

A review of the geographic distribution, status and conservation of Scotland's lampreys

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INTRODUCTION

Lampreys (Petromyzontiformes) are a diverse group of jawless fishes, comprising approximately 45 species distributed in both northern (41 species from one family, Petromyzontidae) and southern hemispheres (four species from two families, Geotriidae and Mordaciidae) (Renaud, 2011; Mateus et al., 2013; Tutman et al., 2017). Larval lampreys are filter-feeding life-stages commonly located in fluvial sediments (Hardisty, 2006). After several years of growth larvae undergo a radical metamorphosis and the distinctive adult lamprey phenotype is produced (Bird & Potter, 1979). Adult lampreys are broadly characterized as being parasitic (feeding on the blood and/or tissue of fishes) or nonparasitic (non-trophic). Nonparasitic species are often referred to as "brook lampreys". Three species of lamprey can be found in Scotland: sea lamprey (*Petromyzon marinus* Linnaeus 1758), European river lamprey (*Lampetra fluviatilis* Linnaeus 1758), and European brook lamprey (*L. planeri* Bloch 1784).

Recent investigations have revealed that in many ways European river and brook lampreys exemplify the lamprey "species problem": one is parasitic (*L. fluviatilis*) the other nonparasitic (*L. planeri*). However, they are found sympatrically across almost their entire range (Renaud, 2011); larvae are distinguishable only during the latter stages of metamorphosis (Bird & Potter, 1979); they frequently share spawning grounds (Huggins & Thompson, 1970; Lasne et al., 2011); can readily hybridize (Hume et al., 2013); and, where they co-exist, are not reciprocally monophyletic (Espanhol et al., 2007; Bracken et al., 2015). In addition, although *L. fluviatilis* is typically anadromous some populations feed exclusively in freshwater lakes (Berg, 1948; Adams et al., 2008; Inger et al., 2010) or for reduced periods of time in marine environments (Abou-Seedo & Potter, 1979; Hume, 2013). The lampreys of Loch Lomond in west-central Scotland are of particular scientific and conservation importance because of the presence of a lake-feeding *L. fluviatilis* population there (Hume, 2013). The species status of both these fishes is open to debate, but such a discussion is out-with the scope of this

study. The distantly related sea lamprey also appears to be more ecologically variable than previously assumed. Some individuals of this typically anadromous species have been found to remain feeding parasitically in freshwater lakes in Ireland (F. Igoe, Irish Char Conservation Group, *pers. comm.*) and may represent the first stages in establishing a freshwater-resident population. There are substantial numbers of angler records of sea lamprey parasitizing brown trout (*Salmo trutta* L. 1758) and northern pike (*Esox lucius* L. 1758) in Loughs Derg, Conn, Cullin and Corrib (Rare Fish Reporter, <http://www.ucd.ie/rarefishreporter/> accessed June 2017). Recently transformed sea lamprey are known to feed within rivers during their downstream migration to the sea (e.g., Silva et al., 2013), so feeding in lakes is not necessarily a complex transition for this species.

The ecological, behavioural and phenotypic variability of lamprey species has profound implications for their management in Scotland, the wider U.K., and elsewhere in Europe. Despite the difficulty in comprehending and assigning the taxonomic designation of "species" to organisms and the restrictions such assignments produce, these artificial constructs are a necessity if we wish to adequately protect our natural heritage from exploitation and/or extinction. Therefore, as a first step we must comprehend the full extent of lamprey biodiversity (phylogenetic, morphological, behavioural and phenotypic) and then seek ways to protect that diversity at both the species and sub-specific level where necessary. The aim of this study was to document the geographic extent of each of Scotland's three lamprey species using information derived from previously published sources. Given the difficulty in identifying larval lampreys to species level only credible adult sightings are presented to give a truer picture of each species' range. Metadata were derived from primary and grey literature, including Government and non-Government sources. Records ranged in date from 1883 to 2016. In addition, the conservation legislation protecting each species and the current status of Scottish populations is also outlined. Some notes on potential

future directions for lamprey conservation and their relevant ecology are also provided.

