# *Aspects of the conservation biology of an exploited population of migratory European river lamprey (Lampetra fluviatilis)*

ALBRIGHT, ATTICUS,JACK

**University of Durham**

Department of Biosciences

# Aspects of the conservation biology of an exploited population of migratory European river lamprey (*Lampetra fluviatilis*)

By

Atticus Jack Albright BSc (Hons)

Thesis submitted for the degree of Master of Science (by Research)

2020

# ABSTRACT

Populations of anadromous lampreys across the globe have declined in recent years as a result of anthropogenic impacts. One such species is the European river lamprey, *Lampetra fluviatilis*, which has declined due to the consequences of factors such as pollution, over-exploitation and anthropogenic barriers. The Humber River Basin contains one of Western Europe's most important populations of *L. fluviatilis* but this population may be threatened by the impacts of anthropogenic barriers and commercial exploitation for angling bait.

This thesis's objectives were two-fold. Firstly, to evaluate the efficiency of a semi-formalised nature like bypass specifically designed, but previously untested, to allow upstream passage of migrating river lamprey past a weir at the tidal limit. Secondly, to determine the proportion of UK coarse predator anglers who use lamprey as bait and to gauge their opinions and knowledge regarding the use of lamprey as bait.

Passive Integrated Transponder and acoustic telemetry indicated that although attraction efficiency into the bypass was high, up to 70.8 % (calculated as the number of acoustically tagged lamprey that entered the bypass as a percentage of those detected downstream of the weir), the bypass was very inefficient with an estimated passage efficiency of 5.4 % (calculated as the number of PIT tagged lamprey which successfully used the bypass to travel upstream of Naburn weir as a percentage of those that were detected within the bypass during the period of time that the most upstream PIT antennas was operational). Most lamprey that passed the weir directly when the weir was drowned rather than using the bypass. It appears that periods of high river stage increased attraction into the bypass but also created conditions unsuitable for passage through the bypass due to high velocities, especially at an undershot control sluice at the upstream end.

Telephone questionnaires of freshwater predator (principally pike, *Esox lucius*) anglers revealed that 67.8 % of participants used lamprey as bait to some degree and 39.1 % of participants would prefer lamprey to be sourced from the UK. Although participants knew little about the source of their lamprey, they generally agreed that bait companies should source their baits sustainably, that lamprey should be conserved and if lampreys were threatened by exploitation, a ban on their use as angling bait should be implemented. However, the results indicate the existence of a subset of anglers who highly value lamprey as bait and so may oppose conservation efforts or restrictions on use.

Overall, this thesis indicates that upstream passage solutions for weaker swimming fish should be focused on removing redundant barriers in waterways rather than creating novel designs for fishways. Additionally, the lack of knowledge surrounding the origin of angling baits combined with the widespread use of threatened species highlights the lack of transparency within the angling bait industry, an issue that deserves further investigation.

# CONTENTS

# <u>DECLARATION</u>

I, Atticus Jack Albright, hereby declare that this thesis entitled:

**"Aspects of the conservation biology of an exploited population of migratory European river lamprey (*Lampetra fluviatilis*)"**

is, to the best of my knowledge, a presentation of my own original work and that no work done by any other person or group is included, except where due reference is given in the text. I have acknowledged any sources of help with written work or field work in my acknowledgements.

# STATEMENT OF COPYRIGHT

# ACKNOWLEDGEMENTS

Firstly, I'd like to thank my supervisor, Martyn Lucas, for giving me the opportunity to pursue this project and his support for my study in both the laboratory and the field. I would also like to thank him for the invaluable feedback and critique he has provided over the course of this Masters. To Angus Lothian, I am incredibly grateful for all the help with installing PIT antennas, installing acoustic receivers, lamprey tagging, data collection, data analysis advice and generally keeping me sane. I do apologise for continually falling asleep during those long car rides. To Damian Bubb I thank for assisting me again with lamprey tagging, data collection and graphing the water velocities. From the Environment Agency, acknowledgements go to Cameron Barker for providing me with vital environmental data. To all members of the University of Hull Institute of Fisheries (HIFI) who were involved in tagging lamprey and the wider project; Jon Bolland, Richard Noble, William Jubb and Jamie Dodd, thank you for aiding me in my project through tagging lamprey on cold winter mornings. To Paul Bird, thank you for providing the titular lamprey for the project. To John Currie from the Pike Anglers Club of Great Britain (PAC) and every angling club, association and network who spread word of my research around, thank you for helping me to gather participants. To every angler who decided to spend time answering my questions, thank you for providing me with data.

Funding for my study was provided by the Marine Management Organisation (MMO) to which I am most grateful.

To all the others in the laboratory; Rui and Shams. Thank you for the advice, chats and occasional chance to sample new foods! To my siblings, thank you for providing a source of both entertainment and annoyance over the last few months. And finally, my most heartfelt gratitude to my parents who have been a never-ending fountain of advice and support during these trying times. You are an importance source of inspiration to me and I hope I make you proud.

# CHAPTER 1: General Introduction

## 1.1. Decline of freshwater and migratory fish

Freshwater ecosystems cover <1 % of the planet's surface and are among the most endangered ecosystems in the world (Strayer & Dudgeon, 2010). Since 1970, freshwater vertebrate populations have decreased by an average of 84 % with almost one third of all freshwater species being threatened with extinction (WWF, 2020). Migratory freshwater fish (MFF) have fared marginally better on a global scale with average declines of 76 % but European declines have been drastic at an average of 93 % (Deinet *et al*., 2020). Migratory species are defined by Dingle & Drake (2007) as species that undertake regular, seasonal movements between critical habitats to complete their life cycle. These declines in the abundance of MFF species can often be attributed to anthropogenic pressures such as habitat degradation, exploitation, pollution and invasive species (Deinet *et al*., 2020).

Anthropogenic pressures on freshwater ecosystems and MFF populations are particularly pronounced on diadromous fish species (Jonsson *et al*., 1999). Diadromous fish are defined by Myers (1949) as "truly migratory fishes that migrate between the sea and fresh water". However, this definition is flawed as it does not reflect the frequency or necessity of migratory behaviour within the species. Consequently, diadromous fish species are better described according to McDowall (1988) who restricts Myers' (1949) definition to "fish that normally, as a routine phase of their life cycle, and for the vast majority of the population, migrate between marine and fresh waters". Diadromy encompasses several life history patterns (Figure 1.1) which are as follows (definitions based on McDowall (1997));

**Catadromy**; Diadromous lifecycles in which most feeding and growth occurs in fresh water prior to migration of fully grown adults to sea to reproduce. There is either no subsequent feeding at sea, or any feeding is accompanied by little somatic growth. The principal feeding and growing biome (fresh water) differs from the reproductive biome (the sea). The anguillid eels demonstrate this life cycle (McDowall, 1997).

**Anadromy**; Diadromous lifecycles in which most feeding and growth occurs at sea prior to migration of fully grown adults into fresh water to reproduce. Either there is no subsequent feeding in fresh water, or any feeding is accompanied by little somatic growth; the principal feeding and growing biome (the sea) differs from the reproductive biome (fresh water). This life cycle can be found in the *Oncorhynchus* genus. Anadromy seems to be the most common form of diadromy, with around half of global diadromous fish species utilising this strategy (McDowall, 1999).

**Amphidromy**; Diadromous lifecycles in which there is migration of young to sea soon after hatching, followed by early feeding and growth at sea, and then a migration of small young juvenile from the sea back into fresh water. There is then further, prolonged feeding in fresh water during which most somatic growth from juvenile to adult stages occurs, as well as sexual maturation and reproduction. The principal feeding biome is the same as the reproductive biome (fresh water). The *Galaxias* genus is an example of this (McDowall, 1997).

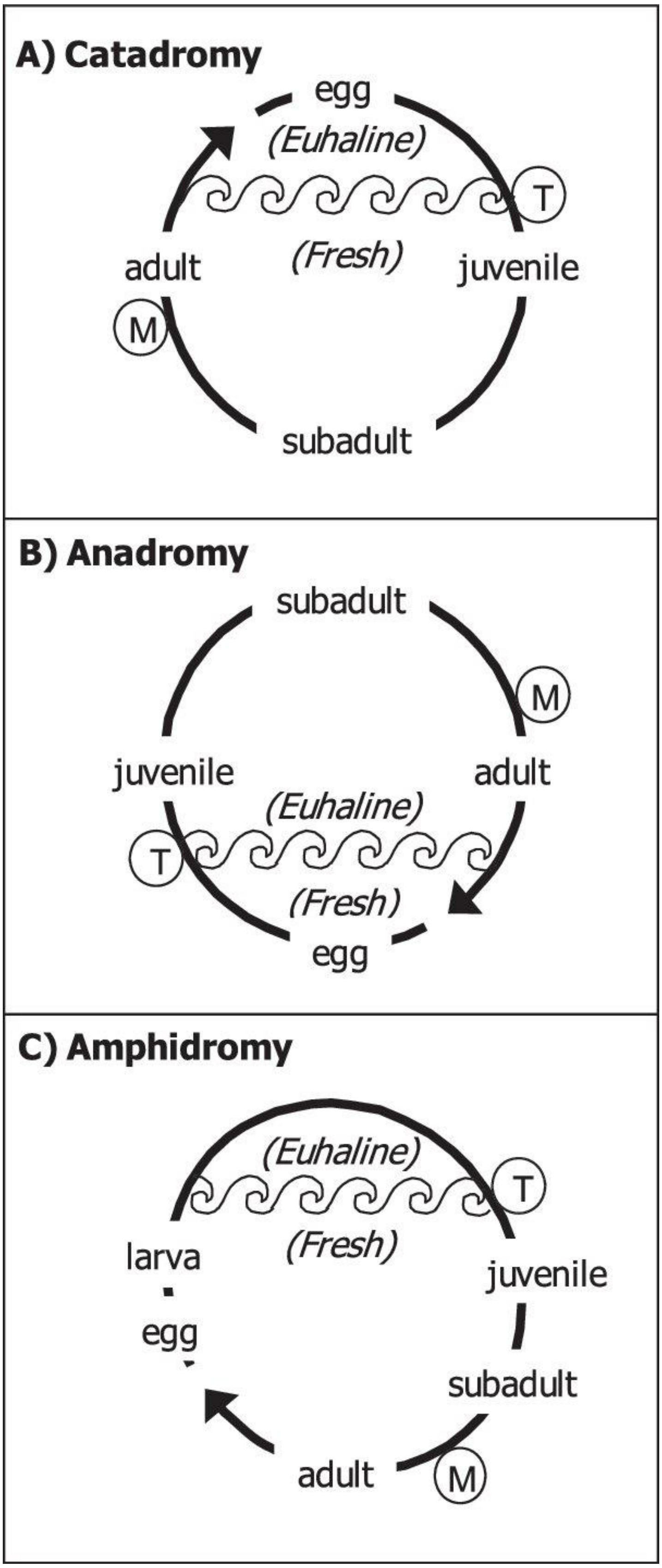



*Figure 1.1: Diagram of the three diadromous life history patterns, T= larval or juvenile physical transformation and M= sexual maturation. Euhaline refers to waters with a salinity between 30 to 35 ppt. Reproduced from McBride & Matheson (2011).*

Diadromous fishes constitute a small component of global biodiversity, a mere 1 % of global fish species (Limburg & Waldman, 2009). They are however disproportionately threatened. Although only 5 % of global fish species are considered endangered, threatened, vulnerable, or of indeterminate status, around 18 % of diadromous fish species are of conservation concern (Jonsson *et al*., 1999). This is problematic as diadromous fish can hold economic and ecological value (Woodby *et al*., 2005; Merz & Moyle, 2006; MacAvoy *et al*., 2008; Stoll *et al*., 2009) and so their declines could have serious ramifications. Lampreys are a group of jawless fish that contains nine anadromous, migratory, species (Potter *et al*., 2015) and so this chapter will cover their ecology, anthropogenic factors that threaten lamprey globally and their value to humanity. It will then focus on the ecology of one species, the European river lamprey *L. fluviatilis* (L. 1758), its status within the UK and within the Humber River Basin.

## 1.2. Ecology of lampreys

Lamprey are an ancient group of jawless fish belonging to the order Petromyzontiformes. Along with the hagfish (Myxinidae), they form the only extant group of agnathans, the monophyletic Cyclostomata (Heimberg *et al*., 2010). Lamprey as a group are thought to date back c. 500 million years (Janvier, 2007), with the earliest fossil records, of *Priscomyzon riniensis*, dating back to the Devonian period 360 million years ago (Gess *et al*., 2006).

Lamprey are clearly identifiable through distinct phenotypic features such as; an anguilliform body, cartilaginous skeletons, sucker like oral discs in the adult, seven pairs of gill pores and a lack of both scales and paired fins (Maitland, 2003). Approximately 40 species of lamprey are currently recognised (Maitland *et al*., 2015). They have an antitropical distribution, generally found north and south of the 20˚ isotherm, potentially due to their lethal temperature of 28 to 32 ˚C (Potter, 1980). The single lamprey order, Petromyzontiformes contains three separate families. The largest of these families are the Petromyzontidae or Northern lampreys, which contain 36 species of lamprey, distributed between 20˚ and 72˚ latitude across the Northern Hemisphere. The remaining lamprey are found within the families Geotridae and Mordaciidae (Renuard, 2011) and are distributed across the Southern Hemisphere. Only three lamprey species are present within the UK; the sea lamprey (*Petromyzon marinus*), the European river lamprey (*Lampetra fluviatilis*) and the European brook lamprey (*Lampetra planeri*). All three species are present across Western Europe but *P. marinus'* range extends over Greenland, Iceland and the Eastern coast of North America (NatureServe, 2013).

The lamprey life cycle is similar across the whole group (Figure 1.2). Spawning adults migrate upstream to reach suitable spawning grounds. These migrations can range between a few kilometres for non-parasitic brook lamprey species to several hundreds of kilometres in some anadromous species (Moser *et al*., 2015). Adult lampreys undergoing a spawning migration are negatively phototaxic, moving upstream in darkness but seeking refuge before dawn (Moser *et al*., 2015). Spawning occurs in spring to early summer with adults breeding in pairs or larger groups before depositing eggs in crude nests or depressions in gravel substrate in shallow, high velocity conditions (Maitland, 2003; Jang & Lucas, 2005). All lampreys are semelparous and die shortly after spawning due to degeneration of internal organs and fungal infection (Hagelin & Steffner, 1958). Lampreys that are unable to find mates or suitable spawning habitat also die, as the process of sexual maturation is linked to degeneration of the intestine and precludes body reconditioning (Docker *et al*., 2019). Occasions of repeat spawning have been reported from the Pacific lamprey (*Entosphenus tridentatus*) (Michael, 1980) but it is likely that these are exceptional circumstances.

After hatching, larval lamprey are known as ammocoetes and generally move downstream through passive or active means to locate suitable feeding habitat although active upstream movement can occur (Kelly & King, 2001; Quintella *et al*., 2005; Kirillova *et al*., 2011). Typical feeding habitat consists of soft, fine sands, with some quantity of organic detritus present (Dawson *et al*., 2015) into which the ammocoetes burrow. These conditions generally occur in areas with low water velocities, where fine sediments are deposited. Ammocoetes filter feed by producing mucus in the pharynx to entrap small particles of organic matter (Moore & Mallat, 1980; Evans & Bauer, 2016).

Ammocoetes feed for a period of three to eight years before undergoing a somewhat synchronized metamorphosis, usually beginning in the summer, typically over the course of three to four months (Manzon *et al*., 2015). The factors explaining the synchronicity of metamorphosis in ammocoete populations are not fully explained but it seems that a rise in water temperature during spring has a large effect (Youson *et al*., 1993). During metamorphosis ammocoetes drastically change, developing features such as complete eyes, fins and the oral disc (Potter *et al*., 1982).

Post metamorphosis, lamprey behaviour is dependent on the species' life history. Out of the approximately 40 species of lamprey; 18

species feed post-metamorphosis (by use of the oral disc and associated keratinous teeth), nine of which are anadromous (Potter *et al*., 2015). These lampreys undergo a second, downstream, migration (Figure 1.2) to reach feeding grounds in marine, estuarine or lacustrine environments (Potter, 1970) whilst species that do not feed, post-metamorphosis, remain in fluvial environments until spawning (Dawson *et al*., 2015). It should be noted that most anadromous species have also established permanent freshwater resident populations (Renaud, 1997).

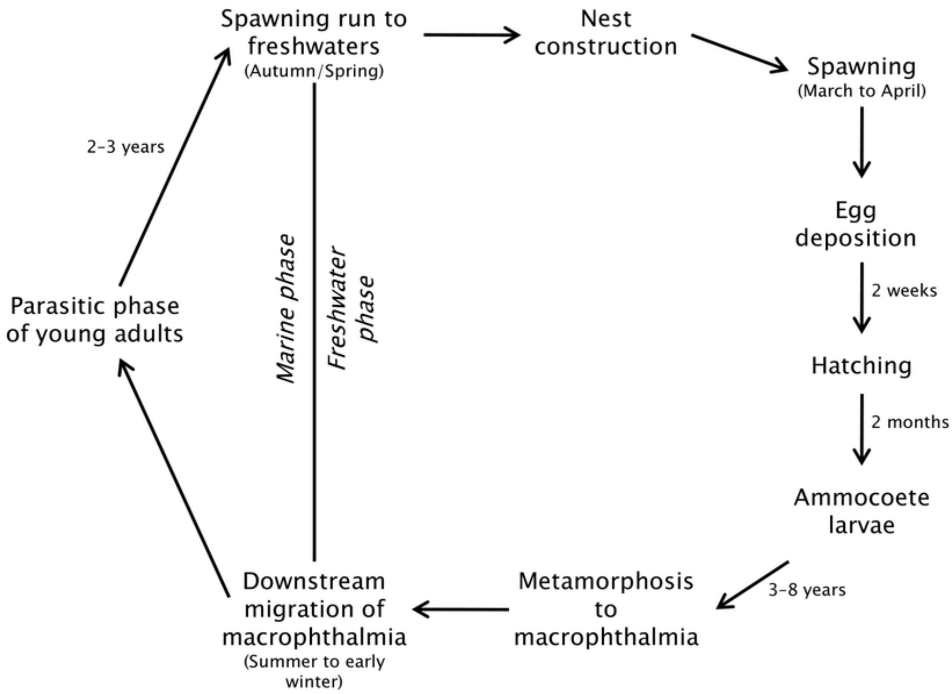



*Figure 1.2: Diagram showing the life cycle of* Lampetra fluviatilis *(reproduced from Stewart-Russon, 2011). Macrophthalmia is a term commonly given to transforming juvenile lampreys, at which point the eyes are very evident.*

Lamprey that feed post-metamorphosis generally have a longer adult lifespan than those that do not, two or more years against less than one year comparatively (Renaud, 2011). Adult lamprey feeding is exclusively parasitic excepting one species (the Caspian lamprey, *Caspiomyzon wagneri*, which is a scavenger of carrion (Renaud, 2011)). Parasitic feeding occurs through three modes; blood feeders, flesh feeders and blood and flesh feeders (Renaud & Cochran, 2019). In all cases, lamprey attach to their prey with their oral disc before either rasping away flesh or puncturing the skin to drain blood. Parasitic lampreys feed on a wide range of fish species and even marine mammals (Kelly & King, 2001; Renaud & Cochran, 2019).

A notable trait of lamprey evolution is the presence of paired species. As non-parasitic lamprey species are often morphologically similar to particular parasitic species it is assumed that non-parasitic species evolved from parasitic species by early metamorphosis, truncating the adult growth stage (Docker, 2009). An example of “paired species” would be *L. fluviatilis* and *L. planeri*. These lamprey have been argued to be conspecifics (Privolnyev, 1964) as they have been found to breed heterospecifically (Johnson *et al*., 2015) and can successfully hybridise through *in-vitro* fertilization (Hume *et al*., 2013). Genetic studies even indicate multiple origins of *L. planeri* from *L. fluviatilis* (Bracken *et al*., 2015) but in this study they are treated as separate species as they have distinctly different life histories, *L. fluviatilis* being an anadromous species and *L. planeri* being a freshwater resident (Maitland, 2003).

## 1.3. Global threats to lamprey

Lampreys are an endangered group with Renaud (1997) stating that of the 34 lamprey species present in the Northern Hemisphere, over half are considered vulnerable, endangered or extinct in at least one part of their range. Population declines at a regional scale have been drastic with *L. fluviatilis* declared as regionally extinct in Spain (Doadrio, 2001). Two lampreys, the Mexican lamprey (*Tetrapleurodon spadiceus*) and the Macedonian brook lamprey (*Eudontomyzon hellenicus*), are classified as "Critically Endangered" by the ICUN whilst the Ukrainian migratory lamprey (*Eudontomyzon sp*) was last seen at the end of the 19$^{th}$ century and so has been declared extinct (Maitland *et al*., 2015). There are numerous reasons for the global decline of lampreys, some of which will be explained below.

