewhat with Pacific lamprey juveniles near the Aleutian Islands (rarely), the Sea of Okhotsk (Morita et al., 2009; Orlov et al., 2014), and in Kamchatka Bay (Shevlyakov and Parensky, 2010). Details of these collections are scant. Shevlyakov and Parensky (2010) observed significantly higher frequencies of wounds on Pacific salmonids caused by feeding juvenile Arctic lamprey compared to Pacific lamprey in the waters off the Kamchatka Peninsula, suggesting Arctic lamprey are the dominant species in this area. Juveniles are common in the Japan Basin of the Sea of Okhotsk, and in the western (Orlov et al., 2014) and eastern Bering Sea (Siwicke and Seitz, 2015). The species is far rarer in the Gulf of Alaska (Orlov and Baitaliuk, 2016). Unsurprisingly, Arctic lamprey juveniles also forage within the Arctic Ocean basin, particularly in the Barents Sea. Makhrov et al. (2013) report that juveniles may stay close to river mouths and are abundant near the mouths of the Northern Dvina and Pechora rivers. Given the shallow and extensive nature of the shelf forming the Bering and Chukchi seas, Arctic lamprey juveniles may disperse widely in this region, penetrating west into the East Siberian Sea. The southern portion of the Barents Sea, where foraging juvenile Arctic lamprey are said to be abundant and targeting herring (Makhrov et al., 2013), contains a wide, shallow shelf with water typically <100 m deep. The majority of juveniles (84%) of this species were captured in the eastern portion of the Barents Sea at depths <40 m (Novikov and Kharlamova, 2018; Fig. 1), although a few were located down to 130 m. A similar preference for shallow water was observed in catches of juveniles from the Sea of Okhotsk and Bering Sea, where >80% of individuals were captured in water <100 m deep, and 90% from <400 m, but juveniles did occur as deep as 1000 m (Orlov et al., 2014). The Yukon River, a large system draining into Norton Sound in the eastern Bering Sea, attracts Arctic lamprey numbers adequate to support a seasonal fishery (Renaud, 2011). This would suggest juveniles form large aggregations in this region, which is rarely >40 m deep. Captures of juvenile lamprey and Pacific cod (*Gadus macrocephalus*) from the Bering Sea suggest Arctic lamprey are likely to be domi-
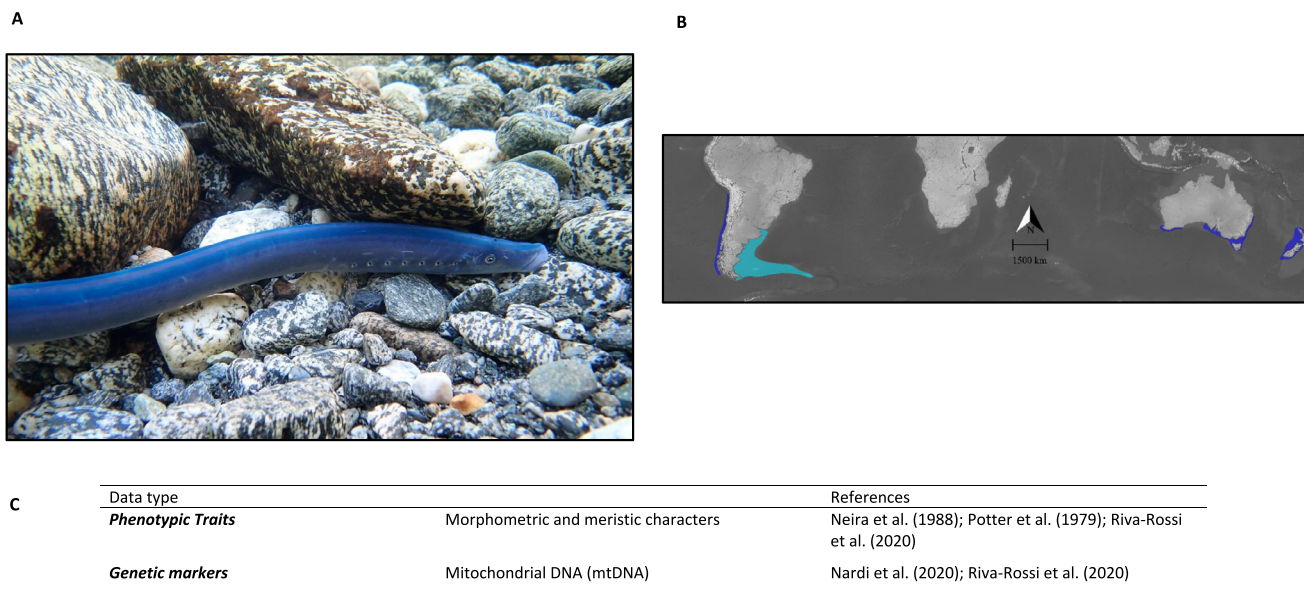
A