GEOGRAPHIC DISTRIBUTION OF ADULT LAMPREYS IN SCOTLAND

Sea lamprey are present in all seven hydrological regions of Scotland. However, the single record from Shetland (Landon Water, dated 1883) may represent a vagrant individual given the species' scarcity in the north (Table 1). Sea lamprey are known to travel extensive distances in the north Atlantic during the juvenile trophic phase, and specimens have been recovered hundreds of kilometers off the coasts of Europe (Lelek, 1973; Pereira et al., 2012). In total, 240 records of adult sea lamprey were identified from 39 river systems (Fig. 1). European river lamprey were recorded in 35 rivers across all regions of Scotland except Orkney and Shetland (Fig. 2). This species is most common in the South West (14 catchments) and Grampian (10 catchments) regions (Table 1). A similar number of records were located for European river (224) and sea lampreys. But only a single occurrence of the species was noted in the Western Isles hydrological region (Glenlussa Water on Kintyre, a mainland site). And surprisingly there are no records from any of the Scottish islands. European brook lamprey were recorded from 62 Scottish river catchments, indicating they are the most widespread species in the country (Table 1). In total, 444 records were obtained from all hydrological regions, again with the exception of Orkney and Shetland (Fig. 3). As with European river lamprey there is a strong regional trend in the distribution of adult records, with most occurrences in the Grampian and South West regions. However, species records were obtained from the Western Isles region (River Broadford on Skye; Laggan on Islay) and two rivers in the far north of Scotland's mainland (Hope and Wick), disjunct from the northern range of the species.

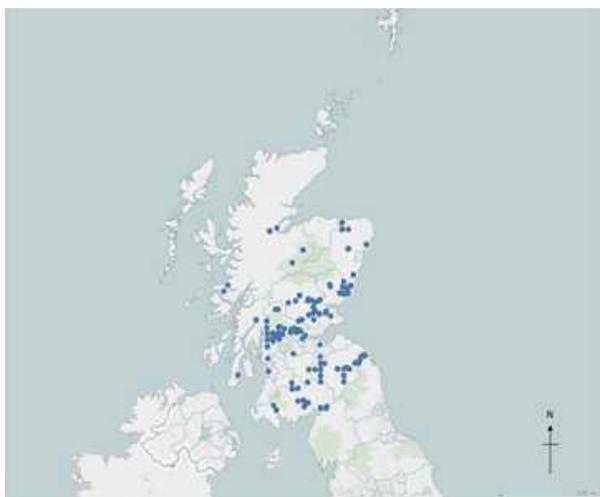


Fig. 1. Geographic distribution of *P. marinus* in Scotland. Only records of adults are indicated.

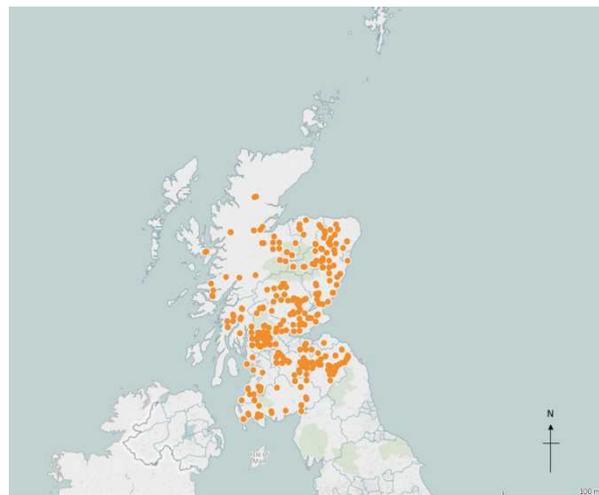


Fig. 2. Geographic distribution of *L. fluviatilis* in Scotland. Only records of adults are indicated.

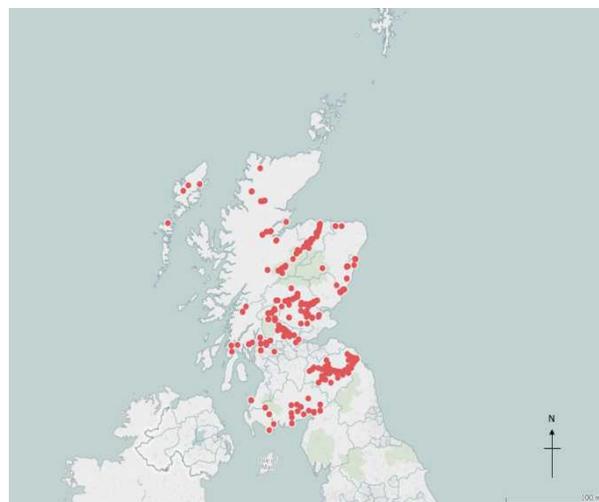


Fig. 3. Geographic distribution of *L. planeri* in Scotland. Only records of adults are indicated.