### 1.3.1. Pollution

Pollution has been a historic issue for lamprey populations, especially across the Northern Hemisphere where declining water quality during the industrial revolution appears to have triggered declines in anadromous river and sea lamprey across the UK as well as the extirpation of *L. fluviatilis* from the rivers Clyde and Thames (Maitland, 2003). Since water qualities in these rivers have improved in the latter half of the 20$^{th}$ Century, river lamprey have re-established in the Clyde but not the Thames (Lucas *et al*., 2020). Pollution seems to have contributed to the decline of lamprey populations and restricted their ranges across the globe (Maitland *et al*., 2015). Initially this seems unexpected as adult lamprey are resilient to many environmental pollutants. Andersen *et al*. (2010) found that with the exception of pentachlorophenol, lamprey display an average or lower sensitivity to many chemicals than other fish. However, lamprey ammocoetes are sensitive to water quality, being negatively impacted by low pH, low oxygen and high iron concentrations (Myllynen *et al*., 1997; Dawson *et al*., 2015). Moreover, the filter feeding lifestyle of larval lamprey may increase their susceptibility to contaminant uptake within sediments as they can accumulate very high levels of pollutants (Merivirta *et al*., 2006;

Bettaso & Goodman, 2010; Nilsen *et al*., 2015; Salmelin *et al*., 2016). Bettaso & Goodman (2010) found that ammocoetes contained mercury levels up to 25 times higher than other filter feeding organisms (*Margaritifera falcata*) at the same site. Research into the potential impacts of these pollutants is lacking but Myllynen *et al*. (1997) show that ammocoete survival decreases with increasing iron concentrations. Thus, sublethal effects from pollution are possible.

Accumulation of pollutants is not restricted to larval lamprey; adults are susceptible to bioaccumulation as they incorporate pollutants from the tissues of prey. *Petromyzon marinus* in the American Great Lakes have mercury levels 10 times greater than their prey species (MacEachen *et al*., 2000). Thankfully, persistent pollutant levels in lampreys have decreased in recent years (Merivirta *et al*., 2001). Another widespread form of pollution affecting lampreys is eutrophication. Increased nutrient input can form bacterial mats (due to increased algal and bacterial production) which creates localised anoxic conditions that ammocoetes are intolerant of (Dawson *et al*., 2015) and smother spawning grounds. On the other hand, this increased productivity, without prolonged hypoxia and habitat impacts, may benefit filter feeding ammocoetes which have been found in high abundance in mildly organically polluted conditions (Maitland *et al*., 2015). However, as 47 % of EU surface waters failed to achieve "Good" ecological status by 2015 under the EU Water Framework Directive (Voulvoulis *et al*., 2017) pollution, at least in the short term, will likely remain an issue for many lamprey populations.

#### **1.3.2. Exploitation**

Lampreys have historically been exploited across the globe. The most common reason for exploitation is for human consumption, lampreys have been consumed since Roman times and are still considered a delicacy in many areas of the world. However, there are other reasons for lamprey exploitation. Arctic lamprey (*Lethenteron camtschaticum*) are valued in Japan as a cure for night blindness and were historically used for fuel by

Alaskan natives (Turner, 1886; Honma, 1960). Pacific lamprey were previously harvested in vast quantities for the production of fishmeal and vitamin oil (Close *et al*., 2002). Lamprey have, historically, been used for commercial fishing and angling (recreational fishing) bait. Adult lampreys were used as bait in the long-line cod (*Gadus morhua*) fishery in the North Sea in the 19$^{th}$ and 20$^{th}$ centuries prior to the advent of trawling (Lanzing, 1959). Renaud (2011) estimated that the English fishing fleet used 450,000 lampreys annually. Numerous species of lamprey ammocoetes have been harvested (both commercially and non-commercially) for angling bait since the start of the 20th century at least (Renaud, 2011). Since the early 1990's, *L. fluviatilis* has been harvested for the UK's recreational angling bait market, often for targeting northern pike (*Esox lucius*) (Foulds & Lucas, 2014).

With lamprey in demand by a variety of markets, it is unsurprising that, in many cases, the magnitude of their exploitation has been immense and potentially unsustainable. The largest *P. marinus* fishery in Europe is the Garonne basin, France, with Beaulaton *et al*. (2008) estimating a mean annual catch of 72 tonnes. This fishery seems to be stable, showing an increasing CPUE (Catch Per Unit Effort) over time, (although care should be taken as CPUE can be drastically affected by advancements in fishing technology). Exploitation has, however, played a major part in the declines of some lamprey species across the globe (Maitland *et al*., 2015). The Japanese catch for Arctic lamprey has fallen from 200 tonnes in 1988 to 5 tonnes per year currently, potentially as a result of over-exploitation (Maitland *et al*., 2015). Clearer evidence for overexploitation can be found through the Baltic catches of *L. fluviatilis*. Catches in countries such as Finland were once immense, with a peak of roughly three million lamprey caught a year, but have since declined (Sjöberg, 2011). Overexploitation likely contributed to this decline as Valtonen (1980) estimates a lamprey fishing mortality of over 80 % in the Kalajoki River, Finland, resulting in unsustainable harvest levels.

Lamprey as a group are naturally vulnerable to overexploitation due to their life history. All lamprey are semelparous and so any individual caught as an ammocoete or migrating adult will have never spawned. As a result, overexploitation can cause the rapid decline of lamprey populations by limiting population recruitment (Masters *et al*., 2006). Moreover, the migratory nature of lamprey, especially the long-distance migrations of anadromous species, adds a complicating factor. Lampreys migrating upstream form spatial and temporal bottlenecks (i.e., converging at spawning grounds) which can easily be exploited through traps (Maitland *et al*., 2015). This results in high catches regardless of the population's actual size and so declines in abundance may be masked. Thankfully, anadromous lamprey are relatively fecund in comparison to other anadromous species such as salmonids (Docker *et al*., 2019). This gives them the potential for rapid recovery from population decline if mortality is reduced. In future, care must be taken when deciding what harvest levels are suitable for lamprey populations.

### 1.3.3. Barriers and river regulation

By far the largest threats to lamprey populations are river regulation and anthropogenic barriers (Maitland *et al*., 2015). Lamprey often spawn in shallow water with gravel substrates and their larvae inhabit areas with fine sediment such as silt beds (see section 1.2.). Consequently, they are vulnerable to the effects of water abstraction and dredging. Dredging removes deposited sediment, removing existing ammocoetes and destroying nursey and spawning habitat, which both result in the decline of lamprey populations (Maitland, 2003; O'Connor, 2006; Quintella *et al*., 2007). These declines are often swift and drastic. King *et al*. (2008) revealed that ammocoete abundance within the River Stonyford, Ireland, reduced by 80 % just seven weeks after dredging. Lowering of water levels for reasons such as irrigation, hydropeaking, or flow regulation also have drastic impacts on ammocoetes populations as they are vulnerable to desiccation and may become stranded on exposed sediments if water levels quickly fall (Streif, 2009). Members of the Karuk tribe provide accounts of thousands of ammocoetes left stranded following a change in flow regulation from the Iron Gate dam, California (Petersen Lewis, 2009). Additionally, lower water levels restrict the area of spawning habitat available to migrating adults and so hinder population recovery (Petersen Lewis, 2009; Chaudhuri *et al*., 2020).

The construction of anthropogenic barriers such as dams, weirs and culverts severely restrict lamprey access to upstream spawning habitat (Lucas *et al*., 2009). Large dams are widespread with over 57,000 worldwide but the abundance of low-head barriers (structures with a head of < 3 m) is estimated to be two to four magnitudes greater and must not be ignored (Lucas & Baras, 2001; Deinet *et al*., 2020). Moreover, low-head barriers are often missing from pre-existing barrier databases, increasing the difficulty in estimating their ecological impacts (Jones *et al*., 2019; Belletti *et al*., 2020). Lamprey are poor swimmers and are considered to be at high risk from the effects of anthropogenic barriers (Mesa *et al*., 2003; Liermann *et al*., 2012). Just seven years after the construction of five dams at the outlet of Elsie Lake, Canada, the resident population of anadromous Pacific lamprey was driven to extinction due to obstruction of upstream and downstream migrations (Beamish & Northcote, 1989). In river basins of the Iberian Peninsula, barrier construction reduced the area of available sea lamprey spawning habitat by up to 96 % (Mateus *et al*., 2012). Additionally, the energy expenditure and temporal delay invoked from crossing anthropogenic barriers may have indirect consequences. Lamprey do not feed during the spawning migration and their spawning cycle is closely linked to water temperature and daylength (Maitland, 2003; Johnson *et al*., 2015). Consequently, even after successful passage lamprey may not be in suitable condition to spawn or may miss the spawning period altogether due to extensive delays at barriers, resulting in poor recruitment.

Anthropogenic barriers pose additional threats to lamprey. Lamprey are able to pass through the turbines of hydropower stations to little effect

(Bracken & Lucas, 2013; Moser *et al*., 2015) which may be due to the absence of a swim bladder which reduces their sensitivity to pressure changes through conventional turbines (Moser *et al*., 2015). However, the protective screens used to divert debris and fish present a hazard to downstream migrating juvenile lamprey. Weak swimming juvenile lamprey are frequently impinged on these screens, with Moursund *et al*. (2003) noting that 70 % of downstream migrating Pacific lamprey were impinged on bar screens within one minute of exposure to water velocities of 0.46 $ms^{-1}$. As a result, hydropower protective screens, typically designed to exclude larger (typically 10-20 cm long) juvenile salmonids, are often a major source of mortality in lamprey populations (Moser *et al*., 2015).

Hydropower stations and anthropogenic barriers have indirect effects on lamprey populations. The creation of reservoirs above barriers as a result of river impoundment transforms habitats from lotic to lentic. Lamprey are rheophilic and spawn in lotic habitats (Dawson *et al*., 2015). Consequently, entering a large body of water with low water velocities may negatively affect their migration and spawning behaviour (Maitland *et al*., 2015). Hydropeaking has been shown to increase erosion rates and ice thickness, removing habitats vital for spawning and larval growth resulting in the rapid decline of lamprey populations (Ojutkangas *et al*., 1995). Cold-water releases will influence the temperature regime of freshwater environments, negatively affecting temperature dependent stages of lamprey biology such as spawning behaviour and embryonic development (Maitland *et al*., 2015). Furthermore, increased freshwater discharge from hydropower stations may draw upstream migrating anadromous lamprey away from more suitable river systems, creating sink populations in highly modified waterways (Birzaks & Abersons, 2011).

Technology to improve the upstream passage of adult/sub-adult lamprey over anthropogenic barriers is ongoing. Lamprey are weak swimmers and often utilise a burst-rest-attachment strategy to clear obstacles in high velocity conditions although some species are very efficient climbers (Reinhardt *et al*., 2008; Kemp *et al*., 2011; Moser *et al*., 2015; Russon *et al*., 2011; Zhu *et al*., 2011). As a result, conventional fishways are often ineffective at providing passage (Hard & Kynard, 1997; Foulds & Lucas, 2013; Castro-Santos *et al*., 2017) which leads some to advocate for the removal of anthropogenic barriers. Barrier removal can result in the rapid recovery of lamprey populations. Hogg *et al*. (2013) found that sea lamprey abundance increased approximately four-fold in just three years after the removal of the lowest dam from the Penobscot River, USA. Unfortunately, barrier removal is not always possible as anthropogenic barriers are costly to remove and many provide vital benefits to human populations such as river level regulation, irrigation and hydropower.

### 1.3.4. Conservation challenges

Another factor that threatens the long-term existence of lamprey populations globally is the limited success of population restoration attempts. Several species of lamprey have been artificially propagated for developmental research and the process has recently been incorporated into conservation strategies to halt the decline of lampreys such as the European river lamprey, Arctic lamprey and Pacific lamprey (Moser *et al*., 2019). The scale of such restoration attempts has been massive in some cases. The Perhonjoki river was stocked with a total of 247 million *L. fluviatilis* larvae between 1997 and 2010 (Aronsuu *et al*., 2019) and the Strīķupe river stocked with 250,000 larvae during 2018 (Aberson, 2019). Unfortunately, both of these programs failed to restore populations of *L. fluviatilis* and so it seems that successful conservation of lamprey population is dependent on understanding the entirety of lamprey lifecycles, not just focusing on one stage.

There are many knowledge gaps surrounding the successful conservation of lamprey. A crucial period for anadromous lamprey is the parasitic stage during which they feed in marine environments. As anadromous lamprey can attain up to 99 % of their growth in weight over this period (Silva *et al*., 2016) this plays a major factor in determining their reproductive potential as fecundity increases with body size in lamprey (Docker *et al*., 2019). However, knowledge surrounding the ecology and behaviour of juvenile lamprey in this feeding phase is very scarce, being deemed a “Black box” by Lucas *et al*. (2020). Consequentially, elements of lamprey biology that could aid conservation efforts such as factors determining the exchange of individuals across river basins are poorly known, despite the utility of multiple population genetic studies (Genner *et al*., 2012; Hess *et al*., 2015; Bracken *et al*., 2015).

These knowledge gaps are not restricted to a single phase of lamprey life history. Many lamprey species are so poorly researched that no population trend or conservation plan has so far been created (Lucas *et al*., 2020). Moreover, there is a noticeable bias in the research towards *P. marinus*, perhaps understandably so given their ecological impacts as an invasive species in the North American Great Lakes. Using a Web of Science search, Docker *et al*. (2015) found that >60 % of the studies that included “lamprey” in the title published between 1864 and 2013 concerned *P. marinus*. The next two most frequent species were also European, *L. fluviatilis* and *L. planeri* comprised 14 % and 6 % of the studies respectively. As lampreys display species specific differences in many aspects of their biology such as mating systems and fish passage efficiency (Moser *et al*., 2015; Johnson *et al*., 2015) this focus on *P. marinus* is troublesome as extrapolating data onto poorly researched species such as the Mexican brook lamprey (*Tetrapleurodon geminis*) could result in the implementation of sub-optimal or even deleterious management strategies.

## 1.4. Importance of lampreys

The aforementioned threats to lamprey populations worldwide are concerning because lampreys possess substantial ecological, economic, scientific and cultural value. Declines in lamprey abundance could have wider ramifications than the loss of a single population or species.

### 1.4.1. Economic value

Firstly, as previously mentioned, lampreys are exploited by humans for a variety of purposes. This has given them considerable economic value. Söberg (2011) estimates the processed Finnish lamprey market alone to be worth € 1.5 million annually. As a culinary delicacy, *P. marinus* often commands a high price, up to € 45 per individual in Portugal, and consequently is subjected to high levels of poaching (Andrade *et al*., 2007). Therefore, lamprey may hold untapped economic potential if invasive populations of *P. marinus* were exploited for export as gourmet food. However, current pollutant levels within invasive *P. marinus* are too high for human consumption (MacEachen *et al*., 2000).

### 1.4.2. Cultural value

Indigenous groups such as Native American tribes in the mid-Columbia Plateau, the Maori of New Zealand and the indigenous people of Yukon, Alaska often relied on lamprey as a subsistence foodstuff due to their high calorific content (Close *et al*., 2002; McDowall, 2011; Renaud, 2011; Nobel *et al*., 2016). The value of lamprey is so great to these groups that they hold great cultural significance and are often used for medicinal or ceremonial purposes (Close *et al*., 2002; Nobel *et al*., 2016).

Lamprey are also culturally and historically significant in Europe. They feature on the coat of arms of the municipality of Arbo, NW Spain, (Figure 1.3) where an annual lamprey festival also occurs (Docker *et al*., 2015). Lamprey biology was a mystery for a long time. The Aberdeen Bestiary (1200) states that lampreys are exclusively female and “conceive from intercourse with snakes”. This misinformation may have resulted in lampreys' contribution to English mythology. The Lambton Worm is a legendary lamprey-like creature from County Durham, NE England, that is the subject of numerous stories, songs, films and even an opera. In more verifiable accounts of English history, lampreys were a favoured food by the ruling class with at least two English monarchs, King Henry I and King John, recorded as having enjoyed lamprey pie, the former allegedly dying after consuming a surfeit of lamprey (Lanzing, 1959). Lamprey are still part of UK tradition with the town of Gloucester presenting a baked lamprey pie to Queen Elizabeth II on her 2012 diamond jubilee (BBC, 2012).

*Figure 1.3: Arbo's coat of arms clearly showing two lampreys, reproduced from heraldry-wiki.com*

**1.4.3. Scientific and medical value**

Lampreys have recently come into the spotlight of scientific interest with over 20,000 manuscripts concerning lamprey as a study organism, the majority of which have been published in recent decades (Docker *et al*., 2015). One reason for this surge of attention is their evolutionary significance. Being one of the two remaining clades of Agnatha and as they appear to have changed very little morphologically when compared to ancestors 360 MYA (Gess *et al*., 2006), lamprey provide valuable insights into early vertebrate evolution (Osório & Rétaux, 2008). Consequently, lamprey have been crucial models for building our understanding of the evolution of vertebrate locomotion, eyes, neuro-endocrine systems, adaptive immune systems and paired limbs (Cooper, 2006; Collin, 2010; Hsu *et al*., 2013; Tulenko *et al*., 2013). Lamprey also have other features that provoke evolutionary interest. Kuraku *et al*. (2012) report evidence of horizontal gene transfer (HGT) between lamprey and their teleost hosts via a DNA transposon. As HGT may accelerate genome innovation and evolution (Jain *et al*., 2003), lampreys may have some impact on the evolution of their prey through their parasitic interactions.

Several parasitic lamprey species secrete anticoagulants from their buccal glands when attached to host fishes in order to prevent blood coagulation and so prolong the feeding period. These secretions comprise of numerous bioactive proteins, named “lamphredin” by Lennon (1954), and have been investigated for their potential medical value. These secretions could be a source for developing new anticoagulants, anaesthetics, thrombolytic agents and immunosuppressants (Sun *et al*., 2010; Xiao *et al*., 2012). The lamprey central nervous system (CNS) is similar in structure and organization to that of other vertebrates and so lampreys are often used as a model organism in neurological studies (Grillner & Jessell, 2009). However, the lamprey CNS appear to be unique amongst vertebrates as it is capable of regenerating spinal cord axons to such a degree that it satisfies the criteria for functional spinal cord regeneration after injury as defined by the National Institute of Neurological Disorders and Stroke (Cohen *et al*., 1988). As a result, lampreys could potentially be used to develop new treatments for spinal cord injury or motor neuron diseases (Cornide-Petronio *et al*., 2011).

### 1.4.4. Ecological value

An often-ignored aspect of lampreys' worth is their contribution to ecosystem functioning. The migratory nature of some lamprey species creates a dependable food resource for predators. For example, gull (*Larus* spp) and goosander (*Mergus merganser*) diel activity patterns have been known to shift to match the timing of lamprey spawning migrations (Sjöberg, 1989) and Steller sea lion (*Eumetopias jubatus*) predate on migrating Pacific lamprey concentrated at river mouths (Beamish, 1980). Lamprey eggs and larvae are readily consumed by a wide variety of fish and macroinvertebrates (Smith & Marsden, 2009).

Filter feeding ammocoetes depend primarily on organic detritus (Dawson *et al*., 2015) and so contribute to the nutrient cycling in the environments they inhabit. Furthermore, ammocoete gut content analysis has revealed that a significant proportion of ammocoete diet originates from terrestrial ecosystems (Dias *et al*., 2019) and so lamprey provide a link between terrestrial and freshwater ecosystems. The density of larval lamprey can be up to 2000 individuals $m^{-2}$ (Dawson *et al*., 2015) and some argue that they act as ecosystem engineers. Their burrowing activity has been shown to increase the oxygen levels of sediments, although the resulting impact on stream biota is uncertain (Shirakawa *et al*., 2013). Hogg *et al*. (2014) argues that lamprey that build nests during spawning can also be considered ecosystem engineers as the physical disturbance increases habitat heterogeneity and the abundance of benthic invertebrates.

Anadromous lampreys have an additional impact on freshwater ecosystems. The spawning migrations of anadromous, semelparous lamprey can be considered analogous to those of anadromous, semelparous salmonids which also attain up to 99 % of their body weight from marine environments (Hilderbrand *et al*., 2004). The environmental impacts of salmonid spawning migrations are well documented in scientific literature as the decay of post spawning salmon releases marine derived energy and nutrients into freshwater ecosystems and adjacent riparian vegetation (Hilderbrand *et al*., 2004; Merz & Moyle, 2006). Historic salmon runs in the Pacific Northwest of the USA delivered over 4,800,000 kg of nitrogen to freshwater environments annually (Gresh *et al*., 2000). As the productivity of many freshwater habitats are phosphorus and nitrogen limited (Jardine *et al*., 2009), this fertilization can have dramatic effects on stream biota. For example, experimental stream supplementation of salmon carcasses increased the rate of algal growth 15 times and the density of macro-invertebrates up to 25 times (Watkinson, 2000). Anadromous lampreys likely form a similar vector of marine derived nutrients into freshwater ecosystems through metabolic waste, unfertilized eggs and body decomposition (Guo *et al*., 2017). Additionally, the different N:P ratio and faster decomposition rates of lamprey comparative to salmonids indicates that lamprey may have a subtly different effect on freshwater ecosystems (Weaver *et al*., 2015).