B

C

Data type		References
Phenotypic Traits	Morphometric and meristic characters	Neira et al. (1988); Potter et al. (1979); Riva-Rossi et al. (2020)
Genetic markers	Mitochondrial DNA (mtDNA)	Nardi et al. (2020); Riva-Rossi et al. (2020)

Fig. 5. A) Pouched lamprey, *Geotria australis* (photo ©Robert Holdaway); B) Distribution of *Geotria* spp. lamprey juveniles in marine waters (Azpelicueta et al., 2001; Beattie, 1920; Bice and Zampatti, 2015; Cobley, 1996; Kitson, 2012; Nardi et al., 2020; Potter et al., 1979; Riva-Rossi et al., 2020); Pouched lamprey are shown in dark blue, Argentinian pouched lamprey (*G. macrostoma*) shown in pale blue; C) Methods used to access population structure in Pouched lamprey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

nant along the continental shelf, and Pacific lamprey forage along the deeper slope where the cod experience only Pacific lamprey wounds (Siwicke and Seitz, 2015).

Arctic lamprey presumably feeding in the same sea basins as juveniles appear to exhibit large differences in body length as mature adults. Orlov et al. (2014) reports that Arctic lamprey spawning in rivers of western Kamchatka Peninsula average 270–290 mm TL, but in the Kuril Islands to the south, mature specimens average just 166 mm TL (see Docker and Potter, 2019). Perhaps owing to the extremely narrow ridge that forms the Kuril Islands (adjacent to several ocean trenches >7000 m deep), juveniles entering the southern Sea of Okhotsk have limited host availability in near shore environments. In contrast, Kamchatka's west coast is fringed by a much broader and shallow shelf <100 m deep where juveniles may better locate their prey.

Pouched lamprey (Geotria australis)

Pouched lamprey have a large range of distribution, spawning in rivers of South America, Tasmania, western Australia, and New Zealand (Fig. 5). As is the case with the Chilean lamprey, the pouched lamprey has not evolved freshwater-resident or praecox forms (reviewed in Docker and Potter, 2019). The majority of pouched lamprey typically measure 530–740 mm TL in Australia (Potter et al., 1983) and 445–570 mm in Chile (Neira, 1984) at the commencement of their upstream migration. Reports of juveniles are rather rare though, leaving large gaps in our knowledge of how connected these populations might be.

Juvenile pouched lamprey may comprise a substantial proportion of the diet of albatrosses in the South Atlantic Ocean (Potter et al., 1979; Prince, 1980; Reid et al., 1996). In South Georgia, Reid et al. (1996) found that pouched lamprey juveniles accounted for up to 79% of the estimated biomass of two albatross species. Given that these birds have limited capacity to dive, mostly restricted to feeding on the surface to <5 m below (Prince et al., 1994), juvenile pouched lamprey must be swimming close to the surface if they are to be preyed upon. In a remarkable case of serendipity, Cobley (1996) reported witnessing a black-browed

albatross *Thalassarche melanophris* plunge into the sea north of the Falkland Islands (Islas Malvinas) and grab a juvenile lamprey ~300 mm TL from near the surface. This predation event happened during daylight hours and the bird was then pursued by several others as it handled the lamprey. Prince (1980) and Reid et al. (1996) report juveniles up to 480 mm TL are preyed on by albatrosses, indicating there is no change in depth preference as they grow.

Potter et al. (1979) report no phenotypic differences between populations of juveniles from South America or Western Australia. However, Neira et al. (1988) found significant morphometric differences in pouched lamprey larvae collected in Argentina compared to Chile. The authors hypothesize that juveniles entering the eastern South Pacific disperse northwards along the coast using the Humboldt Current, which would preclude extensive mixing with juveniles entering the South Atlantic and dispersing east and south towards South Georgia. Neira et al. (1988) also reported that larvae from South America cluster separately from Australasian regions (western Australia, Tasmania, and New Zealand), and that Tasmanian larvae are somewhat separate from the other two. It is possible pouched lamprey foraging in the sea south of Tasmania are less likely to disperse north or east, whereas juveniles may be dispersed with surface currents from New Zealand west across the Tasman Sea to Australia.