STATUS OF LAMPREY POPULATIONS IN SCOTLAND

All three lamprey species present in Scotland are categorized as being of 'Least Concern' (IUCN, 2015). For sea lamprey this designation is based on a large geographic range (eastern North America and western-northern Europe), many sub-populations with substantial population sizes, and a lack of major threats across their range. Scotland is located near the northern limit of the breeding range of sea lamprey (Maitland, 1980), possibly due to the intolerance of embryos to cool water temperatures (Langille & Hall, 1988). As such it has previously been suggested that the species may never have been common in Scottish rivers (Gardiner & Stewart, 1997). However, within the U.K. larval sea lamprey were found to occupy 305 1 x 1 km squares of surveyed habitat (National Biodiversity Network), and 120 of those (39%) were in Scotland (JNCC, 2013a). Unfortunately it is not possible to estimate population sizes based on such grid surveying methods, and despite larvae being widespread in

River System	<i>P. marinus</i>	<i>L. fluviatilis</i>	<i>L. planeri</i>
Allan		X	X
Amhainn Dubh	X		
Annan	X	X	X
Ayr	X		X
Barvas			X
Bervie	X	X	X
Black Cart	X		X
Bladnoch	X		X
Broadford			X
Carron			X
Clyde	X	X	X
Connon	X	X	X
Craigmill			X
Cree	X	X	X
Creed	X		
Dee	X		X
Deveron	X	X	X
Devon		X	
Dighty			X
Don	X	X	X
Doon	X		
Eachaig	X		
Eam	X	X	X
Eden			X
Endrick	X	X	X
Esk	X	X	X
Eye			X
Findhorn			X
Fleet			X
Forth	X	X	X
Garnock	X		X
Girvan	X		X
Glass		X	
Glenlussa		X	
Hope	X		X
Inver	X		
Irvine		X	X
Kelvin	X	X	X
Kirtle		X	X
Laggan			X
Landon	X		
Leith		X	X
Leven	X	X	X
Lochar			X
Lochy	X		X
Lossie			X
Luce		X	X
Lunan		X	X
Monikie			X
Morar			X
Morsgail	X		
Nairn			X
Ness			X
Newhall Burn			X
Nith	X	X	X
North Esk	X	X	X
Oykel	X		
Peffery		X	X
Piltanton		X	X

Shiel		X	X
Shira			X
South Esk	X	X	X
Spey	X	X	X
Stinchar	X	X	X
Tay	X	X	X
Teith	X		X
Tweed	X	X	X
Tyne			X
Urr	X	X	X
White Cart		X	X
Wick			X
Ythan		X	X

Table 1. Rivers in Scotland where adult lampreys have been recorded. Rows in grey indicate river systems that harbour all three species.

Scotland sea lamprey population sizes do appear to be small. Evidence for this comes mainly from monitoring Special Areas of Conservation designated under the EU Habitats Directive (European Commission, 1992), which typically fail to locate areas of suitable larval habitat containing abundant sea lamprey. These sites include the rivers Spey, Tay, Teith and Tweed (Gardiner & Stewart, 1995; Gardiner et al., 1995; Maitland & Lyle, 2000; APEM, 2002, 2004a, 2004b; Bull, 2004; Watt et al., 2008). Failure to detect larval sea lamprey may not necessarily reflect their absence though; it remains possible larval sea lamprey occupy deep water or mainstem habitats not targeted during electrofishing assessments.

Anecdotal evidence, gathered principally from fishery managers, points to general declines in sea lamprey spawning populations in a number of catchments, particularly in the north and west of Scotland. In the River Eachaig in Argyll sea lamprey were once considered common – so much so that the parasitic juveniles were viewed as a pest of coastal salmon nets, where they wounded valuable Atlantic salmon (*Salmo salar* L. 1758) (R. Teasdale, Eachaig Salmon Fishery Board, *pers. comm.*). Yet no larval sea lamprey were located in the Eachaig during the last nation-wide lamprey survey (ERA, 2017) and spawning adults have not been seen in recent years. This situation is paralleled on the River Lochy in Lochaber, where adults are no longer observed by local river managers, anglers or ghillies despite spawning activity being a historically common occurrence (J. Gibb, Lochy Association, *pers. comm.*). And while aggregations of spawning adults have been observed in the River Annan in the south-west of Scotland, these are limited to a short stretch of river below the Newbie Caul, and the total adult population is not thought not to be large (N. Chisholm, River Annan Trust, *pers. comm.*). However, the trend for adult sea lamprey abundance in the U.K. does appear to reflect a general increase in spawning migrants that may stem from ongoing improvements in water quality and access by adults to spawning habitat, or simply greater awareness of the species.