In short, lamprey populations are of conservation concern across the globe. This is an issue that must be taken seriously due to the economic, cultural, scientific and ecological value of lamprey and potential consequences that could arise from their decline. The remainder of this chapter concerns the ecology of one species of lamprey in particular, the European river lamprey, and its status within the Humber River Basin, NE England.

## 1.5. Ecology of the European river lamprey

*Figure 1.4: Pre-adult* Lampetra fluviatilis *captured during its spawning migration in the River Ouse, Yorkshire, NE England. Photo taken on November 5th 2019.*

The European river lamprey, *Lampetra fluviatilis*, (Figure 1.4) is a species of lamprey that is found from the western Mediterranean to the Baltic sea where it inhabits surrounding coastal areas, estuaries and rivers (Figure 1.5) (Maitland, 2003; Sjöberg, 2011; Mateus *et al*., 2012). Within Great Britain, *L. fluviatilis* is found in rivers and lakes south of the Great Glen in northern Scotland (Maitland, 2003). It is also found throughout all but the western part of the island of Ireland. Current populations of *L. fluviatilis* are thought to have originated from the Iberian Peninsula which acted as a refugium during the Pleistocene glaciations (Mateus *et al*., 2012). Three separate forms of *L. fluviatilis* occur;

1) The typical anadromous form which is commonly 260–385 mm long (Berg, 1948) and with an average post larval life of 2.5–2.75 years (Hardisty & Potter, 1971). This form is the most common in the UK and the subject of this study.
2) The smaller, anadromous, praecox form which is commonly 180–245 mm long (Berg, 1948) and with an average post larval life of 1.5–1.75 years (Hardisty & Potter, 1971). This form is less common in the UK and is found in rivers such as the Teme and North Esk (Maitland, 2003).

3) The dwarf freshwater resident form (distinct from *L. planeri*) which is commonly 170–243 mm long and with an average post larval life of under one year (Maitland, 2003). In the UK this form is only found within Loch Lomond, Scotland, where it feeds mostly on powan (*Coregonus clupeoides*) (Maitland, 2003). However, freshwater resident forms can also be found in Russian and Finnish lakes (Maitland, 2003).

As previously mentioned, *L. fluviatilis* and *L. planeri* are paired species, with Bracken *et al*. (2015) finding population genetic evidence indicative of multiple origins of *L. planeri* from *L. fluviatilis*. Both species frequently co-inhabit the same rivers in the UK and interbreed (Johnson *et al*., 2015) but this study only concerns *L. fluviatilis*.

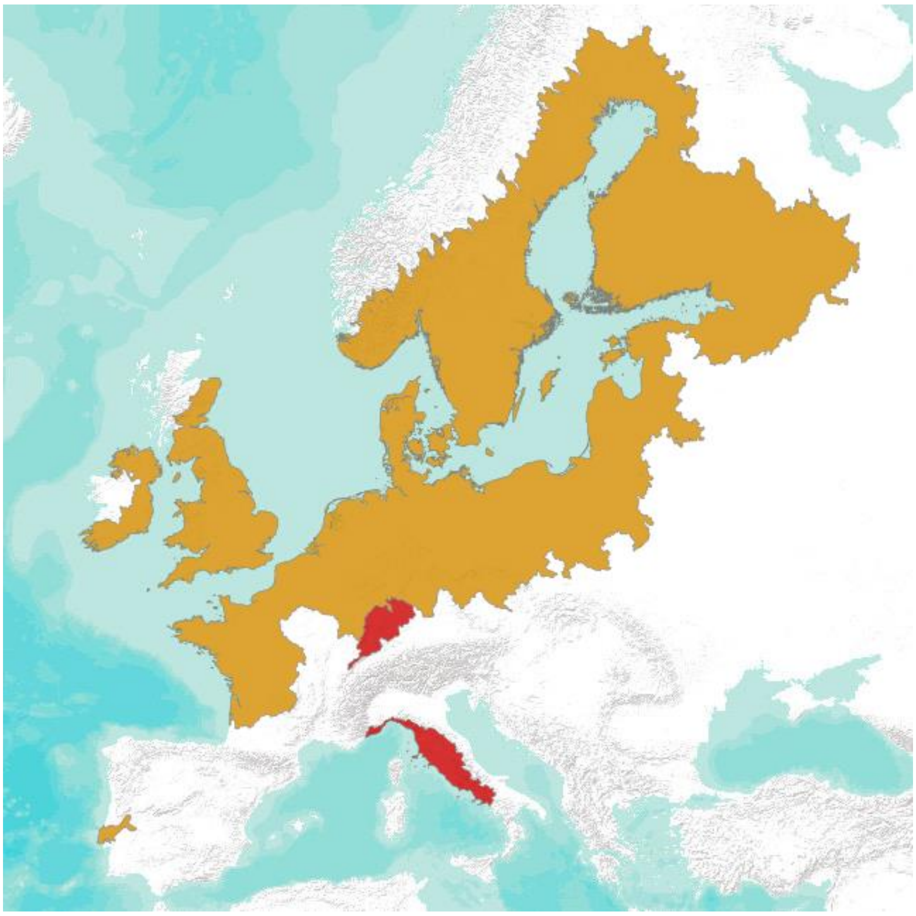


*Figure 1.5: Map showing the distribution of* Lampetra fluviatilis *in Europe, orange shading indicates extant populations, red shading indicates extinct populations. Reproduced from Freyhof (2011)*.

In the UK, *L. fluviatilis'* upstream spawning migration occurs mostly between October to December although the exact timing varies between rivers and spring spawning runs are known to occur (Hardisty & Potter, 1971; Maitland, 2003). Movement generally occurs at night but adult lampreys lose their negative phototaxism as the spawning period continues, leading to 24-hour long activity (Jang & Lucas, 2005). Adults then overwinter in British waterways until water temperatures reach 10-11 ˚C (generally March or April) at which point spawning commences (Morris & Maitland, 1987). Evidence exists that *L. fluviatilis*, like *P. marinus*, is attracted to suitable spawning grounds by larval pheromones produced by ammocoetes present in said habitats (Bjerselius *et al*., 2000; Gaudron & Lucas, 2006). However, it is unclear if this attraction is specifically to the larval pheromones or also to a wide category of organic chemicals present in river water (M. Lucas, pers. comm). *Lampetra fluviatilis*, like other anadromous lamprey, do not exhibit natal homing and will breed in any suitable stream, typically containing conspecific or heterospecific lampreys (Tuunainen *et al*., 1980).

Once adults reach suitable spawning grounds, (typically gravel substrate, water depths between 0.2 m and 1.5 m and just upstream of a riffle), nest construction begins (Jang & Lucas, 2005). Although it appears that males often construct the spawning nest (Hagelin & Steffner, 1958; Aronsuu & Tertsunen, 2015), Jang & Lucas (2005) report that within the Derwent river, females construct nests more frequently than males prior to courtship or spawning. Spawning occurs in a communal, promiscuous system with a slight tendency towards polygyny (Jang & Lucas, 2005). *Lampetra fluviatilis* produce an average of 20,000 eggs per female (Docker *et al*., 2019). Adults usually die within a week after spawning (Hagelin & Steffner, 1958). Many eggs are washed downstream of the gravel nest (Silva *et al*., 2014). Although this appears detrimental, Smith & Marsden

(2009) show that lamprey eggs are readily consumed by predators such as crayfish (*Orconectes* spp). Considering that eggs can successfully develop in non-spawning habitat, the “nest” depression may actually act as an adaptive egg dispersal structure (eggs and sperm tend to be released at the downstream edge of the nest where water flow accelerates) to reduce predation (Silva *et al*., 2014).

After 15 to 30 days of development, dependent on water temperature, the larvae hatch (Maitland, 2003). Newly hatched larvae are temporarily very active and immediately move downstream to a suitable site (Pavlov *et al*., 2014). Initially they hide in pre-existing holes, but when they are >8 mm long they construct their own burrows (Aronsuu & Virkkala, 2014). The larvae prefer habitats with deep, fine sediments such as silt deposits containing a wide variety of particle sizes (Aronsuu & Virkkala, 2014). They are filter feeders, producing mucus in the pharynx to entrap small particles of organic matter (Moore & Mallat, 1980). The ammocoetes feed for three to five years before undergoing metamorphosis in the UK (Maitland, 2003). Metamorphosis occurs between July and September and during this period the larvae undergo many morphological changes such as functional eyes, teeth and the oral disc (Pickering, 1978; Igoe *et al*., 2004; Figure 1.6). From winter to early summer juvenile lamprey migrate downstream into marine or estuarine environments to begin the parasitic phase of their life cycle (Pickering, 1978; Bracken & Lucas, 2013).


*Figure 1.6: A comparison of* Lampetra *ammocoetes, A, (reproduced from Arsento* et al.*, 2018) and of post-metamorphosis* Lampetra fluviatilis, *B, (reproduced from www.lampreysurveys.com).*

*Lampetra fluviatilis* is a flesh feeding species of lamprey, attaching to prey and gouging chunks of flesh off with the oral disc (Renaud & Cochran, 2019). Studies on *L. fluviatilis* feeding behaviour in the parasitic phase are scarce but inference from laboratory studies on the silver lamprey (*Ichthyomyzon unicuspis*) indicate that nocturnal feeding is likely (Cochran & Lyons, 2004). It is known that *L. fluviatilis* feeds upon a wide array of freshwater and marine teleosts including Atlantic herring (*Clupea harengus*), European smelt (*Osmerus eperlanus*) and European sprat (*Sprattus sprattus*) (Birzaks & Abersons, 2011; Renaud & Cochran, 2019).

## 1.6. Status of European river lamprey in Europe and the Humber

### 1.6.1. European river lamprey in Europe

Following improvements in water quality in Central and Western Europe, *L. fluviatilis* has been re-classified from “near threatened” to “least concern” at a global scale by the IUCN (Freyhof, 2011). However, issues have been raised about the re-classification due to a lack of sources and likely issues with data quality (Lucas *et al*., 2020). At a regional level *L. fluviatilis* is often highly threatened. For instance, it is classified as critically endangered in Portugal and even extinct in Italy, Switzerland and the Czech Republic (Freyhof, 2011; Mateus *et al*., 2012). Moreover, it is evident from commercial catch data that populations of *L. fluviatilis* have dramatically decreased comparative to historic levels (Sjöberg, 2011). The scale of threats facing *L. fluviatilis* at regional scales have led to it receiving legal protection across Europe, albeit within a framework that still allows exploitation. This is also the case for the critically endangered European eel (*Anguilla anguilla*) where regulated exploitation is allowed for both recreational and commercial purposes (Dorow & Arlinghaus, 2012).

Partial protection is afforded to *L. fluviatilis* under appendix three of the Bern Convention (1979) and annexes two and five of the Habitats and Species Directive (92/43/EEC). Under the latter, Special Areas of Conservation (SACs), known as Natura 2000 sites outside of the UK and Ireland, have been established in some areas of *L. fluviatilis*’ distribution, including in the UK, to form a European wide network called Natura 2000. SACs for anadromous lamprey should ideally contain; good water quality, clean coarse substrate at spawning grounds, fine sand or silt sediment downstream of spawning areas and access from the sea to spawning areas (Mateus *et al*., 2012). Within England and Wales, 17 SACs currently exist for which the presence of *L. fluviatilis* is a designated feature. Under the Habitat and Species Directive (92/43/EEC), actions (including exploitation) that threaten SACs must be managed on a precautionary basis. When regulatory agencies felt they lacked the direct legal instruments to prohibit taking of lamprey bycatch from eel fisheries in UK tidal waters (Masters *et al*., 2006; Foulds & Lucas, 2014), this was resolved within the Marine and Coastal Access Act (2009) and since then strict numbers of licences, quotas and fishing seasons have been enforced (Foulds & Lucas, 2014), including several complete suspensions of the main fishery in the tidal Ouse, Yorkshire, the most recent of which was between 2017 to 2018.

### 1.6.2. European river lamprey in the UK and Humber River Basin

*Lampetra fluviatilis* is widely distributed in the UK (Figure 1.7) but has disappeared from many areas of its historic range as a result of the effects of anthropogenic barriers and pollution (Maitland, 2003). It is thought that populations of *L. fluviatilis* have increased in UK rivers due to recent pollution abatement (Frear, 2004). A recent Joint Nature Conservation Committee (JNCC) audit (2019) claims that the future prospects for the population in the UK are “favourable” despite stating that the area and quality of occupied habitat is insufficient for the species’ long-term survival.

The Humber River Basin, NE England, (Figure 1.8) has been recognised as the source of one of the UK’s (and western Europe’s) most important populations of *L. fluviatilis* (Masters *et al*., 2006; Lucas *et al*., 2020). The Humber River Basin refers to the drainage area of the Humber river, formed by the confluence of the Rivers Ouse and Trent, and is the largest drainage basin in Britain at around 24,000 km$^2$ (Whitton & Lucas, 1997). The Humber Estuary is the largest coastal plain estuary on the east coast of Britain (Jarvie *et al*., 1997) and a designated SAC, partly due to the population of *L. fluviatilis*. The Humber River Basin allows for the completion of *L. fluviatilis*’ lifecycle, providing suitable spawning, nursery and feeding habitats (Lucas *et al*., 2009). Within the Humber River Basin, the Ouse catchment is thought to support one of the UK’s most important populations of *L. fluviatilis* (Jang & Lucas, 2005). Estimates of the annual spawning run size vary from approximately 300,000 (Masters *et al*., 2006) to 690,000 individuals (Jubb *et al*., unpublished data). The Ouse catchment also supports “favourable” populations of ammocoetes with 11 out of 16 sites containing a mean density of >10 individuals $m^{-2}$ (Nunn *et al*., 2008). However, these ammocoetes could only be identified to genus level (*Lampetra*) and so the proportion of *L. fluviatilis* to *L. planeri* within these populations of ammocoetes is unknown. It appears that *L. fluviatilis* were once abundant within the River Trent. Historical reports of over 3,000 individuals being caught in a single night at Averham weir, lower Trent, exist from the late 19$^{th}$ century (Jacklin, 2006). In recent years, few *L. fluviatilis* have been recorded in the Trent with catch per unit effort (CPUE) of upstream-migrating adults in the tidal Trent being 80 % lower than in the tidal Ouse (Greaves *et al*., 2007) and no larval lamprey being found within the Trent through electrofishing surveys (Jacklin, 2006). Consequently, the River Trent likely supports a small proportion of the Humber River Basin’s population of *L. fluviatilis* when compared to the Ouse. This small population size may be explained by Cromwell weir, which forms a large barrier near the head of tide, and only has a very small salmon ladder present passing <1 % of river flow. Despite the persistence of historic populations and apparent recovery in recent years, *L. fluviatilis* is still affected by numerous anthropogenic pressures within the Humber River Basin.

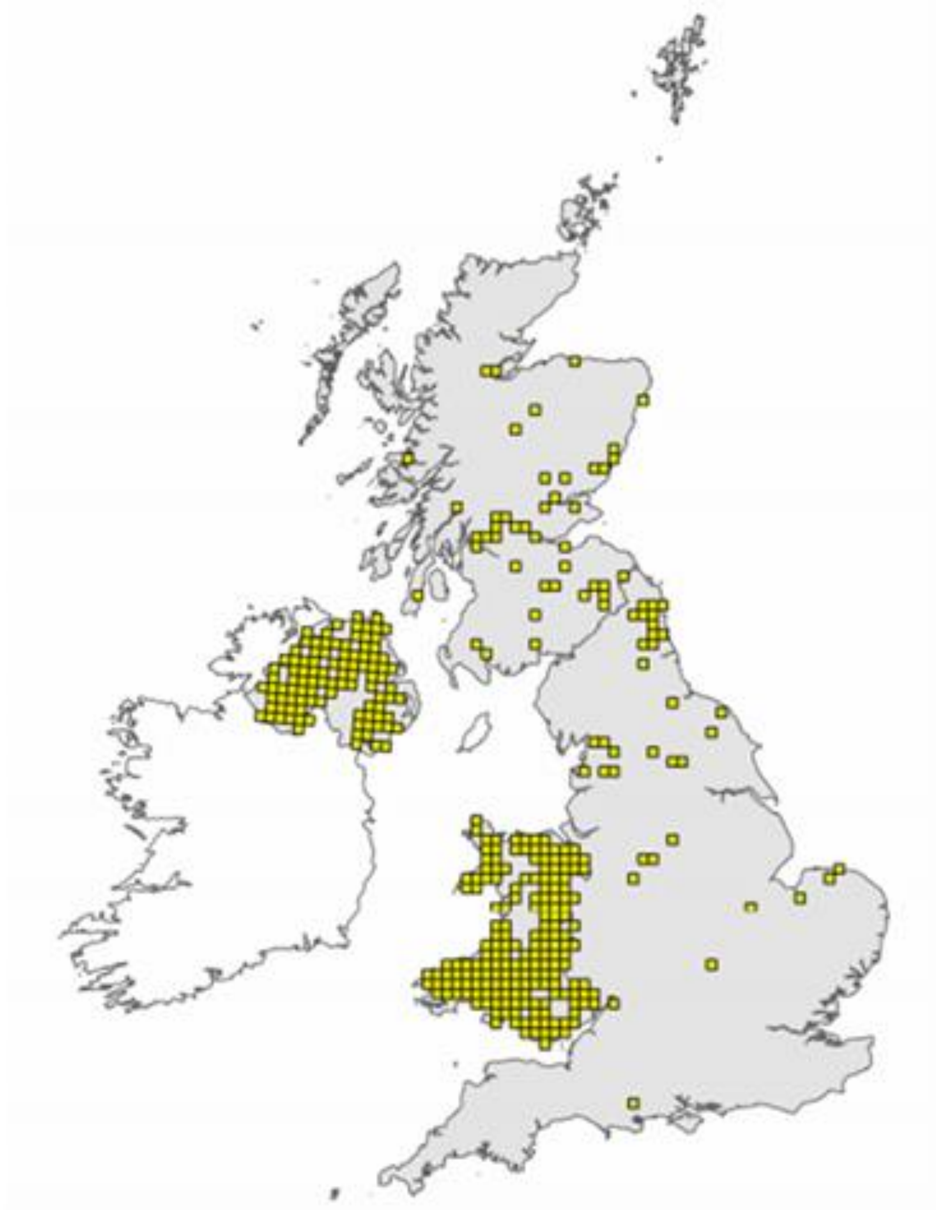


*Figure 1.7: Distribution map for* Lampeta fluviatilis *within the UK, reproduced from JNCC (2019). It is noteworthy that not only whether or not this map refers to the presence of juvenile or adult* L. fluviatilis *is unknown, the known widespread distribution throughout the Yorkshire Ouse subcatchment (see above text) is almost entirely contradicted within this map.*


*Figure 1.8: Map of the Humber River Basin district, NE England. Reproduced from EA (2016).*

## 1.6.3. Key anthropogenic factors affecting European river lamprey in the Humber

### 1.6.3.1. Anthropogenic barriers and fishways

As previously mentioned, lampreys are vulnerable to the impacts of river regulation and anthropogenic barriers (see section 1.3.3.). As NE England has a rich industrial heritage, the Humber River Basin contains large numbers of low head barriers with Nunn and Cowx (2012) assessing the impact of 67 potential barriers to migrating lamprey within the Humber. These barriers are known to limit the spawning migration of *L. fluviatilis*. Barmby Barrage, the first barrier found at the River Derwent (a tributary in the lower Ouse, which is also an SAC for this species), has been shown to be a major barrier to upstream migrating lamprey (Lucas *et al*., 2009; Silva *et al*., 2017). The former study results strongly suggest a cumulative effect of multiple partial barriers on upstream migration. This restriction to migration results in concentration of spawning events into a handful of areas, increasing vulnerability to disturbance (Jang & Lucas, 2005). Although 98 % of suitable spawning habitat within the Derwent occurs >51 km upstream, just 1.8 % of spawning individuals were found within this area (Lucas *et al*., 2009). The remaining percentage of spawning occurs disproportionately within a single site, Stamford Bridge, which Jang & Lucas (2005) identified to host >80 % of the spawning that occurs in the lower 80 km of the Derwent. Within the Trent it appears that a leading cause of the decline of *L. fluviatilis* populations from historic levels was the construction of Cromwell weir (Foulds, 2013). It is therefore vital that successful mitigation schemes are implemented within the Humber River Basin to improve the chances of *L. fluviatilis*' long-term survival with the Humber's tributaries.