Recently, using mtDNA genes, Nardi et al. (2020) and Riva-Rossi et al. (2020) suggested the existence of a new specific taxon, the Argentinian pouched lamprey, a sister species of *G. australis* which the latter authors (also by analysis of morphological characters) suggested should be revalidated as *Geotria macrostoma* (Burmeister, 1868). *Geotria macrostoma* can now be considered as a distinct species inhabiting Argentinian Patagonia, with a distinct evolutionary potential.

European river lamprey (Lampetra fluviatilis)

The European river lamprey is widely distributed throughout Europe, occurring in the Northeast Atlantic Ocean and associated freshwater drainages in Europe as far north as Scandinavia and
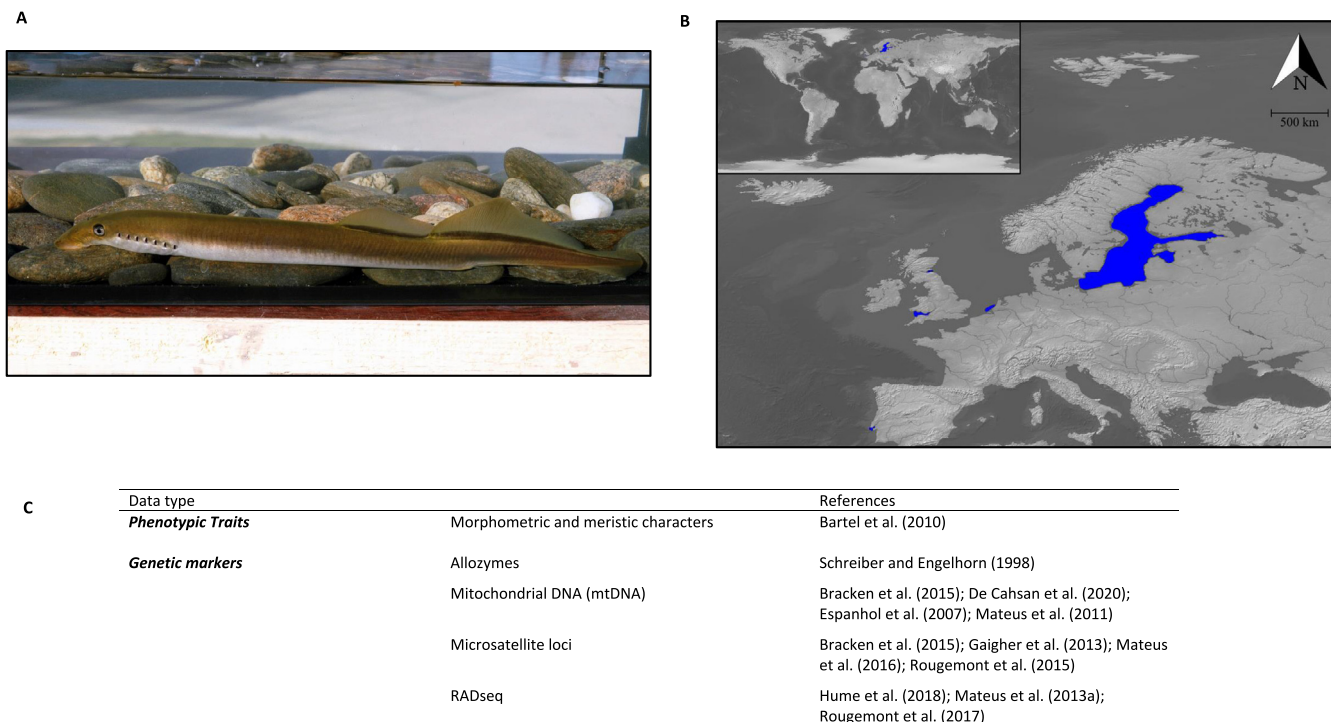
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Data type		References
Phenotypic Traits	Morphometric and meristic characters	Bartel et al. (2010)
Genetic markers	Allozymes	Schreiber and Engelhorn (1998)
	Mitochondrial DNA (mtDNA)	Bracken et al. (2015); De Cahsan et al. (2020); Espanhol et al. (2007); Mateus et al. (2011)
	Microsatellite loci	Bracken et al. (2015); Gaigher et al. (2013); Mateus et al. (2016); Rougemont et al. (2015)
	RADseq	Hume et al. (2018); Mateus et al. (2013a); Rougemont et al. (2017)