And it should be noted that adult lampreys are not routinely surveyed, and therefore may be more common than presently believed.

European river lamprey are considered to have recovered significantly from population declines resulting from pollution in rivers throughout west-central Europe (Maitland et al., 2015). A generally high abundance of the species in some European states (e.g., Baltic Sea nations) appears to outweigh concern over local scarcity in some other regions (Maitland, 2000). In Scotland though, the population trends is considered to be ‘Stable’ (JNCC, 2013b). Most populations of the species are in the southern-central parts of the country, in particular around the Solway coast, Ayrshire and Clyde coasts as well as the Forth and Tweed areas, resulting in the most restricted range of the three Scottish lampreys. Further north, the species appears to be very scarce and north of the Great Glen found only in the rivers Shiel and Conon, although larval records have been identified from the rivers Glass and Peffery previously (ERA, 2017). National Biodiversity Network data identifies 310 1 x 1 km grid squares as being occupied by larval European river lamprey in the U.K. (JNCC, 2013b). Of these, 61 records (c. 20%) were located in Scotland.

The range of European brook lamprey largely overlaps that of the closely related European river lamprey, and the same is true in Scotland. It can be regarded as the most widespread and abundant of the three lamprey species present in the country. Records and survey data gathered during the previous national lamprey survey confirm the relatively high abundance of European brook lamprey compared with either of the other two species (ERA, 2017). As with European river lamprey though, uncertain larval identification makes assessments of status difficult throughout the country as records may be confused between both species (typically referred to as *Lampetra* spp. in surveys). It is present throughout Scotland, with the exception of Orkney and Shetland and the far northwest mainland. They are present but

apparently uncommon in the Hebrides, with only two populations identified in the Inner Hebrides and one in the Outer Hebrides. The presence of this species in the Hebrides is of significant interest, and the conservation value of the Skye population in the River Broadford has already been highlighted by Maitland & Lyle (1991). However, despite considerable survey effort in the Hebrides only two additional populations have been identified since then: one in the River Barvas on Lewis and one in the River Laggan on Islay (ERA, 2017). Interestingly, larval lamprey in the Barvas were found in substrates composed almost entirely of peat or coarse sand, something not yet observed elsewhere. It is likely that all three populations are relatively small, as a consequence of catchment size and limited availability of suitable larval rearing habitat. A U.K. wide assessment of the larval distribution of this species identified their presence in 1379 1 x 1 km grid squares (National Biodiversity Network), with 121 (c. 9%) in Scotland (JNCC, 2013c). The species' long term trend in Scotland is considered to be 'Stable'.

LEGISLATION PROTECTING LAMPREYS IN SCOTLAND

Several pieces of legislation protect lampreys in Scotland, including the preservation of important habitat features for larval, juvenile and adult life-

stages, in addition to their protection from overexploitation (Tables 2 & 3). Although *P. marinus* does not receive direct protection through the Wildlife & Countryside Act 1981 (as amended), it is listed under Annex II of the EU Habitats Directive (European Commission, 1992) allowing for its inclusion as a qualifying feature within SACs. *Lampetra fluviatilis* is also listed under Annex II of the Habitats Directive, as well as Annex V. This latter legislative measure, as well as its inclusion in Schedule 3 of the Conservation Regulations (Anon, 1994) and Appendix III of the Bern Convention (Council of Europe, 1979) provides the means to restrict and regulate exploitation of *L. fluviatilis*. European river lamprey are fished commercially on a small scale in the U.K. (Masters et al., 2006), and more so in mainland Europe (Sjöberg, 2011), typically to provide bait for fishermen (Foulds & Lucas, 2008). *Petromyzon marinus* is listed under Appendix III of the Bern Convention, which also limits its exploitation. However, in Scotland it is not subject to the types of exploitation seen in France and the Iberian Peninsula, where targeted fisheries for the species exist (Beaulaton et al., 2008; Stratoudakis et al., 2016). *Lampetra planeri* is listed under Annex II of the Habitats Directive and Appendix III of the Bern Convention.

Scientific name	U.K. BAP	Habitats Directive Annex	Conservation Regulations Schedule	Bern Convention Appendix	IUCN Red List category (2015)
<i>Petromyzon marinus</i>	Y	II	n/a	III	LC
<i>Lampetra fluviatilis</i>	Y	II, V	3	III	LC
<i>Lampetra planeri</i>	N	II	n/a	III	LC

Abbreviations as follows: BAP, Biodiversity Action Plan; IUCN, International Union for Conservation of Nature.