Barrier removal is likely an optimal course of action to improve *L. fluviatilis*'s longitudinal passage through the Humber River Basin. The method has already proven effective for *P. marinus* elsewhere (Hogg *et al*., 2003). However, barrier removal is unlikely within the Humber River Basin as many low-head barriers in the UK are important for purposes such as water level management and small-scale hydropower generation (Entec, 2010; Birnie-Gauvin *et al*., 2017). Because of this, fishways are often constructed to provide adequate passage over barriers. Unfortunately, most UK fishways are biased towards providing passage for strong swimming salmonids whilst *L. fluviatilis* is a weak swimming species that utilises a burst-rest-attachment strategy in high velocity conditions (Kemp *et al*., 2011; Noonan *et al.,* 2012). Unlike some other species of lamprey, *L. fluviatilis* is incapable of climbing vertical or strongly sloping structures using its sucker (Kemp *et al*., 2011). Due to its poor swimming performance, *L. fluviatilis* is unable to ascend many types of fishway with a high degree of success. Tummers *et al*. (2016) show that *L. fluviatilis*' passage efficiency (number successfully exiting fishway divided by the number that entered the fishway multiplied by 100) at an unmodified Larinier super active baffle fishway was 0.3 % whilst Foulds & Lucas (2013) show that passage efficiency of Denil and pool and weir fishways for the same species to be 0 % and 5 % respectively. Nature-like bypasses have been proposed as an alternative to conventional fishways and may provide greater passage efficiency of *L. fluviatilis* by replicating natural sections of waterways, but they have not yet been evaluated. Therefore, it is vital to assess the utility and efficacy of nature-like bypasses for *L. fluviatilis* passage to determine if they are an acceptable solution.

#### 1.6.3.2. Hydropower and water abstraction

Studies regarding the impingement and entrainment (whereby lamprey are drawn through a hydropower or water extraction site) of lamprey within the Humber River Basin are scarce. Bracken & Lucas (2013) found a damage rate of 1.5 % for juvenile *L. fluviatilis* entrained within an Archimedes screw hydropower station on the Derwent. Although this is a low percentage, the authors warn that the cumulative impact of numerous hydropower stations within a single catchment could be significantly higher (Bracken & Lucas, 2013). Additionally, Teague & Clough (2011) note that, from February 2009 to March 2009, 235 juvenile *L. fluviatilis* were entrained at a Yorkshire Water water abstraction site located on the Derwent, with a survival rate of 89.7 %. However, an unspecified number of lampreys also received significant injuries which may have led to mortality prior to spawning.

Recorded impingement rates can be noticeably higher than entrainment, with Proctor & Musk (2001) finding an impingement rate of 482 *L. fluviatilis* per 24 hrs at the water intake of the South Humber Bank Power Station in June, 2000. Impinged lamprey were most likely juveniles undergoing their downstream migration. The scale of impingement and entrainment on lamprey populations within the Ouse catchment may be significant, as the residual loss of juvenile *L. fluviatilis* from entrainment at the Elvington water treatment works was estimated to be 3.4 % of the Derwent's population (APEM, 2009). However, it is difficult to estimate the population size of juvenile lamprey within the Humber River Basin and so this figure may be inaccurate. Nonetheless, it is important to investigate the scale of impingement and entrainment of *L. fluviatilis* across the Humber River Basin as well as technologies to reduce their impacts if necessary.

1.6.3.3. Commercial exploitation

The Humber River Basin has been the site of commercial exploitation of *L. fluviatilis* since the late 19$^{th}$ century at least (Maitland, 2003; Masters *et al*., 2006). The purpose of this recorded exploitation was to fulfil the bait demand generated by the North Sea long-line fishing fleet rather than for direct human consumption (see section 1.3.2.). The River Ouse provided the majority of this historic exploitation (Masters *et al*., 2006). Catch rates were high, with estimates ranging between 25,500 lampreys captured from 1913-14 to 54,500 from 1910-1911 (Masters *et al*., 2006). This fishery, along with all the other lamprey fisheries in the UK, ceased as trawling replaced long-line fishing in the North Sea (Lanzing, 1959).

The UK lamprey fishery was revived in the early 1990's through bycatch of licenced European eel (*Anguilla anguilla*) fisheries in the tidal reaches of the Ouse and Trent rivers (Masters *et al*., 2006). However, the introduction of the Marine and Coastal Access Act (2009) which enabled the licencing and restriction of lamprey fishing by the Environment Agency (EA), combined with the dramatic decline of *Anguilla anguilla,* led to a shift in the fishery to treat *L. fluviatilis* as the primary target rather than bycatch (Foulds & Lucas 2014; M. Lucas, pers. comm). These lampreys are sold to tackle shops as bait for predatory freshwater fish, notably pike (*Esox lucius*). Two lamprey fishers on the Ouse were identified by Foulds & Lucas (2014) who estimated an exploitation level of >20 %. As these fisheries are close to the Humber Estuary SAC (for which the presence of *L. fluviatilis* is a listed feature) it is crucial to manage the current lamprey fishery in the UK to ensure the persistence and recovery of *L. fluviatilis* in the Humber River Basin without detriment to that SAC or the nearby Derwent SAC.

## 1.7. Research direction

It is important to understand the individual efficacies of the multiple fish way designs *L. fluviatilis* may encounter during migration. Within the Humber River Basin, *L. fluviatilis* encounter many low-head barriers and so should be provided upstream passage through installed fishways. Despite this, conventional fishways have demonstrably failed to successfully provide *L. fluviatilis* with passage in sufficient quantities (Foulds & Lucas, 2013; Tummers *et al*., 2016a). It may be that *L. fluviatilis* depends on periods of high flow to cross barriers directly, without the aid of fishways which puts them at risk if extended low flow periods prevent upstream passage (Lucas *et al*., 2009). Although nature-like bypasses have been suggested as an effective alternative for lamprey passage (Lucas *et al*., 2009), there have been no quantitative studies to assess their suitability for *L. fluviatilis*. Consequently, chapter two aims to:

1) Evaluate the efficacy of a semi-formalised nature-like bypass for upstream migrating *L. fluviatilis* using Passive Integrated Transponder (PIT) and acoustic telemetry.
2) Investigate the impacts of environmental factors such as water temperature and river stage (level) on passage success and time.
3) Evaluate if this form of bypass is suitable for wider application to provide passage to migrating non-climbing lampreys and recommend potential improvements.

The re-emergence of the commercial lamprey fishery within the Humber River Basin is also a cause for concern. Although lower than historic exploitation levels within the Humber and current exploitation within the Baltic, an exploitation level of >20 % is still worrying because *L. fluviatilis* is a semelparous species and so is vulnerable to large scale exploitation (Valtonen, 1980; Sjöberg, 2011; Foulds & Lucas, 2014). The purpose of this exploitation is to provide bait to anglers and although the structure of the lamprey bait market in Britain has already been revealed (see Foulds, 2013; Foulds & Lucas, 2014) the opinions and attitudes of the consumers, coarse predator anglers, have not been investigated. It is essential to take consumer attitude and opinions regarding the use of lamprey as coarse predator bait into consideration in order to properly manage the exploitation of *L. fluviatilis*. As a result, chapter three aims to:

1) Understand the general fishing behaviour and attitudes of UK coarse predator anglers.
2) Determine the proportion of anglers using lamprey as bait and for what purpose.
3) Establish the knowledge and opinions of anglers regarding lamprey as bait.
4) Determine how willing anglers are to replace lamprey with alternative baits.

# CHAPTER 2: Inefficiency of a semi-formalised nature like bypass used by European river lamprey for upstream passage

Research reported in this chapter originates from part of a Marine Management Organisation funded project on the exploitation and migration of river lamprey in the River Yorkshire Ouse. The study rationale was created by J. Bolland, University of Hull (UoH) and M. Lucas, Durham University (DU). The study was designed by A. Lothian, A. Albright (2019-20 season), M. Lucas (all DU) and J. Bolland (UoH). Raw data were collected in the 2018-2019 study period by A. Lothian (DU) and W. Jubb (UoH). Raw data in the 2019-2020 study period were collected by A. Albright, A. Lothian, D. Bubb (DU) and W. Jubb (UoH). Telemetric tagging of lamprey was conducted by W. Jubb, J., Bolland, R. Nobel, J. Dodd (all UoH) and A. Lothian (DU) across both study periods. Data analysis, interpretation and writing was done by A. Albright, with comments by M. Lucas.

## 2.1. Abstract

Impacts of river barriers are particularly pronounced for migratory fishes. Due to their historic legacy, fishways, created to aid fish passage across anthropogenic barriers, have been designed with a bias towards strong-swimming species e.g., salmonids, but are ineffective for weaker swimming species. Most conventional fishways are ill-suited to provide passage to lamprey although species specific differences exist. As a consequence of this, research into providing fish passage for a wider range of fish species, including lamprey, across anthropogenic barriers is ongoing. One promising concept is that of nature like bypasses which aim to replicate the heterogeneity of hydraulic conditions found within streams, thus assisting the upstream movement of weaker swimming. However, the efficacy of nature like bypasses has not been formally tested for lamprey. This study used PIT and acoustic telemetry to measure the attraction and

passage efficacy of *Lampetra fluviatilis* through a semi-formalised nature like bypass with an undershot control sluice at the upstream end, during the upstream pre-spawning migration period. Although this bypass was designed with an intention to permit upstream migration of lamprey and eel, it had not been tested. The bypass exhibited a high attraction efficiency of up to 70.8 % (calculated as the number of acoustically tagged lamprey that entered the bypass as a percentage of those detected downstream of the weir). However, passage efficiency through the bypass was low with a minimum estimate of 5.38 % (calculated as the number of PIT tagged lamprey which successfully used the bypass to travel upstream of Naburn weir as a percentage of those that were detected within the bypass during the period of time that the most upstream PIT antennas was operational). Acoustic telemetry results indicate that, rather than using the bypass, most lamprey passed Naburn weir directly when the weir was drowned out. Most passage attempts within the bypass and across the weir occurred during periods of high river stage when the weir was drowned out. During these periods the flows through the bypass increased attraction into the bypass but also created conditions unsuitable for passage through the bypass due to high velocities, especially at an undershot control sluice at the upstream end. Although the bypass passage efficiency calculated is likely to be an underestimate, due to periods of PIT antenna failure, this design of semi-formalised nature like bypass is not recommended to aid upstream lamprey passage. Recommendations for a thorough analysis of lamprey swimming performance and technologies to assist passage such as attractant/repellent semiochemicals are made.

## 2.2. Introduction

Migratory freshwater fish are highly threatened, especially in Europe (see section 1.1.). Numerous threats have contributed to these declines such as exploitation, pollution and disease, however one of the largest issues is the blocking of migration pathways through anthropogenic barriers in rivers (Deinet *et al.,* 2020). Waterways are highly fragmented globally, with only 23 % of rivers >1000 km in length free flowing to the sea (Grill *et al*., 2019). Fragmentation in the UK is more intense as Jones *et al.* (2019) show that only 1 % of rivers in England, Scotland and Wales are free of artificial barriers. Large dams are often seen as the predominant form of anthropogenic barrier. They do cause noticeable impacts to freshwater ecosystems such as habitat modification, habitat degradation and favouring the spread of non-native species (Santucci Jr *et al*., 2005; Dudgeon *et al*., 2006; Poff *et al*., 2007; Zeng *et al*., 2017; Turgeon *et al*., 2019). However, the impacts of smaller low-head barriers (structures with a head of <3 m such as weirs or culverts) are often overlooked (see section 1.3.). Belletti *et al*. (2020) estimate that out of the 1.2 million instream barriers in Europe, 68 % are low-head barriers. As the demand for hydropower rises it seems likely that the number of anthropogenic barriers is set to increase, with Chile projecting a 6.8-fold increase in barriers by 2050, and so they will have an increased ecological impact in future (Zarfl *et al*., 2015; Lucas *et al*., 2020).

Unsurprisingly, efforts to mitigate the impacts of anthropogenic river barriers are ongoing. Barrier removal has been shown to trigger rapid recovery of rheophilic biodiversity (Hogg *et al*., 2013; Birnie-Gauvin *et al*., 2017) but this is rarely done, possibly due to the large cost of barrier removal in some cases and potential hydrological effects downstream (Silva *et al*., 2018; Birnie-Gauvin *et al*., 2019). As a result, fishways are often selected as an alternative method. Fishways (see Figure 2.1 for conventional 'technical' designs) are defined by Silva *et al.* (2018) as structures deliberately created to facilitate safe and timely fish movement past an obstacle, upstream and/or downstream. Fishways date back to over 300 years ago (Clay, 1995). Fishways can provide effective upstream passage across barriers for multiple species of fish (Noonan *et al*., 2012; Baker, 2014; Dodd *et al*., 2018) but must be carefully designed to produce suitable hydraulic conditions for passage. Flow volumes and velocities at the entrance of the fishway must be sufficiently high to prove attractive to fish to encourage them to enter whilst flow velocities and other hydraulic features such as turbulence are low enough to allow successful passage (Castro-Santos *et al*., 2009; Williams *et al*., 2012). However, fishways were initially designed to provide upstream passage to migrating salmonids and, in most cases, have not been re-designed for other taxa (Mallen-Cooper & Brand, 2007). Noonan *et al.* (2012) give evidence of a salmonid bias as they show that salmonids have significantly higher passage efficacy than non-salmonids across all forms of fishway. It is vital to design fishways that provide multiple species passage. This requires understanding of the behaviour and swimming capabilities of multiple fish taxa.

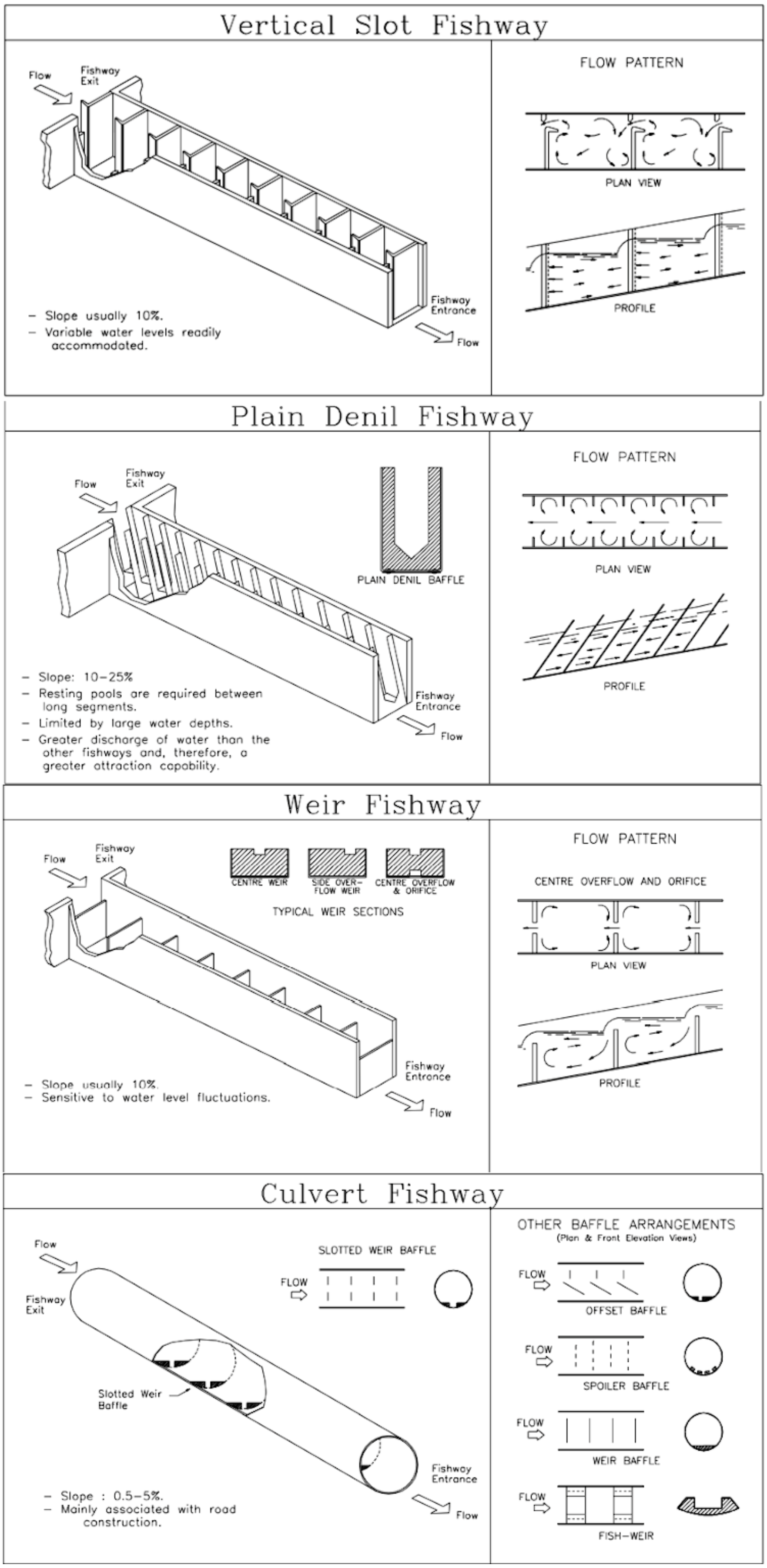



*Figure 2.1: Examples of technical fishway designs. Reproduced from Katopodis (1992).*

Migratory lampreys are a group of fishes at high risk from anthropogenic barriers such as dams (Liermann *et al*., 2012). In the past, lampreys were rarely considered during the design of fishways (Moser *et al*., 2011). The majority of lamprey passage research has focused on two areas. Firstly, preventing invasive *Petromyzon marinus* from completing their upstream migration into spawning tributaries of the North American Great Lakes and so contributing to their control (Lavis *et al*., 2003; Sherburne & Reinhardt, 2016). Secondly, increasing the passage of Pacific lamprey (*Entosphenus tridentatus*) over hydroelectric dams in North America, which has so far been successful (Moser *et al*., 2010; Goodman & Reid, 2017).

Although the latter area seems to indicate that measures are being successfully enacted to reduce the impact of anthropogenic barriers on lamprey, care must be taken when comparing behaviour and swimming capabilities across species. Pacific lamprey are unusual (together with the southern hemisphere lamprey, *Geotria* and *Mordacia*) as the pre-adults are able to scale wetted vertical surfaces through powerful axial undulation and oral disc attachment (Reinhardt *et al*., 2008; Zhu *et al*., 2011) and so are successful at passing through fishways that incorporate specially built smooth surface ramps and rest stations (Moser *et al*., 2010). Pre-adult lampreys occurring in Europe such as *P. marinus* and *L. fluviatilis* do not exhibit this behaviour, but rather utilise a burst-rest-attachment strategy to traverse obstacles in high velocity conditions (see section 1.3.3.). This may explain why the passage success of different fishway designs varies across species. For instance, whilst *E. tridentatus* has a passage efficiency of >90 % on "pool and weir" fishways (Keefer *et al*., 2013), Castro-Santos *et al*. (2017) recorded a passage efficiency of 29-55 % for *P. marinus* in a similarly designed fishway. Additionally, *L. fluviatilis* is a smaller species than *E. tridentatus* or *P. marinus* and so is likely a weaker swimmer in absolute terms. Russon & Kemp (2011) note that *L. fluviatilis* has a maximum burst speed of 2.12 $ms^{-1}$ at 12.6 ˚C whilst the larger *P. marinus* is capable of burst speeds of over 4 $ms^{-1}$ (Hoover & Murphy, 2018).

Consequently, *L. fluviatilis* is poorly suited to crossing anthropogenic barriers, with flume tests indicating that they struggle to pass even small weirs (Russon *et al*., 2011). Furthermore, *L. fluviatilis* have very low passage efficiency across many types of technical fishway such as Denil, pool and weir and super-active baffle fishways (Foulds & Lucas, 2013; Tummers *et al*., 2016a). This is problematic as adult lamprey often must traverse anthropogenic barriers to reach suitable spawning grounds. Lamprey undergoing their pre-spawning migration have a fixed energy budget as they do not feed during this period, their intestines atrophy and they have a single opportunity to spawn (see section 1.2.). Additionally, their spawning cycle is closely linked with day length and water temperature (Maitland, 2003; Johnson *et al*., 2015). As a result, delay or obstruction of migration due to poor passage at barriers may prevent lamprey from reaching many potential spawning grounds or cause them to miss the spawning period. Evidence of this is seen in the Derwent river of the Humber River Basin, NE England, where although 98 % of suitable spawning habitat occurs >51 km upstream the effects of barriers means that only 1.8 % of recorded spawners occur that far upstream (Lucas *et al*., 2009). Thankfully, research into "lamprey friendly" fishways is ongoing (Moser *et al*., 2015; Lucas *et al*., 2020) but many of the current solutions, such as retro-fitting barriers with studded tiles, have only shown modest success (Vowles *et al*., 2017; Tummers *et al*., 2018; Lothian *et al*., 2020).