Fig. 6. A) European river lamprey, *Lampetra fluviatilis* (photo ©Bernardo Quintella); B) Distribution of European river lamprey juveniles in marine waters (Baer et al., 2018; Bartel et al., 2010; Maitland et al., 1984). Note: The absence of data on some locations (e.g., the French coast) is more likely due to a lack of study than a real absence; C) Methods used to access population structure in European river lamprey.

as far south as Portugal and Italy (Fig. 6), with a number of established freshwater populations in western Russia, Norway, Finland, and the British Isles (Docker and Potter, 2019; Elliott et al., 2021; Potter et al., 2015). A wide range of sizes has been reported for this species, with geographical variation in size, ranging from 200 to 492 mm TL (Mateus et al., 2016; Renaud and Cochran, 2019).

The first population genetic study in European river lamprey was performed with allozyme markers and revealed low differentiation (G_{ST} = 0.054) among populations from the Rhine, Elbe, and Warnow rivers (Schreiber and Engelhorn, 1998; Table 2). Population structure was further investigated with mitochondrial markers mainly in the Iberian Peninsula and United Kingdom (Bracken et al., 2015; Espanhol et al., 2007; Mateus et al., 2011, 2016), but Mateus et al. (2016) performed an extensive analysis that also included samples from Germany, Finland, Sweden, France, the Netherlands, and Denmark (Fig. 6C and Table 2). In general, these studies revealed low structure among lamprey populations, which is consistent with a scenario of recent founder expansion events.

The first microsatellite markers for European river lamprey were described by Gaigher et al. (2013). Bracken et al. (2015) used these markers together with cross-amplified microsatellites from other species to infer the population genetic structure of European river and brook lampreys, and the freshwater-resident form of European river lamprey in the UK. European river lamprey samples appear as a single mixed population showing low differentiation among nine populations (F_{ST} = 0–0.025), and a significant pattern of isolation by distance was detected (r^2 = 0.40). These authors found evidence of ongoing gene flow between European river and brook lampreys where they occurred sympatrically (Loch Lomond, Scotland, F_{ST} = 0.019), but five parapatric populations revealed to be distinct from river lamprey populations and from each other (F_{ST} = 0.060–0.191; all F_{ST} values significant). In France, Rougemont et al. (2015) also reported a weak genetic structure (F_{ST} = 0.022, from 0 to 0.102) among ten European river lamprey

populations using 13 microsatellites markers (Gaigher et al., 2013). A pattern of isolation by distance was also detected ($r_{spearman}$ = 0.79). Mateus et al. (2016) used another set of cross-species amplified microsatellite loci to genotype three populations of European river lamprey from Portugal, Germany, and Finland. At such a large spatial scale, the differentiation between German and Finnish populations was low (F_{ST} = 0.011; not significant at the 0.1% level) and moderate between European river lamprey from Portugal vs Germany and Finland (F_{ST} = 0.110 and 0.146, respectively; P < 0.001; Table 2).

Recent migration rates among migratory populations revealed that European river lampreys from Portugal is the most isolated population. This is likely due to its persistence in the Iberian glacial refugia during glacial periods. In previously glaciated areas from northern Europe, however, there is evidence of strong recent gene flow among populations, which might themselves have been colonized from lampreys expanding out of Iberian refugia (Mateus et al., 2016). This pattern is also evident in the differentiation between European river and brook lampreys in different regions. Mateus et al. (2016) found that this pair is apparently at different stages of speciation in different locations, showing evidence of high reproductive isolation between more ancient, sympatric populations, in the southern refugium (F_{ST} = 0.317), and low differentiation in the north. Previously, Mateus et al. (2013a) used RAD-seq in order to infer the genetic differentiation between brook and European river lampreys in the Sorraia River, Portugal, finding strong genetic divergence between species (F_{ST} = 0.37). Rougemont et al. (2017) also used a RAD-seq approach in nine population pairs of European river lamprey and brook lamprey in France and found a pattern of low differentiation among river lamprey populations, similar to the one observed with microsatellite markers (F_{ST} = 0.01, from 0 to 0.024; Table 2). They also found a low differentiation between species in sympatry (F_{ST} = 0.04–0.14) and a moderate level of divergence in parapatry (i.e., within the