Table 2. Summary of conservation legislation protecting lampreys in Scotland.

Legislation	Schedules and appendices
U.K. BAP	UK BAP priority fish species list Annex II – designation as qualifying feature within SACs for the species listed.
EC Habitats Directive	Annex IV – special protection for the species listed. Annex V – exploitation may be subject to management.
The Conservation (Natural Habitats etc.) Regulations 1994	Schedule 2 – European Protected Species in Great Britain. Schedule 3 – animals that may not be taken in certain ways.
Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats)	Appendix III – regulation of the exploitation of species listed. CR – Critically Endangered. VU – Vulnerable.
IUCN Red Lists	LC – Least Concern. EX – Extinct.

Abbreviations as follows: BAP, Biodiversity Action Plan; SAC, Special Areas of Conservation; EC, European Commission; IUCN, International Union for Conservation of Nature.

Table 3. Description of relevant conservation legislation schedules and appendices protecting lampreys in Scotland.

Both *P. marinus* and *L. fluviatilis* are listed as a priority species under the U.K. Biodiversity Action Plan (JNCC, 2007), indicative of their ecological importance and identification as requiring conservation. More recently, both species have been identified as a Priority Marine Feature (PMF) in Scottish territorial waters (Howson et al., 2012). This designation will help support advice concerning action affecting marine biodiversity, and assist with delivery of new marine planning and licensing systems as set out in the Marine (Scotland) Act 2010. It is noteworthy that some PMFs are being used to underpin the selection of Nature Conservation Marine Protection Areas in Scottish seas, which could protect foraging habitats and a prey base for these anadromous lampreys.

The distribution of lampreys in freshwaters of the U.K., particularly sea lamprey, is not reflected in the proportion of SACs identifying them as qualifying features of interest in Scotland; only four out of 23 of these sites aimed at protecting sea lamprey and their habitats (excluding the Solway Firth and Tweed estuary) are located in Scotland. Similarly, only four of 21 sites for European river lamprey (again excluding the Solway and Tweed estuaries) are located in Scotland. Fewer SACs include European brook lamprey (four in Scotland, out of 18 in the U.K.), and perhaps this reflects their greater and more widespread abundance. A review of all consents and licenses for discharge and abstractions affecting rivers in Scotland was recently completed, which will further prevent significant reductions in water quality and habitat access stresses on lampreys (Scottish Environmental Protection Agency, River Basin Management Plan 2015 - 2027). This publication outlines the means to protect and improve Scotland's water resources by reducing activities affecting notified features in designated sites (SACs), and includes a programme of measures to address them.

CONCLUSIONS & RECOMMENDATIONS

It is clear that lampreys are distributed broadly across Scotland, with the exception of Orkney, Shetland and the north-west mainland. Independent records ($N = 910$) of adult lampreys from 72 different river systems were collated and presented in this review. The European brook lamprey is the most commonly encountered species and it would appear that it has the best long-term prospects given it lacks large-scale migratory movements and can reside in relatively small headwaters, where it may be buffered from climate shifts and the introduction of invasive species. Both of these are highlighted as threats to lampreys in Scotland (JNCC, 2013 a, b, c). In-stream barriers can still isolate populations within certain river systems though, and we lack a good understanding of their water quantity and quality requirements (Maitland, 2003). European brook lamprey populations have evolved independently more than once throughout their

European range, including in the U.K. (Espanhol *et al.*, 2007; Bracken *et al.*, 2015), and a high degree of genetic divergence exists between some populations elsewhere in Europe (Mateus *et al.*, 2013). Maitland (2004) and Maitland & Lyle (1991) highlight the presence and conservation value of "dwarf" European brook lamprey in the Scottish Hebrides. Data collected during the last national lamprey survey suggest that these very small lamprey represent part of a wider geographic variation in European brook lamprey size (ERA, 2017). It is not clear whether such phenotypic differences have a genetic basis or whether they reflect local adaptation to smaller, perhaps nutrient poor streams. In either case, the maintenance of phenotypic diversity is likely to require the species' preservation across the full range of river types and hydrological regions.