Providing effective, multi-species passage over anthropogenic barriers is required to remediate the impacts of anthropogenic barriers. A potential solution is the construction of nature-like bypasses. Nature-like bypasses (Figure 2.2) aim to recreate sections of natural waterways, constructing low gradient passes with natural materials (Jungwirth, 1996; Jungwirth *et al*., 1998; Katopodis *et al*., 2001). Nature-like bypasses have been shown to provide passage to multiple species of fish (Santos *et al*., 2005; Calles & Greenberg, 2007; Kim *et al*., 2016), including weaker swimming species (Tummers *et al*., 2016b), and can even compensate for the loss of lotic habitat (Tamario *et al*., 2018). *Petromyzon marinus* has been recorded as successfully passing through a nature-like bypass (Santos *et al*., 2005). Aronsuu *et al*. (2015) even shows that all acoustically tagged *L. fluviatilis* that entered a 1:40 gradient nature like rock ramp fishway successfully traversed it. However, this occurred with a very small sample size (*n*= 10). Consequently, this study evaluated the efficacy of a semi-formalised nature-like bypass for *L. fluviatilis* during their adult spawning migration and the impact of environmental factors on passage, through the use of Passive Integrated Transponder (PIT) and acoustic telemetry.

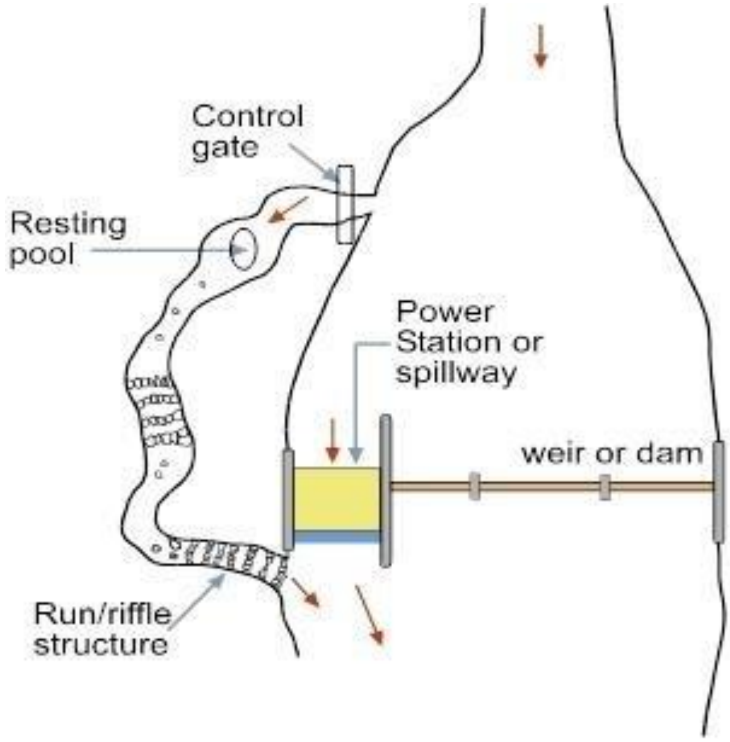



*Figure 2.2: Hypothetical example of a nature like bypass design. Reproduced from Franklin* et al. *(2018).*

## 2.3. Methodology

### 2.3.1. Study site

The study was conducted at Naburn weir (Latitude: 53.893614, Longitude: -1.099192), the tidal limit of the River Ouse, North Yorkshire, North East England. The Ouse has a low average gradient (c 0.1 m $km^{-1}$), an average width of 40 m and an average depth of 3 m (Lucas *et al*., 1998). It has a mean freshwater flow of 51.4 $m^3s^{-1}$, measured at Skelton, with a catchment area of 10,704 $km^2$ (https://nrfa.ceh.ac.uk/). It is one of the two principal sub-catchments of the Humber, draining from the north and west, while the Trent drains from the south, together forming the largest drainage basin in the UK at around 24,000 $km^2$ (Figure 2.2) (Whitton & Lucas, 1997). It has a low base flow index of 0.45 resulting in a strong response to precipitation (https://nrfa.ceh.ac.uk).

When compared to most other UK rivers, the Ouse contains a diverse fish fauna dominated by cyprinids (Lucas *et al*., 1998). The Humber Estuary is macrotidal and a designated SAC, partly due to the population of European river lamprey, *L. fluviatilis*, a large proportion of which spawn in key tributaries of the Ouse, comprising the Swale, Ure and Nidd which join upstream of Naburn, and the Wharfe which joins downstream, near Cawood (Figure 2.2).

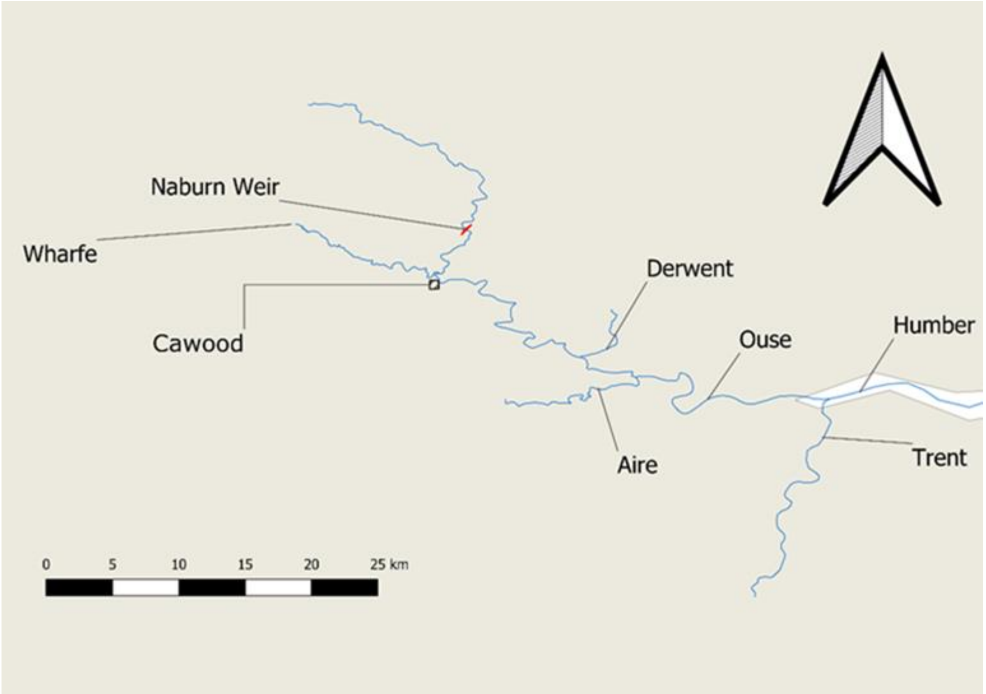



*Figure 2.2: The rivers in the study area; Ouse, Derwent, Trent, Aire and Wharfe. The Ouse and Trent join to form the Humber Estuary. Naburn weir and Cawood are also marked on the map.*

The Humber Estuary provides feeding grounds for developing parasitic juvenile river lamprey and its tributaries such as the Swale, Ure, Nidd, Wharfe and Derwent contain habitats suitable for spawning and larval development (Lucas *et al*., 2009). This has led to the Humber containing one of the UK's (and Western Europe's) most important population of *L. fluviatilis* (Jang & Lucas, 2005; Lucas *et al*., 2020). Out of the 15 largest weirs within the Humber river basin, Naburn weir has been marked as a high priority site for passage improvement by Nunn & Cowx (2012). This is because it is the first barrier that upstream-migrating diadromous fish (including *L. fluviatilis*) encounter on the Ouse, Naburn weir being the artificial tidal limit of the River Ouse. The study occurred over two separate periods; November 2018 to April 2019 and November 2019 to April 2020, broadly reflecting migration periods by adult river lamprey in the Ouse (Masters *et al*., 2006; Lucas *et al*., 2009).

**2.3.2. The bypass**

Naburn weir was built in 1741, as a triangular weir, and predates the navigation lock at the same site which was opened in 1757 to improve navigation along the Ouse and was expanded in 1888. Naburn weir is approximately 38 m across and has been raised from its original crest height of 3.24 meters from the river bed to the top of the weir crest to 3.71 m. This results in Naburn weir crest currently being 4.91 meters above ordnance datum (mAOD). Regardless of this raising, Naburn weir is frequently flooded during periods of high freshwater flow combined with high tide. An Environment Agency gauging station is present at the weir on the left bank that records river stage both upstream and downstream of Naburn weir. The navigation lock is approximately 250 m long and 20 m wide, the lock gates are opened only to allow traffic through the lock but may provide passage to fish through holes in the lock gates (A. Albright, personal observation).

A pool and weir salmon ladder, constructed of iron and concrete in 1936 is present on the right bank of the weir. The salmon ladder consists of seven pools (each approximately 4.8 m long and 2.4 m wide with an approximate 0.3 m drop between each pool). Overall, the salmon ladder gains approximately 2.7 m in height from the downstream entrance to upstream exit. The salmon ladder’s outflow overlaps with that of a semi-formalised nature like bypass that is also present on the right bank (Figure 2.3, Figure 2.5). The semi-formalised nature-like bypass was installed on the right bank by the Environment Agency in 2014, semi-formalising an existing haphazard channel and large hole in the wing wall which was created by erosion during floods. This erosion channel has been known to be used for upstream passage by *L. fluviatilis* since 2002 (Masters *et al.*, 2006; M. Lucas, unpubl. data). Due to the fear of wing wall failure and lamprey poaching the Environment Agency repaired the wall, created a semi-formal bypass and constructed a security fence. The bypass is approximately 50 m long, has an approximate 1:30 gradient, and was constructed out of cobbles set in concrete which forms a series of pools and small step weirs connected by drops no greater than 100 mm (Figure 2.3). The height difference between the downstream entrance and upstream exit is approximately 3.5 m, but this is somewhat variable throughout the tidal cycle. The downstream entrance is approximately 10 m downstream of the salmon ladder entrance and the upstream exit is approximately 5 m upstream of the salmon ladder exit. An adjustable sluice gate within the wing wall at the upstream end of the bypass aimed to provide suitable flow conditions for the upstream migration of eels in summer (by adjusting the sluice gate opening to a height of 30 cm) and river lamprey in winter (by adjusting the sluice gate opening to a height of 60 cm). Although the project was given the ICE (Institution of Civil Engineers) Sir John Fowler Award in 2015, the efficiency of lamprey passage across the bypass had not been tested prior to this study. It is important to note that the bypass present at Naburn weir is not a true nature-like bypass as it is too short and possess too steep a gradient to accurately mimic surrounding waterways. Consequently, the results of this chapter should not be deemed representative of *L. fluviatilis*'s passage capability over true nature like bypasses, but rather an evaluation of this specific design to see if it is suitable for broader application.

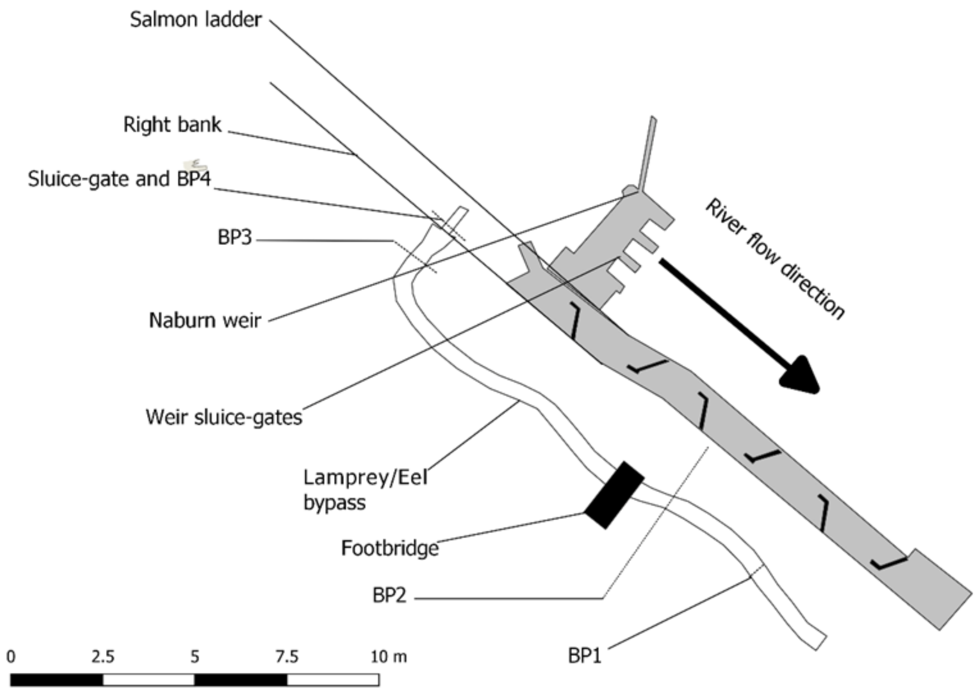



*Figure 2.3: Structure of the nature-like bypass and pool and weir salmon ladder present at the right bank of Naburn weir. Only part of the weir channel width is shown. The PIT antennas installed across the bypass are marked (BP1-4)*

*Figure 2.4: The semi-formalised nature-like bypass present at Naburn looking towards the downstream entrance for fish. The sluice is positioned immediately to the left of the image, out of shot.*

*Figure 2.5: Birds eye view of the Salmon ladder and semi-formalised nature-like bypass at Naburn. Reproduced from (www.youtube.com).*

**2.3.3. Telemetric methods**

Both Passive Integrated Transponder (PIT) and acoustic telemetric methods were deployed to record the movement of *L. fluviatilis* through the bypass and surrounding area. PIT telemetry was selected for the majority of *L. fluviatilis* as it provides a cost-effective method to track movement over small-scale structures with minimal adverse effects on swimming performance (Lucas and Baras, 2000). Moreover, PIT telemetry has been utilised in previous studies of *L. fluviatilis* passage (Calles & Greenberg 2007; Foulds & Lucas 2013, Tummers *et al*., 2016a, Tummers *et al*., 2018,) and so was deemed to be suitable for the purposes of this study. Acoustic tags are larger than PIT tags and so are more likely to affect swimming performance (Thorstad *et al*., 2013). Nevertheless, they were used alongside PIT telemetry because acoustic telemetry, using arrays of receiver-loggers with omnidirectional hydrophones, can be used to track the movements of tagged individuals in real time over much larger areas than PIT telemetry (Cooke *et al*., 2012). As acoustic tags generate sonic pulses to form their signals, they are operational in brackish environments (that would be frequently experienced at a tidal weir such as Naburn) unlike radio signals, which are rapidly attenuated by the dissolved salts in such waters (Thorstad *et al*., 2013). Acoustic tagging has also been shown to not significantly affect the swimming performance of the Pacific lamprey, *Entosphenus tridentata*, (Close *et al*., 2003) and Silva *et al*. (2017) found no apparent effect of acoustic tagging on the behaviour of *L. fluviatilis* released within the Ouse. Therefore, it was decided that a subset of the captured tagged lamprey would be both PIT and acoustically tagged with the remainder being only PIT tagged. A total of 2934 *L. fluviatilis* were PIT tagged during the course of the study, 120 of which were additionally acoustically tagged. This large quantity of lamprey were tagged in order to maximise the chances of recaptures (a separate study under the control of Hull University). Additionally, when considering the potential effects of predation and the various routes lamprey could have taken post-release, this large quantity of lamprey were tagged in order to maximise the chances that a sufficient number of lamprey reached Naburn weir for meaningful statistical analysis to occur.

2.2.3.1. Lamprey capture and tagging procedure

*Lampetra fluviatilis* were captured for tagging along a 10 km stretch of the Ouse centred at Cawood (a site approximately 9 km downstream of Naburn) from November to December across both study years by an experienced commercial fisherman using a total of 40 Apollo II type eel pots divided across three trap lines. This downstream section of the Ouse was selected for trapping as it has shown a higher CPUE (Catch Per Unit Effort) than other areas of the tidal Ouse or Trent for *L. fluviatilis* (Lucas *et al*., 2009, Masters *et al*., 2006). It also meant that tagged lamprey were unlikely to have visited the weir previously. Traps were checked weekly and lamprey were landed at Cawood, maintained in aerated tanks and processed by a team of taggers. Lamprey were sedated in a buffered solution of tricaine mesylate and river water (MS-222, 0.1 g $L^{-1}$) in groups of two – three at a time. Total body length (to the nearest mm) and body weight (to the nearest gram) were recorded. Tagging was carried out under the Home Office license and direction of J. Bolland, University of Hull. All *L. fluviatilis* over 320 mm had a 23 mm HDX PIT tag (Oregon RFID, 3.65 x 23 mm, 0.6 g in air) inserted into the body cavity through an incision (approx. 4 mm long) in the ventral side under Home Office licence. PIT tag incisions were not closed with sutures or glue as *L. fluviatilis* (*n*= 60) were found to exhibit no PIT tag loss over a 5-month period when incisions were not closed (M. Lucas, unpublished data). A subset of the captured *Lampetra fluviatilis* with a body length exceeding 380 mm were additionally acoustically tagged with a 69 kHz acoustic tag inserted into the body cavity via a mid-ventral incision (approx. 8 mm long) after PIT tagging. The acoustic tag model changed between study years; V7-2L in 2018 (VEMCO, 7 mm x 20 mm, 1.6 g in air) and V7-4L in 2019 (VEMCO, 7 mm x 22.5 mm, 1.8 g in air). Acoustic tag incisions were closed with sutures due to the larger incision size. Acoustic tags were set to transmit every 60 (± 30) seconds. Expected tag lifespan varied between study years; 132 days in 2018 and 197 days in 2019. In both cases, it was expected that acoustic tags would continue operation until after May the following year. This would cover the duration of the study period. The minimum size for tagging was implemented to reduce any potential tagging effects. The combined weight of PIT and acoustic tag exceeded 2 % of the lamprey's total body weight in rare cases. However, the validity of the 2 % rule of thumb is debatable (Jepsen *et al*., 2005) and *L. fluviatilis* have been acoustically tagged before, seemingly to minimal effect (Lucas *et al*., 2009; Silva *et al*., 2017) therefore it was unlikely that the added weight from the combined tags had a significant impact on *L. fluviatilis*' behaviour compared to untagged fish. Tagged lamprey were electronically scanned to confirm that tags were operational and to record each tag's unique identification code. All lamprey were allowed to recover in aerated water (minimum 30 minutes) before release at Cawood in mid to late afternoon.

As previously mentioned, 2934 *L. fluviatilis* were PIT tagged and released at Cawood, 1660 in the 2018-2019 period and 1274 in the 2019-2020 period. Of these lamprey, 120 were additionally acoustically tagged, 61 in the 2018-2019 period and 59 in 2019-2020 period. Table 2.1 shows the number of lamprey released across 12 separate dates as well as the average bodyweight and body length recorded per release date.