same river but separated by migration barriers: F_{ST} = 0.07–0.21). The level of introgressive hybridization was moderate in the majority of UK watersheds (Bracken et al., 2015), although it was high in Loch Lomond (Hume et al., 2018). Hume et al. (2018) used RAD-seq to investigate gene flow between three lamprey sympatric ecotypes from Loch Lomond: brook lamprey, anadromous European river lamprey, and a freshwater-resident form of European river lamprey. The non-parasitic brook lamprey was highly admixed with the other two, suggesting extensive gene flow occurs, whereas the freshwater-resident parasitic lamprey was highly genetically distinct from its presumed anadromous ancestor. These data suggest both the resident populations (parasitic and non-parasitic) share a common, freshwater ancestor that likely colonized post-glacially in the Loch Lomond basin.

Other factors determining population structure in lampreys are the distributional range and dispersal capacities, size, and life cycle. Juveniles of European river lamprey are rarely observed while feeding in marine environments. Maitland et al. (1984) reported that high numbers of juveniles could be found in the Firth of Forth, on Scotland's east coast (Fig. 6). This is a large (~45 km long), shallow estuary (<10–20 m deep), and it harbors abundant hosts such as Atlantic herring (*Clupea harengus*) and European sprat (*Sprattus sprattus*), which appear to be favored by European river lamprey (Maitland et al., 1984). Here, the species may be restricted to the estuary as even fully grown individuals (>300 mm TL) forage here. In the Baltic Sea, the species is likely to be widely distributed and feed in large numbers, as tributaries of this shallow sea support consistently high spawning runs (Bartel et al., 2010). In fisheries-dependent and fisheries-independent surveys, Elliott et al. (2021) found that European river lamprey were recorded closer to the coast than sea lamprey. European river lamprey may express preference for shallower water compared to Pacific and sea lampreys, although its depth distribution is similar to Arctic and western river lampreys. The Baltic Sea, where the species is numerous, is on average only 55 m deep and nowhere exceeds 500 m. Juveniles may aggregate in the many large embayments such as the Gulfs of Bothnia, Finland, and Riga (Bartel et al., 2010). Juveniles are also common in large, shallow estuaries of the UK (Firth of Forth, Severn Estuary) at depths <20 m, but they are less commonly encountered on the continental shelf of the North Sea (Maitland et al., 1984). The Rhine River produces a large number of juveniles as well (Baer et al., 2018), indicating that the shallow margins of the North Sea near major river mouths may be particularly attractive to juveniles. Such areas should experience significant freshwater input and be less saline, which may be a factor for either juveniles or their prey. The North Sea in general is a shallow shelf environment averaging 95 m deep, but it is not known how far from the coast juvenile European river lamprey disperse.