European river and sea lampreys undertake migratory movements between fluvial larval rearing habitats and juvenile foraging habitats in marine environments. This renders them susceptible to population reductions *via* habitat fragmentation caused by in-stream barriers. Although restoring connectivity between these habitats is a priority to SEPA under the Water Framework Directive (River Basin Management Plan 2015 - 2027) effective fishway technologies conducive to lamprey passage remain elusive. Evidence suggests European river lamprey, although readily attracted to technical fish passes, fail to pass in numbers sufficient to sustain populations (Foulds & Lucas, 2013; Tummers *et al.*, 2016; Silva *et al.*, 2017). Sea lamprey similarly suffer from poor passage efficiency when utilizing traditional fishway designs (Rooney et al., 2015; Castro-Santos et al., 2016; Pereira et al., 2017). Therefore, substantial improvements in this area must be realised before there is widespread adoption of technical fish passes as mitigation measures for these threats to migratory lampreys. There is strong evidence that providing access to spawning habitat through barrier removals will result in relatively rapid recolonization by migratory lampreys in areas where they were extirpated or restricted from (Hogg et al., 2013; Lasne et al., 2015; Magilligan et al., 2016).

New technologies, in particular the advent of environmental DNA (eDNA) as a tool for assessment, also presents an opportunity for the rapid and efficient (i.e., less costly) survey of rivers for the presence/absence of lampreys prior to and following management actions. Assays for sea lamprey have already been developed (Gustavson et al., 2015) and ongoing research seeks to establish methodologies to extend the capacity of eDNA to estimate their abundance. This new line of surveying technology represents a significant improvement over electrofishing surveys. However, currently it is not possible to distinguish between European river and brook lampreys using molecular genetics, rendering

the applicability of eDNA to the assessment of these species less useful.

Molecular evidence indicates that although genetic differences in sea lamprey populations do exist across large spatial scales (Rodriguez-Muñoz et al., 2004; Waldman, 2004), sea lamprey do not home to natal rivers (Bergstedt & Seelye, 1995) and individual river populations are not discrete. Therefore, it is probable that Scottish river catchments do not contain discrete sea lamprey genetic stocks as a result of constant exchange of adults. Whether Scottish regional populations exist (e.g., north vs. south) is unknown. As the Scottish metapopulation is unlikely to be large, a precautionary approach should be adopted and threats to all existing river populations identified and, where possible, reduced (JNCC, 2013a). The migratory behaviours of European river lamprey are not well understood, but anadromous populations in the U.K. do belong to a single panmictic population, sharing genes throughout their range (Bracken et al., 2015). As direct manipulation of lamprey populations *via* exploitation and stocking are largely absent, positive management for European river lamprey populations is likely to be generic - involving avoidance and mitigation of known threats (JNCC, 2013b; Maitland et al., 2015). The relatively restricted geographic range of the species in Scotland means that catchments supporting European river lamprey are often in close proximity to one another. As there is likely to be a high degree of gene flow between adjacent rivers, long term sustainability of stocks, especially in smaller rivers, may be partly dependent on immigration from proximal sites.

The designation of large Scottish river catchments like the Spey, Tay and Tweed as SACs where lampreys are a qualifying feature is consistent with the presence of abundant, high quality spawning and larval rearing habitat, and the potential for such habitat to support large populations. Additional sites could be identified by extending this approach to assessing the benefits of future management actions, such as barrier removal or bypass. The amount of suitable spawning and larval habitat made available could be quantified following the removal of in-stream barriers, or their mitigation with sufficient fishway installations. Priority could then be given to those actions that would maximize potential access to newly available habitat at the lowest cost (Jensen, 2017). For example, it has been suggested that weirs in the lower reaches of Scottish rivers may restrict lamprey access to large extents of these catchments (ERA, 2017), but passage efficiency has not been evaluated. Opportunities to ease passage at these locations might be viewed as a higher priority than removal of barriers on smaller systems, or higher up catchments where less suitable habitat would be made available following intervention. Prioritization based on catchment size could be fine-tuned where

data on physical habitats exist in the form of remote sensing databases, aerial photographs or recent surveys, which could help identify the extent of key habitat features for lampreys.

Additional studies that examine contemporary *vs.* historical distributions, the relationship of spatial use in association with threats, and the efficacy of current and future assessment tools for lampreys will be extremely helpful in guiding management actions for all three species in Scotland. Populations that express atypical ecological traits (e.g. island populations of European brook lamprey; freshwater feeding European and sea lampreys) should be prioritized. Such populations are likely expressing local adaptations to environmental conditions, and their continued presence is a significant contribution to Scotland's natural heritage and biodiversity.

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