*Table 2.1: The number of lamprey tagged and released per day split by tagging methodology (PIT or acoustic and PIT tags), as well as the average bodyweight (g) and body length (mm) recorded per release day. Standard deviation for the bodyweight and body length recorded are also included.*

| Release Date | Telemetric Tags Inserted | Number Tagged | Average Weight ± SD (g) | Average Length ± SD (mm) |
|---|---|---|---|---|
| 11/07/2018 | PIT | 148 | 72.3 ± 10.9 | 346.3 ± 14.6 |
| 11/07/2018 | Acoustic and PIT | 7 | 109.6 ± 18.3 | 392.0 ± 11.6 |
| 11/14/2018 | PIT | 282 | 76.5 ± 38.6 | 352.8 ± 20.2 |
| 11/14/2018 | Acoustic and PIT | 12 | 94.0 ± 21.1 | 391.8 ± 8.3 |
| 11/21/2018 | PIT | 338 | 73.9 ± 14.7 | 353.0 ± 25.7 |
| 11/21/2018 | Acoustic and PIT | 11 | 96.3 ± 10.9 | 391.7 ± 13.3 |
| 11/27/2018 | PIT | 329 | 77.4 ± 14.5 | 358.3 ± 18.1 |
| 11/27/2018 | Acoustic and PIT | 11 | 105.1 ± 8.6 | 394.0 ± 9.3 |
| 12/05/2018 | PIT | 351 | 81 ± 15.0 | 364.7 ± 20.6 |
| 12/05/2018 | Acoustic and PIT | 10 | 100.8 ± 11.7 | 396.5 ± 12.3 |
| 12/10/2018 | PIT | 151 | 78.3 ± 12.3 | 361.2 ± 17.2 |
| 12/10/2018 | Acoustic and PIT | 10 | 99.4 ± 7.9 | 396.2 ± 9.2 |
| 11/08/2019 | PIT | 134 | 74.6 ± 11.6 | 352.2 ± 13.9 |
| 11/08/2019 | Acoustic and PIT | 7 | 101 ± 8.7 | 391.6 ± 8.2 |
| 11/15/2019 | PIT | 255 | 76.7 ± 11.2 | 356.6 ± 16.0 |
| 11/15/2019 | Acoustic and PIT | 14 | 103.3 ± 9.7 | 391.6 ± 12.0 |
| 11/22/2019 | PIT | 298 | 79.5 ± 13.8 | 359.1 ± 19.0 |
| 11/22/2019 | Acoustic and PIT | 11 | 105.8 ± 13.6 | 396.9 ± 15.3 |
| 11/29/2019 | PIT | 199 | 80.1 ± 14.1 | 362.0 ± 19.7 |
| 11/29/2019 | Acoustic and PIT | 10 | 103.4 ± 15.8 | 396.4 ± 13.6 |
| 12/05/2019 | PIT | 175 | 86.1 ± 15.9 | 368.0 ± 21.2 |
| 12/05/2019 | Acoustic and PIT | 10 | 108.7 ± 8.5 | 400.1 ± 11.7 |
| 12/10/2019 | PIT | 154 | 83.2 ± 14.9 | 366.7 ± 19.9 |
| 12/10/2019 | Acoustic and PIT | 7 | 113.6 ± 9.0 | 408.6 ± 13.5 |

2.2.3.2. PIT telemetry data collection

A series of PIT antennas were installed throughout the bypass to detect tagged *L. fluviatilis* moving through it. The structure of the PIT antenna array changed between study periods with BP2 and BP4 being added prior to the start of the 2019-2020 study period. A swim through loop PIT antenna spanning the depth and width of the bypass channel was established at the base of the bypass (BP1). This was followed by a figure-eight shaped flatbed antenna (Castro-Santos *et al*., 1996) crossed over at the middle to improve detection (10 m by 0.4 m) (BP2). This antenna exceeded the bypass channel width and extended horizontally in order to detect lamprey swimming outside of the channel during periods of high river stage. At the top of the bypass two swim through loops were installed, BP3 was within the bypass and again spanned the depth and width of the channel whilst BP4 was fitted to a wooden frame constructed 30 cm upstream of the sluice gate at the outside exit of the bypass, above the weir (Figure 2.3). All PIT antennas were range tested to ensure a minimum detection range of 30 cm. It is important to note that BP4 could only detect PIT tags on the outside edge of the bypass i.e., once they had passed through the sluice-gate, due to metal interference from the sluice-gate preventing detections from within the bypass.

As previously mentioned, the structure of the PIT antenna array changed between study periods. BP2 was added as it was evident, during 2018-2019, that lamprey could evade BP1 during high river stage period by swimming outside of the bypass channel, potentially resulting in an inaccurate estimate of attraction efficiency. BP4 was added because without a PIT antenna covering the exit to the bypass it would be impossible to know how many lampreys successfully traversed the bypass upstream. It was not initially added (in 2018-2019) due to the expectation of metal interference from the sluice-gate affecting the detection efficiency of a PIT antenna. Accordingly, passage efficacy of the bypass could only be calculated for the 2019-2020 study period. Although two PIT antennas were installed across the pool and weir salmon fish ladder in the 2018-2019 study period (at ~30% of length from entrance, and at upstream exit), they were destroyed by debris swept downstream by high freshwater flow events at the start of the 2019-2020 study period and could not be repaired. Consequently, the salmon fish ladder PIT data was removed from this study as it could not be compared across study periods. Unfortunately, this meant that the efficiency of the semi-formalised nature-like bypass could not be compared to a traditional bypass design in almost identical environmental conditions.

In the 2018-2019 study period BP1 and BP3 were controlled by a single HDX PIT reader unit (Texas Instruments SX2000) with readers configured as a master (BP1) and slave (BP3) to interrogate and read synchronously. In the 2019-2020 study season two separate PIT units, each configured as Master-Slave were employed. BP1 and BP3 were master drives and BP2 and BP4 were the respective slave drives. Each set of antennas was synchronously interrogated eight times a second. Across both study seasons antenna tuners were fixed on posts above low water level adjacent to each antenna. The tuners connected to the readers through shielded twin-ax cables. The reader units and antennas were powered by three to eight 110 Ah 12 V leisure batteries that were replaced upon each visit to the site (every three to seven days). Readers and battery power supplies were kept in secured boxes positioned on platforms approximately 1 m above normal water levels to reduce chance of flood damage. Data collected (PIT tag identification number, time and date of PIT tag detection and antenna of detection) were stored on compact flash cards within the reader units. Data were downloaded on each site visit, at which point readers were reset to correct times. Before and after each battery change a, test PIT tag was passed through each antenna and the data downloaded to ensure the equipment was operational. Detection efficiency of PIT antennas was tested by repeatedly passing a test PIT tag perpendicular to the antenna at 1 $ms^{-1}$ ten times with a five second interval per pass. This was repeated at five separate points across the antenna for each antenna. It was found that the PIT antenna array had a detection efficiency of 95 %.

The 2018 season for collection of PIT data was ended in late December 2018 due to extensive battery failure and the 2019 season was ended in early February 2020 due to potential damage to equipment from flooding from Storm Ciara (requiring equipment removal). Consequently, the study's estimate for the bypasses' attraction efficiency may be an underestimate if some lamprey reached the bypass after the equipment was removed. BP1, BP2 and BP3 were operational for >95% of the study period but due to equipment malfunction BP4 was only operational after 10.00 December 10$^{th}$ 2019, approximately 55 % of the 2019-2020 study period. In order to account for this, when calculating the passage efficiency of the bypass, only lamprey that entered the bypass during the period that BP4 was operational were included.

#### 2.2.3.3. Acoustic telemetry data collection

An array of acoustic receivers (VEMCO VR2W - 69 kHz) were installed across the area surrounding Naburn weir to detect approaches from acoustically tagged upstream migrating *L. fluviatilis*, successful passage events and passage routes (Figure 2.6). A total of six receivers were utilised in the study, two downstream of the weir (R9 & R10) and four upstream (R11-R14). Numbering of these receivers reflects the fact that other receivers, not part of the study reported here, occurred downstream and upstream. Receivers were installed in non-turbulent water in September during low tide periods. Receivers were attached to weighted ropes (c. 10 kg) and tied to a secure position on the bank (such as a jetty), for both ease of recovery and to prevent the receivers from being washed downstream. Receivers were positioned so that they were approximately vertical and the hydrophone was pointing upwards. Each receiver was secured so that it was covered by at least 1 m of water at low tide. All receivers were powered by a 3.6 V lithium-thionyl chloride battery that provided a constant power output and an expected operational lifespan of 15 months. Receivers detected and interpreted the unique code of pulses generated by acoustic tags and recorded the tag identity and time of detection. R12 was installed within the navigation channel to detect lampreys taking that route upstream. R13 and R14 were included as it was realised that the detection range of R11 could overlap the weir during periods of flood, detecting tagged lamprey downstream of the weir and so two receivers were required further upstream. Two receivers (R9 & R10) were positioned downstream of the weir as the noise of the weir may have reduced the effective range of a receiver meaning a single receivers' range could not span the entire width of the Ouse. Multiple receivers also gave a degree of redundancy in case of loss of one. Receivers were inspected monthly for damage and to ensure none had been lost to flood events or vandalism. Data was offloaded wirelessly through Bluetooth. Data from acoustic receivers were collected from October 30$^{th}$ 2018 to March 31$^{st}$ 2019 and October 30$^{th}$ 2019 to March 31$^{st}$ 2020 during which time all receivers remained operational throughout. Detection range and efficiency of the acoustic receivers were tested by placing a sample acoustic tag (attached to a meter stick) approximately 1 m below the surface for two minutes ten times with a two-minute interval each time. This was repeated for each receiver between 0 and 50 m at five-meter increments. Receivers within the array was found to have a detection efficiency of > 90 % and a detection range of 40 m.

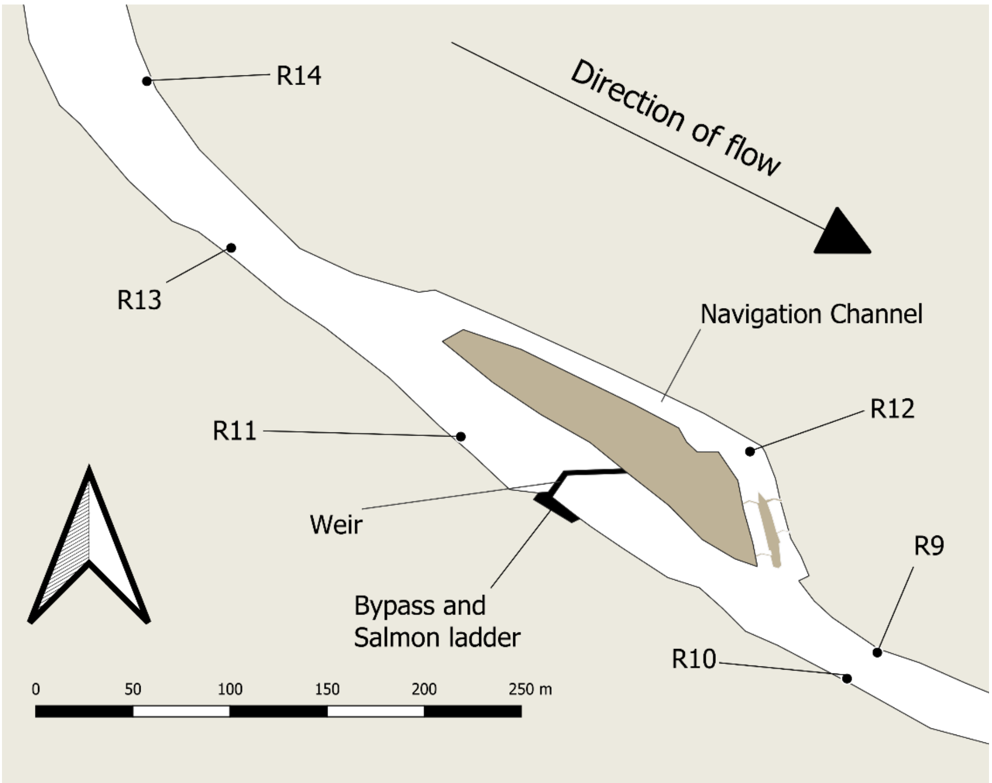



*Figure 2.6: Overhead view of Naburn showing the position of the acoustic receivers, the weir, the bypass and salmon ladder and the navigation channel. Tagged lampreys were released approximately 9 km downstream at Cawood.*

**2.3.4. Flow measurement and other environmental variables**

In order to characterise the environmental conditions that upstream migrating *L. fluviatilis* experienced within the bypass, water velocity and depth measurements were taken. To do this a 0.5 m x 0.5 m grid was manually fitted across the bypass, at each point in the grid water depth (to the nearest cm) was first recorded using a meter stick before the water velocities (in $ms^{-1}$) were taken at the 10 %, 50 % and 90 % water depths using an electromagnetic velocity meter (Valeport Model 801 EMGlow). This process was repeated on three separate dates; June 16th 2020, May 3rd 2020 and January 20th 2020, reflecting low (Q 85.8), medium (Q 31.1) and high stage (Q 9.7) conditions respectively. For the bypass sluice location, known to be a high-velocity locality when river level (and head) is elevated, five measurements were taken across the width of the sluice-gate at each of the 10 %, 50 % and 90 % water depth levels. Measurements were taken using sluice position settings at those adopted by the Environment Agency for lamprey migration conditions (60 cm opening of sluice-gate). GPS coordinates across the whole-bypass grid were extracted using a prior, simplified, diagram of the bypass and the data associated with each point was interpreted and extrapolated in QGIS to produce maps of the water depths and velocities across the bypass and water velocities across the sluice-gate cross-section.

Fifteen-minute river stage records over the study periods and daily mean stage records covering the last ten years were provided by the Environment Agency's downstream gauging station at Naburn Lock. Tidal cycles were not recorded as the tidal cycle was represented through the downstream stage recorded at the gauging station. Hourly average water temperature measurements were taken by a VEMCO VR2Tx - 69kHz acoustic receiver situated approximately 4 km downstream of Naburn weir. Sunrise and sunset times were taken from an online source (www.timeanddate.com).

### 2.3.5. Analysis

For this study attraction efficiency of the bypass was estimated in two ways. Firstly, for PIT tagged lamprey, the number detected within the bypass as a percentage of the number released at Cawood. Secondly, for double tagged lamprey, the number of lamprey PIT detected within the bypass as a percentage of the number lamprey acoustically detected immediately downstream of Naburn weir (at R9/R10).

New passage attempts were identified by the presence of a period between two subsequent detections of an individual tag exceeding 33 minutes for PIT tags (and so attempts within the bypass) and periods exceeding 39 minutes for acoustic tags (and so attempts to cross Naburn weir). This was determined by calculating the time interval between all subsequent detections and identifying the first interval where no detections occurred which was greater than 30 seconds (Castros-Santos &

Perry, 2012). River stage, water temperature, whether the attempt occurred between sunset and sunrise, and whether Naburn weir was flooded (stage exceeded 4.91 mAOD) were determined per attempt using the first detection of each attempt for PIT attempts within the bypass and the first and last downstream acoustic detection for attempts by double tagged lamprey across the weir.

Passage efficiency of the bypass was determined to be the number of lamprey detected on BP4 that had been detected on BP1, BP2 or BP3 prior to that detection and were not subsequently detected on BP1, BP2 or BP3 within 33 minutes of that detection on BP4 as a percentage of the number of lamprey detected within the bypass during the period of time that BP4 was operational. This was because, after a break in detections exceeding 33 minutes, a new passage attempt was deemed to have begun. The passage time within the bypass was determined to be the period of time between the detection at the start of the successful attempt and the first or only detection on BP4. Passage time for acoustically tagged lamprey was determined to be the period of time between the last downstream detection (R9/10) and the first upstream detection (R13/14), with R11 and R12 only being used to help interpret route of passage and continuity of movement. Acoustically tagged lamprey were determined to have used the bypass to travel upstream if they were detected on one or more of BP1, BP2 or BP3 and subsequently detected on BP4 between their last downstream detection and first upstream detection. Acoustically tagged lamprey were determined to have used the navigation lock to travel upstream if they were detected within the lock (R12) and were not detected on R11 prior to said detection between their last downstream detection and first upstream detection. Any detection of acoustically tagged lamprey downstream subsequent to their first detection upstream was ignored as it was deemed that any lamprey moving downstream had done so of their own volition and to remove the issue of one lamprey potentially making multiple successful passage attempts during the study.

To determine what factors affected the numbers of passage attempts lamprey made (both PIT and acoustic), the river stage and water temperature recorded across each lamprey's attempts were averaged, these mean values along with the lamprey's recorded weight and length on tagging were included as factors in a Poisson regression against the number of attempts each lamprey made. Final models were selected by comparison of ΔAIC (Akaike, 1974; Richards, 2008) and investigated by Wald tests. To determine what factors affected the chance of an attempt to pass the weir being successful, the weight and length of the lamprey as well as the river stage, water temperature, whether the weir was flooded and whether the attempt was between sunset and sunrise on the last downstream detection of each lamprey were included as factors in global logistic regression model against if the lamprey was detected upstream, final models were determined by comparison of ΔAIC (Akaike, 1974; Richards, 2008) and investigated by Wald tests. To determine what factors affected the passage time of lamprey travelling upstream, the weight and length of the lamprey as well as the river stage, water temperature, if the weir was flooded and if it was after sunset on the last downstream detection of each lamprey that was subsequently detected upstream were included as factors in a global linear regression model, final models were determined by direct comparison of ANOVA testing of global models and removal of non-significant factors (Rouder *et al.*, 2016). In all cases, separate models were created for the 2018-2019 study season and 2019-2020 study season data sets respectively. Pearson's $X^2$ tests with Yate's continuity correction applied were conducted to see if significantly more attempts or successful attempts to cross either the bypass or Naburn weir occurred after sunset or when naburn weir was drowned out. To account for multiplicity and correct for Type I errors, all model testing was conducted at a 5% significance level with the Holm–Bonferroni method applied. Fishway figures were drawn with QGIS (v3.12.2) and data analysis was conducted in R (v3.6.2).

## 2.4. Results

### 2.4.1. Stage and velocity measurements

During the 2018-2019 PIT telemetry study period (November 8$^{th}$ 2018 to January 4$^{th}$ 2019) the average stage was 3.82 ± 0.02 mAOD and Naburn weir was drowned out (stage >4.91mAOD) for 27.1 % of the study period. During the 2018-2019 acoustic telemetry study period (November 8$^{th}$ 2018 to March 31$^{st}$ 2019) the average stage was 3.17 ± 0.01 mAOD with Naburn weir being drowned out for 14.6 % of the study period. Over the entire 2018-2019 study period the maximum stage recorded was 7.71 mAOD, the minimum stage was 1.65 mAOD (Figure 2.7) and the average temperature was 5.73 ± 0.03 ˚C.

During the 2019-2020 PIT telemetry study period (November 8$^{th}$ 2019 to February 2$^{nd}$ 2020) the average stage was 4.57 ± 0.01 mAOD and Naburn weir was drowned out for 41.4 % of the study period. Over the 2019-2020 acoustic telemetry study period (November 8$^{th}$ 2019 to March 31$^{st}$ 2020) the average stage was 5.04 ± 0.01 mAOD and Naburn weir was drowned out for 50.7 % of the study period. Over the entire 2019-2020 study period the maximum stage recorded was 8.35 mAOD, the minimum stage was 2.09 mAOD (Figure 2.7) and the average temperature was 5.47 ± 0.02 ˚C. Water depths within the bypass ranged between 3 to 85 cm whilst water velocities ranged between 0.1 to 2.5 $ms^{-1}$ (Figure 2.8), with increased velocities at higher river stage, especially at the sluice opening.