European river lamprey exhibit high levels of inter-population variation in terms of morphology and life-history strategy. In this species, population structure has been mainly inferred with molecular markers, but marked differences in body length have been observed among populations. In the Baltic Sea, such differences have been observed in lamprey beginning their spawning migration. Bartel et al. (2010) report that length is negatively correlated with latitude, lamprey from Bothnian Bay (65° N) measured 200–396 mm TL whereas in Polish waters (52–54° N), they measured 290–510 mm TL. It is possible that, because Bothnian Bay regularly freezes in the winter, juvenile European river lamprey may have a shorter period of time in which to feed compared to the milder winters of the southern Baltic Sea. In France, individuals from the Oir population (Normandy) are much smaller (220 mm on average) than in all other studied populations located either in more southern Atlantic rivers (250–290 mm) or further north in the Channel area (300–330 mm) (Rougemont et al., 2015). Such variations may be linked to the duration of juvenile feeding at sea or to differences in food sources. A similar pattern is observed in the population from the Tagus basin, Portugal (Mateus et al., 2016), where total length averaged 260 mm TL. The genetic isolation of this southern population, together with the relatively small size of individuals, was suggested by the authors as indicative of reduced levels of mobility during the parasitic phase, probably associated with their permanence in the large Tagus estuary (~300 km²) and adjacent coastal area (Mateus et al., 2016). This differentiation of a southern population in relation to the more abundant northern
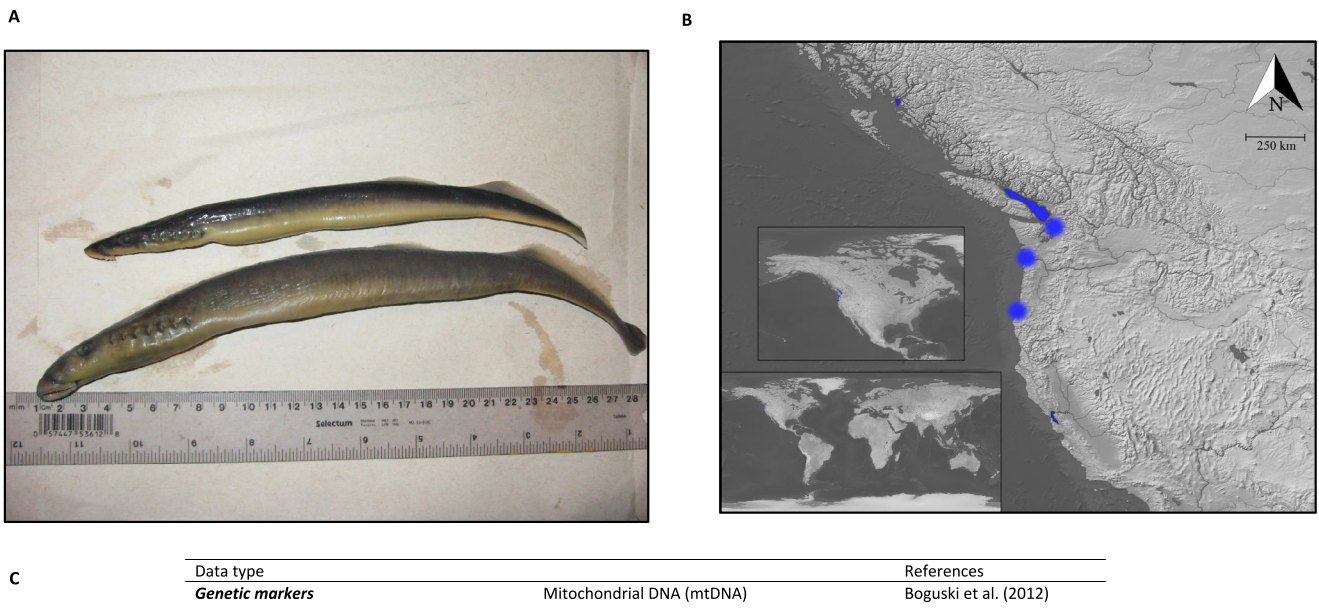
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C

Data type		References
Genetic markers	Mitochondrial DNA (mtDNA)	Boguski et al. (2012)

Fig. 7. A) Western river lamprey, *Lampetra ayresii* (photo ©Joy Wade); B) Distribution of western river lamprey juveniles in marine waters (Beamish, 1980a; Beamish and Neville, 1995; Bond et al., 1983; Wade and Beamish, 2016; Weitkamp et al., 2015; Withler, 1955); C) Methods used to access population structure in western river lamprey.

populations may represent a disadvantage in a scenario of climate change, where southern populations are more prone to extinction. For instance, European river lamprey is classified as Critically Endangered in Portugal and Italy (Cabral et al., 2005; Bianco et al., 2013), but of Least Concern globally (Freyhof, 2011). Understanding population structure can thus help to identify populations and regions that may need special attention regarding urgent conservation actions.

Western river lamprey (Lampetra ayresii)

The western river lamprey is endemic to nearshore ocean and estuaries of the North American Pacific Coast. This distribution includes freshwater drainages in North America, from British Columbia south into California (Potter et al., 2015; Fig. 7). It is the smallest anadromous lamprey, with adults ranging from 168 to 236 mm in TL (Docker and Potter, 2019). Compared to Pacific lamprey, there has been little research conducted on genetic population structure in the western river lamprey, partly due to its relatively restricted distribution, but largely due to the general inability to distinguish it from the western brook lamprey during the long larval stage when these species are most frequently encountered (Docker, 2009; Docker and Potter, 2019). However, the results of Boguski et al. (2012) suggest that there may be fixed mtDNA sequence differences between western river lamprey from widely separated populations, although it should be noted that sample sizes of adult specimens (i.e., where species identification was confirmed) were small. Western river lamprey from the Nass and Fraser river systems (N = 2), Yaquina River drainage (N = 1), and Sacramento Delta (N = 2) systems did not share any cytochrome *b* haplotypes, and sequences among these three locations differed by 1.1–1.5 % (Boguski et al., 2012). Clearly, however, larger sample sizes and a clearer understanding of the distribution of this species (i.e., whether its apparently disjunct distribution is due to inadequate sampling in the intervening regions) are required.

The western river lamprey appears to have a highly restricted distribution compared with other anadromous lamprey species, being found only near the mouths of large rivers draining the Pacific coast of North America. It is thought to occur predominantly as widely separated populations, generally remaining in surface waters in larger estuarine systems rather than dispersing more widely at sea (Boguski et al., 2012; Moyle, 2002). In California, most records for this species are from the lower Sacramento–San Joaquin River system; in Oregon, they have been reported only in the Columbia and Yaquina river systems; and in British Columbia, they appear common only in the Skeena, Nass, and Fraser river systems, although they have "not really been looked for" in most other streams (Boguski et al., 2012; Moyle, 2002).

Juvenile western river lamprey are most frequently encountered while foraging in the Strait of Georgia, although reports from the Skeena River mouth (Withler, 1955), Yaquina Bay (Bond et al., 1983), and Columbia River mouth (Weitkamp et al., 2015) exist. In the Strait of Georgia, where juveniles have been most intensely studied, approximately 3 million individuals enter the sea from the Fraser River each year and prey extensively on Pacific salmonids and herring (Beamish and Neville, 1995). The restricted distribution of this species might be due to close association with schools of prey such as herring, which aggregate within the strait each summer (Beamish, 1980a) (Fig. 7). This species appears to overlap ecologically with European river lamprey, which also tends to aggregate near shore in reduced salinity environments rather than disperse along the continental shelf.

Although juvenile western river lamprey are found throughout the Strait of Georgia, the majority have been sampled in surface waters (0–4 m) where they feed heavily on salmonids and herring (Beamish, 1980a; Beamish and Neville, 1995; Wade and Beamish,

2016; Weitkamp et al., 2015; Fig. 1). Sampling in midwater has revealed western river lamprey rarely forage in depths >50 m (Beamish, 1980a), and suggests the strong countershading evident on juveniles of the species is associated with a preference for foraging at the surface (Kan, 1975).

Conclusions

In this review, we demonstrate that population structure of anadromous lampreys can be determined by several factors, such as distributional range, dispersal capacities, body size, life cycle, stream geology, and anthropogenic actions. For instance, wide-ranging, large-bodied anadromous species (e.g., sea lamprey, Pacific lamprey, Arctic lamprey) show minimal population structure over relatively large spatial scales, while smaller-bodied parasitic lampreys (e.g., European river lamprey) show more limited dispersal and greater population structuring. This is particularly evident in the western river lamprey, which is, on average, the smallest of all anadromous lampreys. Historical factors are also reflected in current population structure; for instance, signals of refugial persistence during the Quaternary glaciations and subsequent colonization of newly available habitats are revealed by the use of genetic markers capable of detecting historical and contemporary gene flow and migration rates.

Making use of a variety of distinct methods, it has been possible to identify considerable intraspecific diversity (which is often hidden by similar morphology), understand ancient relationships between migratory and resident species, identify marine stocks, and understand evolutionary processes acting in lampreys. Thus, with these recent methodological advances and renewed efforts there is now a clearer understanding of the past and present distribution of populations and species at broader geographic scales, and of the effects of anthropogenic actions on patterns of genetic diversity. The complexity of life histories and the fact that anadromous lampreys tend to be highly dispersive and show no homing has imposed challenges for the vastly different goals of conservation and population control. Some species are still relatively poorly studied, especially species in the Southern Hemisphere, where better delineation of population structure could help in their conservation and management. However, several years of testing different markers and methods allow a more comprehensive understanding of what needs to be done in the future to fulfill existing knowledge gaps. New genomic tools are increasingly being implemented to complement ecological knowledge such as dispersal tendencies, and are being combined with population genetic analyses and local adaptation studies. Our synthesis of past and current methods for assessing population structure in lampreys—each with strengths and limitations—provides a roadmap for the continuing development of effective research on movement and connectivity in 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.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2021.08.024.

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