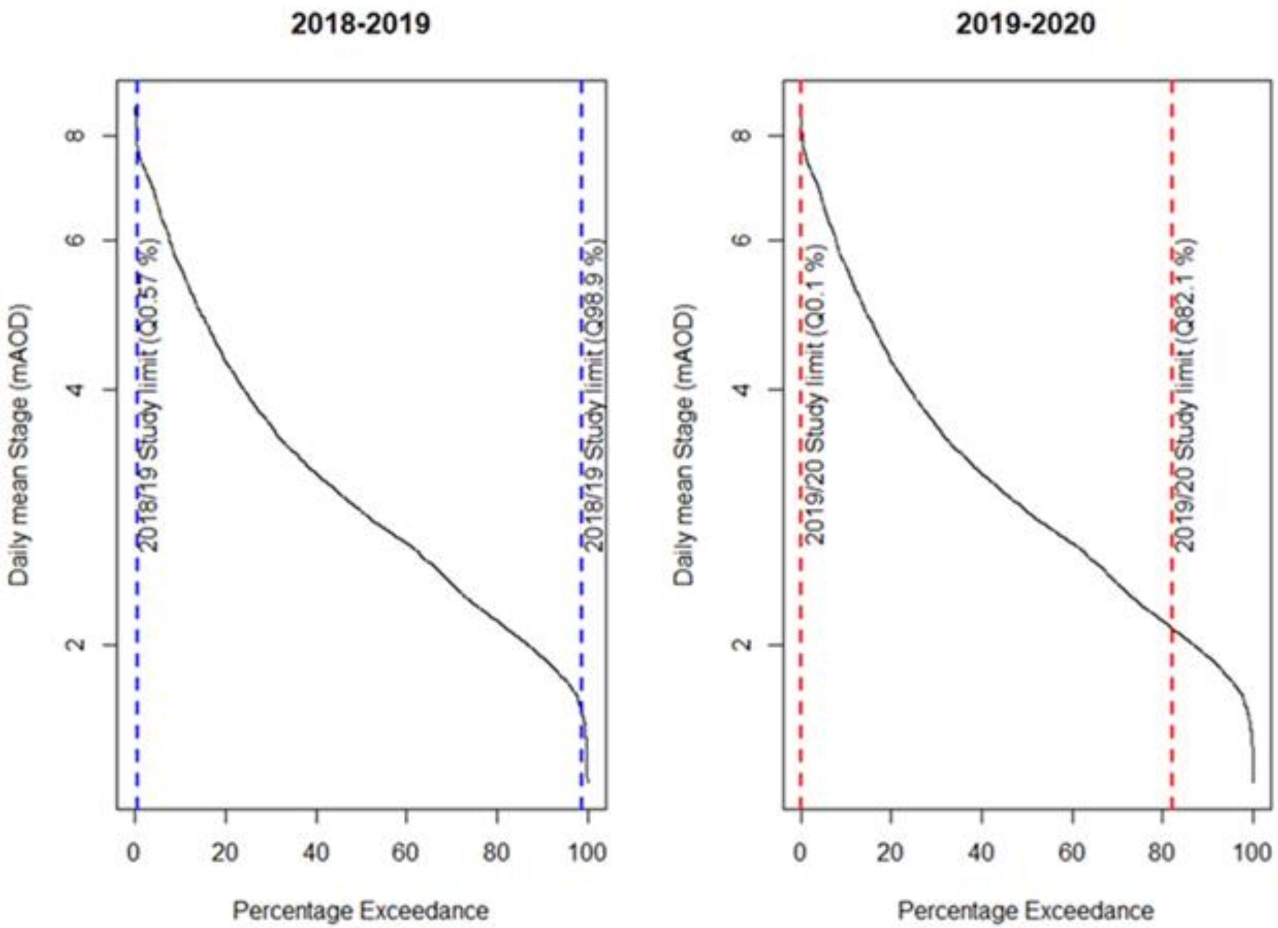



*Figure 2.7: Percentage exceedance curve of the Naburn daily stage means (log scale) recorded from January 1st 2010 with the maximum and minimum stage values of the 2018-2019 and 2019-2020 periods marked.*

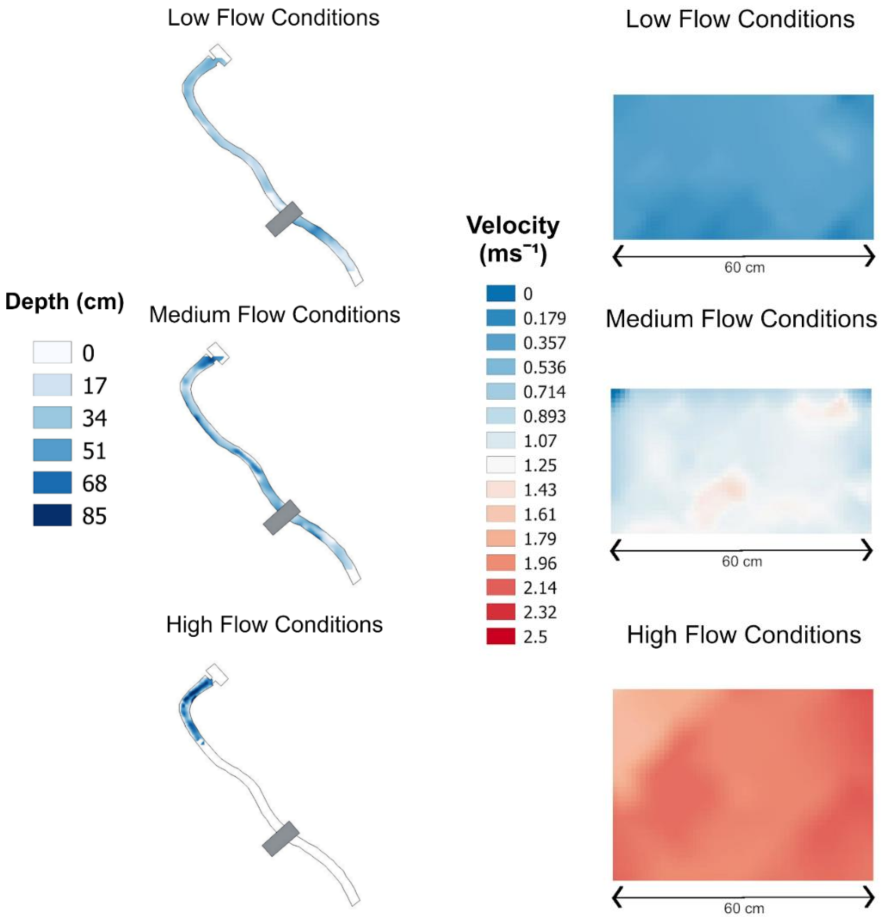



*Figure 2.8: Water velocity across the cross section of the sluice gate exit along with water depth and velocity of flow through Naburn weir lamprey bypass at 10%, 50% and 90% depth across Low, Medium and High flow conditions. Measurements were taken at; June 16th 2020 (Low flow conditions, stage= 2.02 mAOD, 2.89 m below weir crest), January 20th 2020 (Medium flow conditions, stage= 3.55 mAOD, 1.36 m below weir crest) and March 5th 2020 (High flow conditions, stage = 5.63 mAOD, 0.72 m above weir crest). Only the top bend was measured during high flow conditions as below this point the area was flooded and overtopped the bypass channel banks. The grey block represents the bridge over the bypass channel. Figure continues below.*

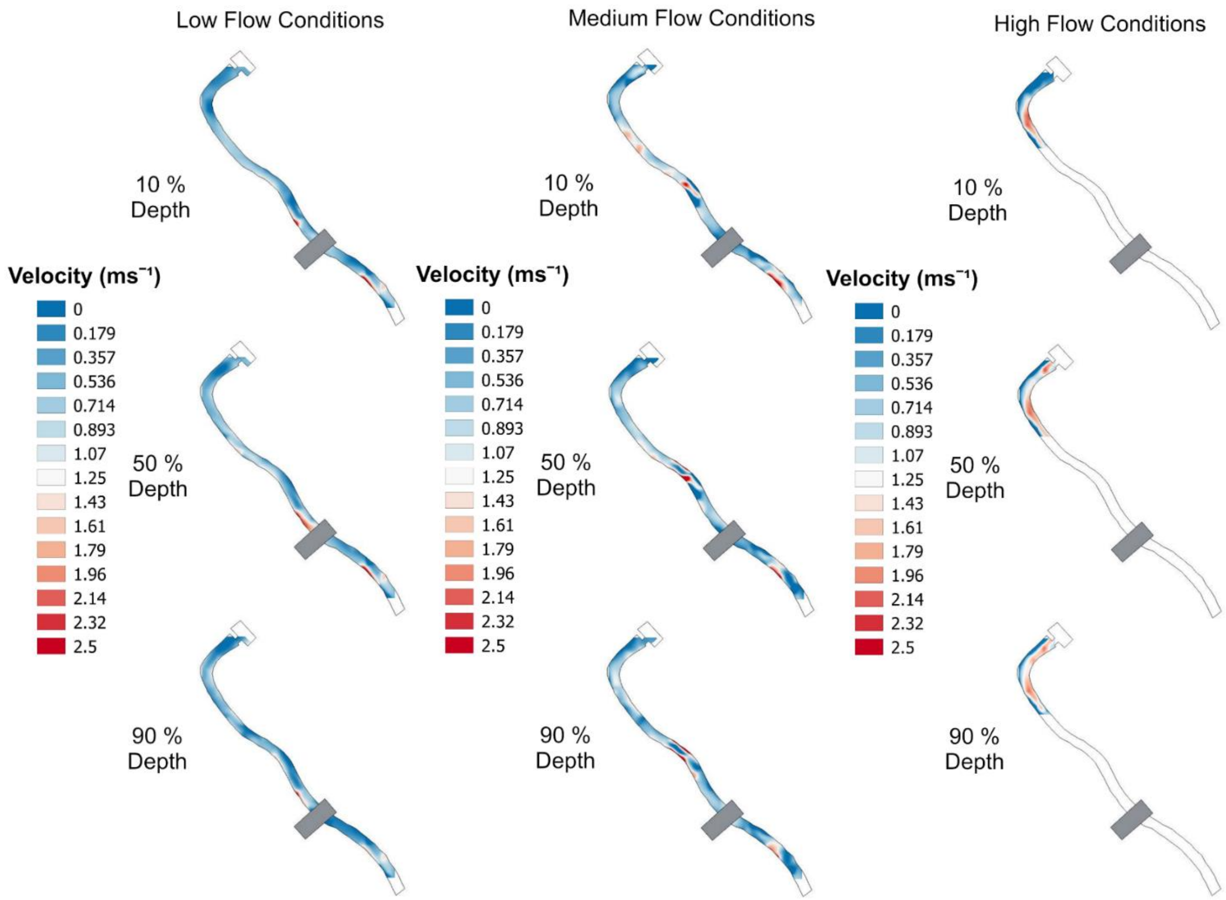



*Figure 2.8 (continued): Velocity of flow through Naburn weir lamprey bypass at 10%, 50% and 90% depth across Low, Medium and High flow conditions. Only the top bend was measured during high flow conditions as below this point the area was flooded and overtopped the bypass channel banks. The grey block represents the bridge over the bypass channel.*

#### 2.4.2. 2018 study season PIT telemetry

Of the 1660 PIT tagged lamprey (average weight= 77.8 ± 0.5 g, average length= 358.1 ± 0.5 mm) released at Cawood, 474 (average weight= 78.7 ± 0.7 g, average length= 359.0 ± 1.2 mm) were detected within Naburn bypass between 07/11/2018 to 04/01/2019. This generates an estimated minimum attraction efficiency (MAE, assuming 100% survival and movement to immediately downstream of Naburn weir) of 28.6 %. Tagged lamprey took 199.6 (± 8.1) hours on average, to be detected within the bypass post release but this was highly variable, ranging between 12.6 to 955.2 hours with 10.8 % (*n*= 51) of lamprey detected within 24 hours from release. Two hundred and eighty lamprey (59.1 % of all lamprey detected within the bypass) were detected on BP1 and 460 (97.0 % of all lamprey detected) on BP3. Figure 2.9 shows the number of lamprey detected within the bypass per day alongside the river stage during the 2018-2019 study season.

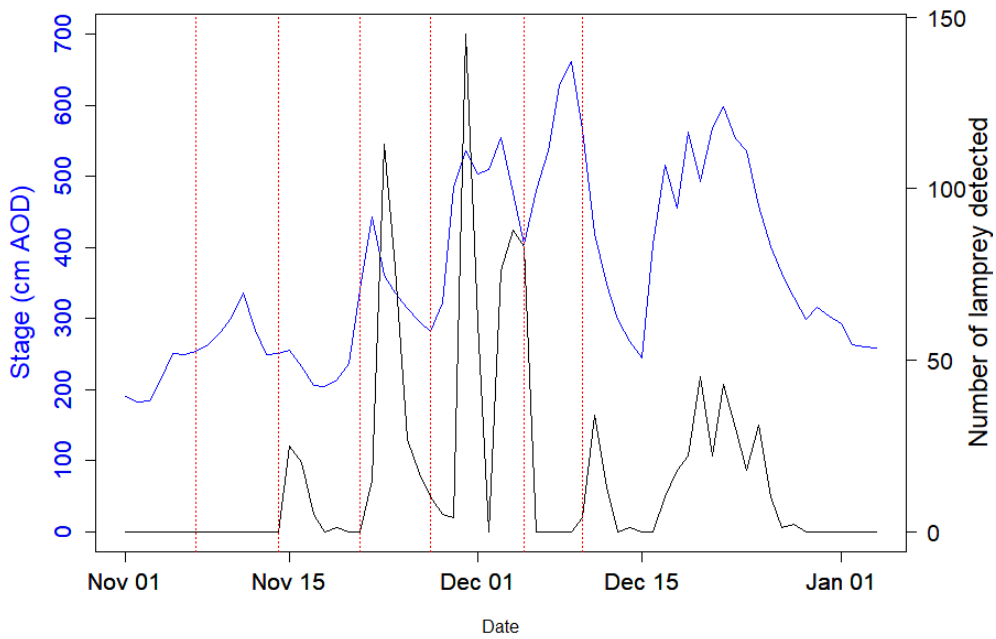



*Figure 2.9: The number of lamprey detected within the bypass alongside the downstream Naburn river stage (in centimetres above ordnance datum) from November 1st 2018 to January 4th 2019. Red vertical lines mark the release dates of tagged lamprey at Cawood.*

A total of 1714 attempts to traverse the bypass were made during the 2018-2019 study period. The number of attempts per lamprey ranged from 1 to 30 with an average of 3.6 ± 0.2 attempts per lamprey. Forty-three percent of attempts (*n*= 739) occurred when the weir was drowned out and 73.7 % of attempts (*n*= 1264) occurred after sunset. Significantly more attempts occurred when the weir was drowned out (Pearson's $X^2$ test with Yate's continuity correction applied, $X^2$= 222.53, df= 1, $p$< 0.001) and after sunset (Pearson's $X^2$ test with Yate's continuity correction applied, $X^2$= 386.58, df= 1, $p$< 0.001) than expected. A Poisson model containing the factors; the mean stage across attempts, the mean water temperature across attempts, the lamprey's weight, lamprey's length and if the lamprey was double tagged was initially created. The last factor was then dropped as it had an insignificant effect and was likely to have a negligible effect on swimming behaviour, unlike lamprey weight and length, which was kept. A negative binomial model was selected as the final model as it had a lower ΔAIC when compared to a Poisson model with the same factors. The number of attempts made to traverse the bypass decreased as mean stage (Wald test, $z$= -3.40, $p$< 0.001) and mean temperature (Wald test, $z$= -3.13, $p$= 0.002) across attempts increased (Figure 2.10). Once the Holm–Bonferroni method was applied, all of these factors remained significant under the new significance levels of 0.013 and 0.017 respectively. Due to the lack of a PIT antenna at the upstream bypass exit, the number of PIT tagged lamprey which successfully traversed the bypass during the 2018-2019 study season is unknown and so the passage efficiency cannot be recorded.

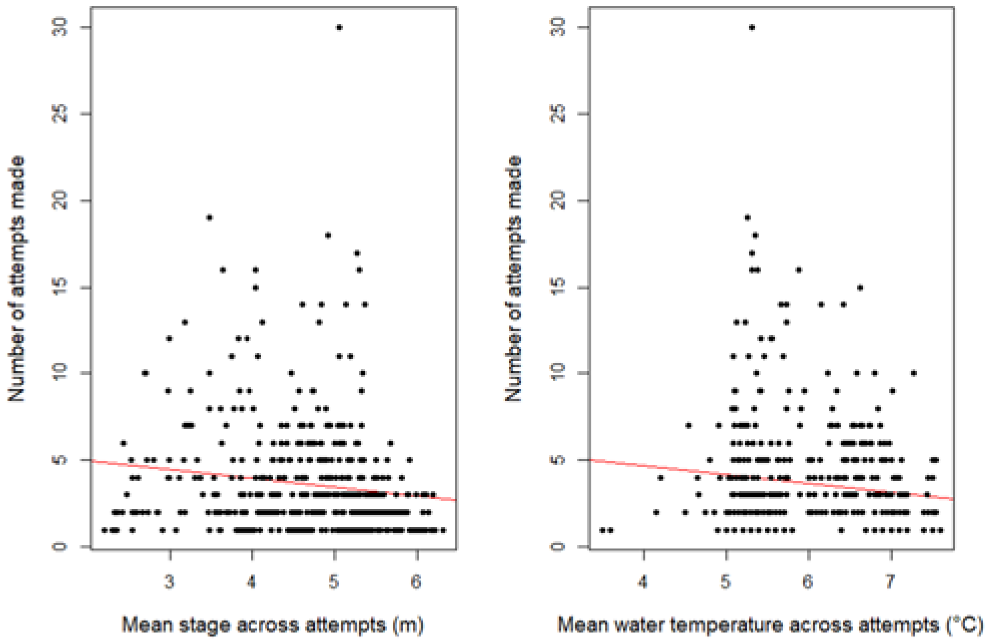



*Figure 2.10: The number of attempts made by each PIT tagged lamprey detected within the bypass between November 1st 2018 and January 4th 2019 against the mean stage (mAOD) downstream of Naburn weir and mean water temperature (˚C) recorded across said lamprey's attempts.*

**<u>2.4.3. 2019 study season PIT telemetry</u>**

Of the 1274 PIT tagged lamprey (average weight= 81.1 ± 0.4 g, average length= 362.2 ± 0.6 mm) released at Cawood, 645 (average weight= 81.7 ± 0.6 g, average length= 363.0 ± 0.8 mm) were detected within Naburn bypass between November 8th 2019 to Feburary 2nd 2020. This results in an estimated MAE (assuming 100% survival and movement to downstream of Naburn weir) of 50.6 %. Tagged lamprey took 139.2 (± 7.6) hours on average, to be detected within the bypass post release but this was highly variable, ranging between 6.8 to 1488.3 hours with 23.4 % ($n$= 151) of lamprey detected within 24 hours from release. The time taken to be detected within the bypass after release significantly differed across study periods (2018 vs 2019, Welch's two sample $t$-test, $t$= 5.42, df= 1068.1, $p$< 0.001). A total of 306 lamprey (47.4 % of all lamprey detected within the bypass) were detected on BP1, 475 (73.6 % of all lamprey detected within the bypass) on BP2, 454 (70.4 % of all lamprey detected within the bypass) on BP3 and 11 (1.7 % of all lamprey detected within the bypass) on BP4. Figure 2.11 shows the number of lamprey detected within the bypass per day alongside the river stage during the 2019-2020 study season.

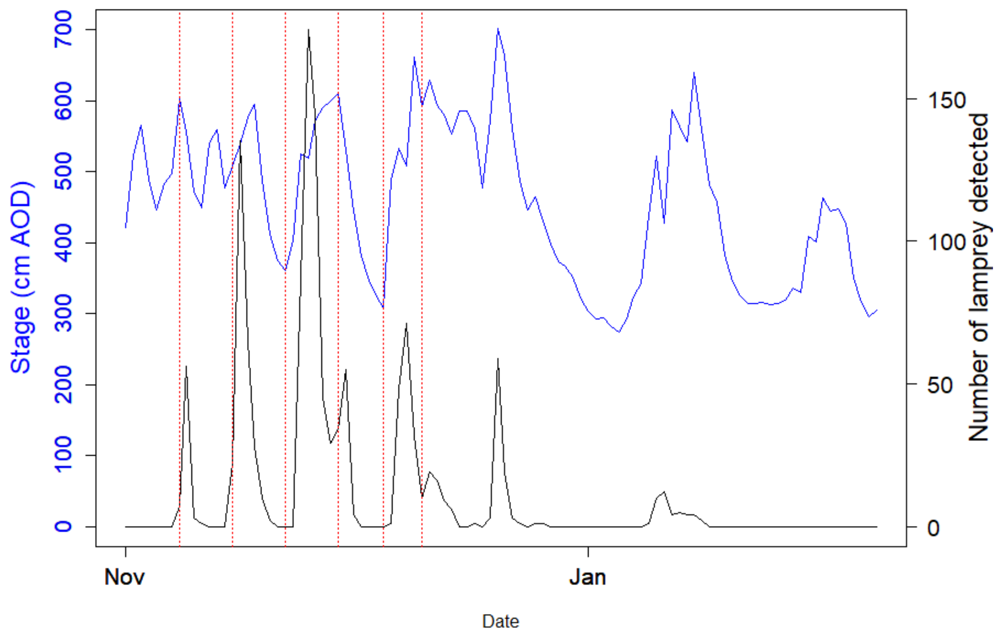



*Figure 2.11: The number of PIT tagged lamprey detected within the bypass alongside the downstream Naburn river stage (in centimetres above ordnance datum) from November 1st 2019 to February 7th 2020. Red vertical lines mark the release dates of tagged lamprey at Cawood.*

A total of 2408 attempts to traverse the bypass were made during the 2019-2020 study period. The number of attempts per lamprey ranged from 1 to 26 with an average of 3.7 ± 0.1 attempts per lamprey. Ninety percent of attempts (*n*= 2168) occurred when the weir was drowned out and 90.1 % (*n*= 2170) of attempts occurred after sunset. Significantly more attempts occurred when the weir was drowned out (Pearson's $X^2$ test with Yate's continuity correction applied, $X^2$= 2368.8, df= 1, $p$< 0.001) and after sunset (Pearson's $X^2$ test with Yate's continuity correction applied, $X^2$= 1568.2, df= 1, $p$< 0.001) than expected. A Poisson model containing the factors; the mean stage across attempts, the mean water temperature across attempts, the lamprey's weight, lamprey's length and if the lamprey was double tagged was initially created. The last factor was then dropped as it had an insignificant effect and was likely to have a negligible effect on swimming behaviour, unlike lamprey weight and length, which was kept. A negative binomial model was selected as the final model as it had a lower ΔAIC when compared to a Poisson model with the same factors. It was found that the number of attempts to traverse the bypass per lamprey increased with average temperature during attempts (Wald test, $z$= 2.41, $p$= 0.016) but decreased as lamprey weight (Wald test, $z$= -3.14, $p$= 0.002) and average river stage during attempts (Wald test, $z$= -8.79, $p$< 0.001) increased (Figures 2.12). Once the Holm–Bonferroni method was applied, all of these factors remained significant under the new significance levels of 0.025, 0.017 and 0.013 respectively.

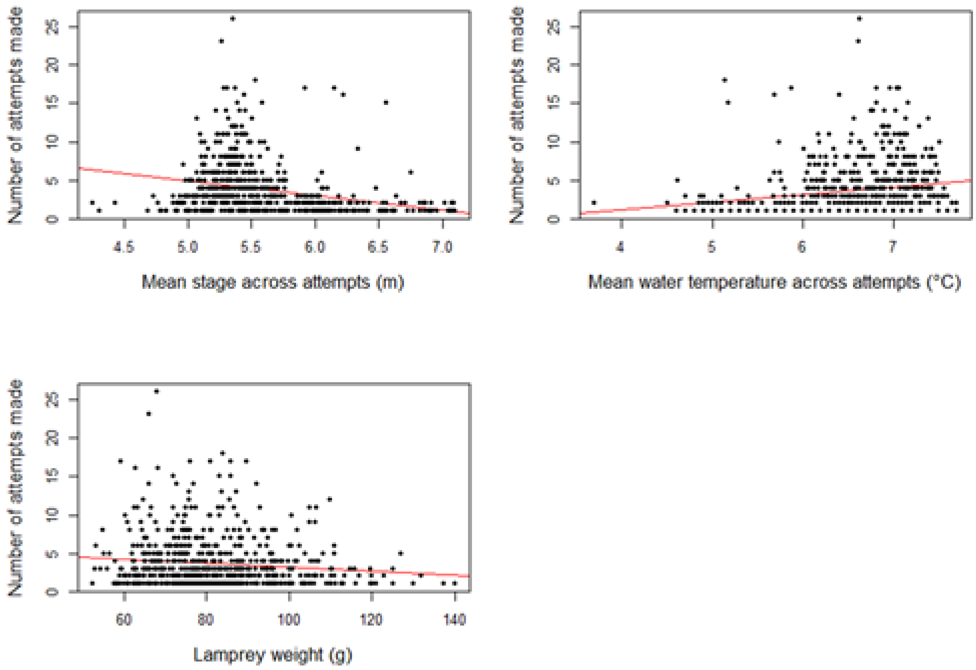



*Figure 2.12: The number of attempts made by each PIT tagged lamprey detected within the bypass between November 1st 2019 and Feburary 7th 2020 against the mean stage (mAOD) downstream of Naburn weir and mean water temperature (˚C) recorded across said lamprey's attempts as well as the lamprey's recorded weight upon tagging.*

A total of 11 PIT tagged lamprey were detected on BP4 during the period that BP4 was operational (December 10th 2019 to February 7th 2020). However, only seven of these lamprey were detected on a PIT antenna within the bypass prior to their detection on BP4 with the other four being detected on a PIT antenna downstream of BP4 shortly after detection on BP4. This indicates that only seven PIT tagged lamprey successfully traversed the bypass. With a total of 130 PIT tagged lamprey detected within the bypass (BP1 – BP3) from December 10th 2019 to February 7th 2020 an estimated minimum passage efficiency of 5.38 % can be calculated. A logistic regression containing the factors; if the weir was flooded on the last downstream detection, if the last downstream detection was between sunset and sunrise, the lamprey's weight and the lamprey's length was selected as the final model as it contained all the factors that may have affected lamprey swimming performance. No factors were found to significantly affect the chances of successfully traversing the bypass on an attempt (Wald tests, $p > 0.05$), but of all attempting individuals the sample size of successfully passing lamprey was very small. The time taken to successfully traverse the bypass ranged from 1.17 to 592.24 hours with an average of 201.46 ± 98.03 hours. Five of the successful attempts occurred when the weir was drowned out and all occurred between sunset and sunrise. Significantly more successes occurred after sunset than expected (Exact Binomial test, $n= 7$, $k= 7$, $p= 0.008$).

**2.4.4. 2018 study season acoustic telemetry**

Of the 61 acoustic + PIT tagged lamprey (average weight= 100.2 ± 1.8 g, average length= 394.0 ± 1.4 mm) released at Cawood, 71.1 % ($n= 43$ [average weight= 100.5 ± 2.5 g, average length= 395.7 ± 1.7 mm]) were detected on R9/10 and so approached Naburn weir. Tagged lamprey took an average of 31.8 ± 10.9 hours to be detected downstream post release, but this was highly variable, ranging between 5.2 to 322.5 hours with 74.4 % ($n= 32$) of lamprey detected within 24 hours from release. The number of double tagged lamprey detected on the acoustic receivers and within the bypass varied (Table 2.2). Detections generally occurred during periods of high stage and first upstream detections almost exclusively occurred when Naburn weir was drowned out (Figure 2.13).

*Table 2.2: The number of acoustic + PIT tagged lamprey detected on the acoustic receivers and within the semi-formalised nature-like bypass and that number as a percentage of acoustic + PIT tagged lamprey detected downstream during the 2018-2019 study season. Approximate location of acoustic receivers are given and can be seen in Figure 2.6.*

| Receiver and location | No of lamprey detected | No of lamprey detected as a % of those detected downstream ($n= 43$) |
|---|---|---|

| | | |
|---|---|---|
| R9 (Left bank, downstream) | 43 | 100.0 |
| R10 (Right bank, downstream) | 38 | 88.4 |
| PIT antennas in bypass | 17 | 39.5 |
| R11 (Right bank, just upstream of Naburn weir) | 26 | 60.5 |
| R12 (Left bank, within the navigation lock) | 6 | 14.0 |
| R13 (Right bank, upstream) | 24 | 55.8 |
| R14 (Left bank, upstream) | 24 | 39.5 |

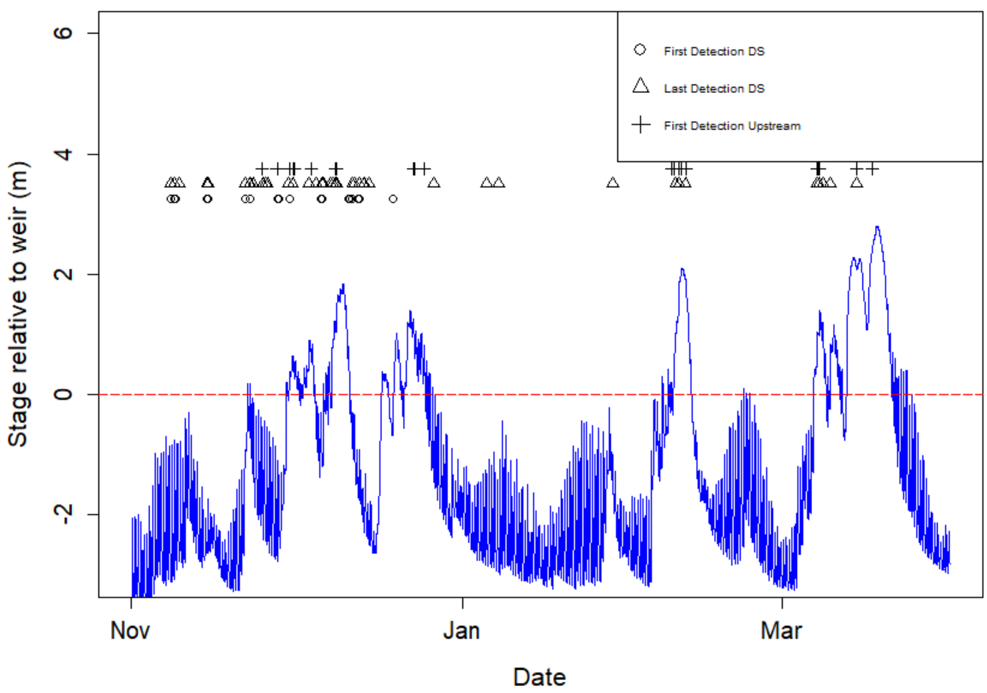



*Figure 2.13: The first and last downstream detections as well as the first upstream detection for each acoustically tagged lamprey detected from November 1st 2018 to March 31st 2019 compared to the downstream river stage relative to Naburn weir crest (m). The horizontal red line shows the stage at which Naburn weir is drowned out (4.91 mAOD).*

A total of 311 attempts to pass the weir were made by acoustic tagged lamprey downstream over the course of the 2018-2019 study period. The number of attempts per lamprey ranged from 1 to 77 with an average of 7.2 ± 2.0 attempts per lamprey. Twenty-seven percent of attempts ($n$= 86) occurred when the weir was drowned out and 77.5 % ($n$= 241) of attempts occurred after sunset. Significantly more attempts occurred when the weir was drowned out (Pearson's $X^2$ test with Yate's continuity correction applied, $X^2$= 42.5, df= 1, $p$< 0.001) and after sunset (Pearson's $X^2$ test with Yate's continuity correction applied, $X^2$= 94.0, df= 1, $p$< 0.001) than expected. A Poisson model containing the factors; the mean stage across attempts, the mean water temperature across attempts, the lamprey's weight, lamprey's length was created as the initial model as these were the factors deemed likely to affect lamprey swimming behaviour. A negative binomial model was selected as the final model as it had a lower ΔAIC when compared to a Poisson model with the same factors. It was found that the number of attempts to traverse the weir per lamprey decreased as the average temperature across attempts increased (Wald test, $z$= -3.10, $p$= 0.002) (Figure 2.14). Once the Holm–Bonferroni method was applied, this factor remained significant under the new significance level of 0.013.

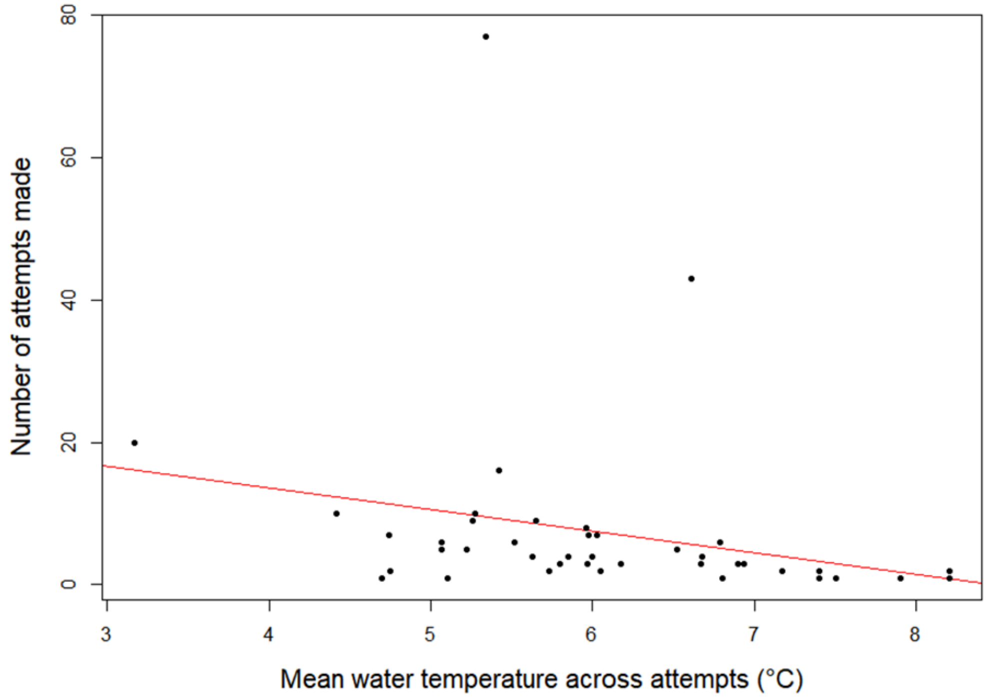


*Figure 2.14: The number of attempts by each acoustically tagged lamprey detected downstream of Naburn weir between November 1st 2018 and March 31st 2019 against the mean water temperature recorded across said lamprey's attempts.*

Twenty-five acoustically tagged lamprey (58.1 % of the lamprey who were detected downstream) were recorded as successfully passing the weir (detected on R13/14) during the 2018-2019 study period. Ten of the successful attempts started when the weir was drowned out, 21 of the successful attempts started after sunset. Significantly more successful attempts than expected started when the weir was drowned out (Exact Binomial test, $n$= 25, $k$= 10, $p$= 0.002) or after sunset (Exact Binomial test, $n$= 25, $k$= 21, $p$< 0.001). A logistic regression containing the factors; downstream stage of last recorded downstream detection, downstream temperature of last recorded downstream detection, lamprey's length, lamprey's weight, if the last recorded downstream detection occurred between sunrise and sunset and if the last recorded downstream detection occurred when the weir was drowned out to investigate what factors affected the chance of a lamprey successfully traversing the weir as these factors were deemed likely to affect lamprey swimming performance. Of these factors, if the last recorded downstream detection occurred between sunrise and sunset and if the last recorded downstream detection occurred when the weir was drowned out were removed from the final model as they both had an insignificant effect and the model was improved by their removal (ΔAIC was reduced).

It was found that although the chance of a lamprey successfully traversing the weir increased with the downstream stage recorded at the last recorded downstream detection of that lamprey, it was an insignificant effect (Wald test, $z = 1.72$, $p > 0.05$) (Figure 2.15). By checking that detections within the navigation lock (R12) were not preceded by a detection within the river channel upstream of the weir (on R11) and that these detections did not occur in periods of low stage (which would be indicative of calm water conditions, increasing detection range), the results indicate that one lamprey may have utilised the navigation lock to travel upstream whilst the remaining 24 successful attempts most likely crossed the weir directly.

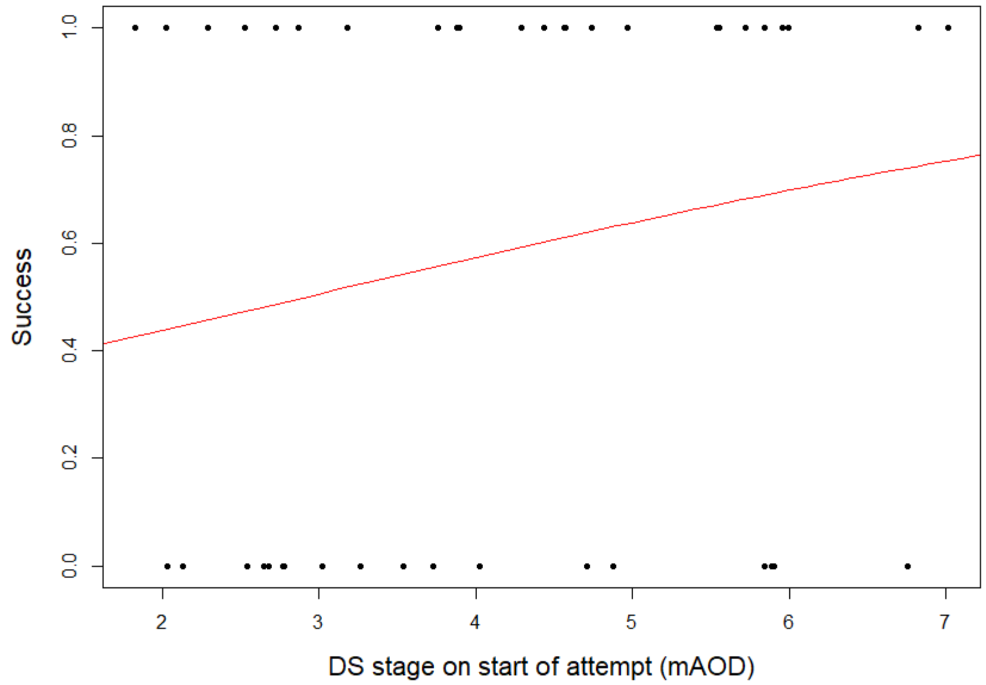



*Figure 2.15: The probability of success or failure of acoustically tagged lamprey that approached Naburn weir to travel upstream between November 1st 2018 and March 31st 2019 against the downstream stage (mAOD) recorded at the start of their last recorded attempt (last downstream detection).*

Passage time past the weir varied from 1.10 to 2535.34 hours with an average of 638.49 ± 167.38 hours. A linear regression containing the factors; lamprey length, lamprey weight, stage recorded at last downstream detection, temperature recorded at last downstream detection, if the last recorded downstream detection occurred when the weir was drowned out and if the last recorded downstream detection occurred between sunset and sunrise was initially created. Of these factors, temperature recorded at last downstream detection, if the last recorded downstream detection occurred when the weir was drowned out and if the last recorded downstream detection occurred between sunset and sunrise were found to have an insignificant effect and so were dropped from the final model. Although it was initially found that passage time reduced as downstream stage increased (Linear Regression, $F_{1,21}$= 4.79, $p$= 0.040, $R^2$= 0.256) (Figure 2.16), once the Holm–Bonferroni method was applied, this downstream stage was found to have an insignificant effect under the new significance level of 0.017.

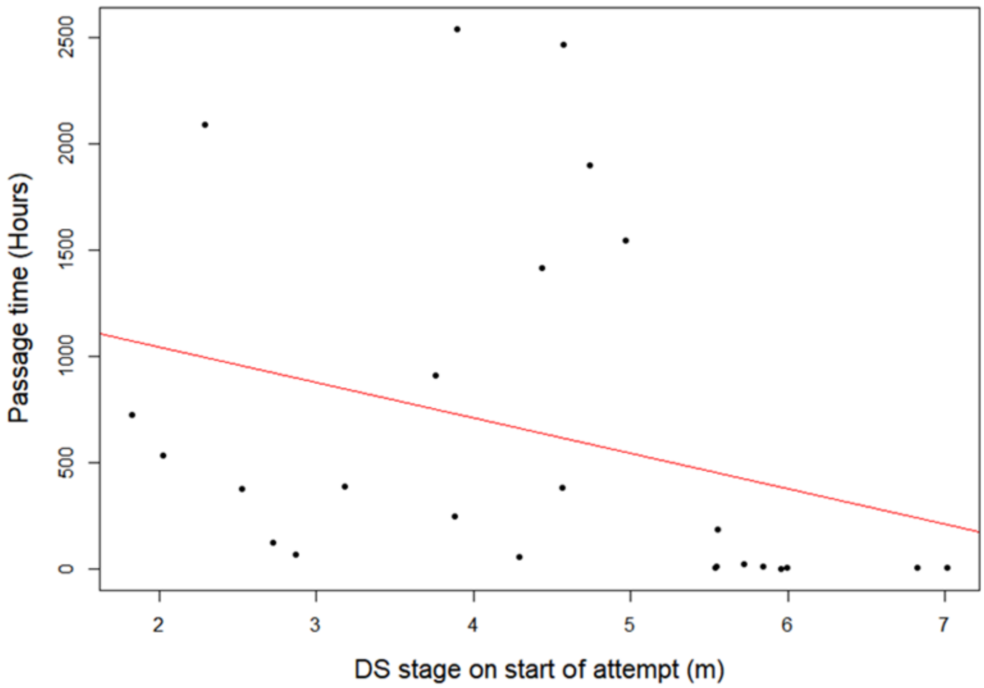



*Figure 2.16: The passage time of successful attempts made by acoustically tagged lamprey recorded upstream of Naburn weir between November 1st 2018 and March 31st 2019 compared against the downstream stage recorded at the start of the attempt (last downstream detection prior to first upstream detection).*

## 2.4.5. 2019 study season acoustic telemetry

Of the 59 acoustic + PIT tagged lamprey (average weight= 105.6 ± 1.5 g, average length= 396.9 ± 1.7 mm) released at Cawood, 81.4 % (*n*= 48 [average weight= 106.2 ± 1.6 g, average length= 396.7 ± 2.0 mm]) were detected down stream of Naburn weir (R9/10) and so were determined to have approached the weir. Tagged lamprey took an average of 107.9 ± 23.5 hours to be detected downstream post release, but this was highly variable, ranging between 8.2 to 873.1 hours with 39.6 % (*n*= 19) of lamprey detected within 24 hours from release. The number of double tagged lamprey detected on the acoustic receivers and within the bypass varied (Table 2.3). Detections generally occurred during periods of high stage and first upstream detections almost exclusively occurred when Naburn weir was drowned out (Figure 2.17).

*Table 2.3: The number of acoustic + PIT tagged lamprey detected on the acoustic receivers and within the semi-formalised nature-like bypass and that number as a percentage of acoustic + PIT tagged lamprey detected downstream during the 2019-2020 study season. Approximate location of acoustic receivers are given and can be seen in Figure 2.6.*

| Receiver and location | No of lamprey detected | No of lamprey detected as a % of those detected downstream (*n*= 48) |
|---|---|---|
| R9 (Left bank, downstream) | 48 | 100 |
| R10 (Right bank, downstream) | 48 | 100 |
| PIT antennas in bypass | 34 | 70.8 |
| R11 (Right bank, just upstream of Naburn weir) | 39 | 81.3 |
| R12 (Left bank, within the navigation lock) | 12 | 25.0 |
| R13 (Right bank, upstream) | 39 | 81.3 |
| R14 (Left bank, upstream) | 19 | 39.6 |
| | | |

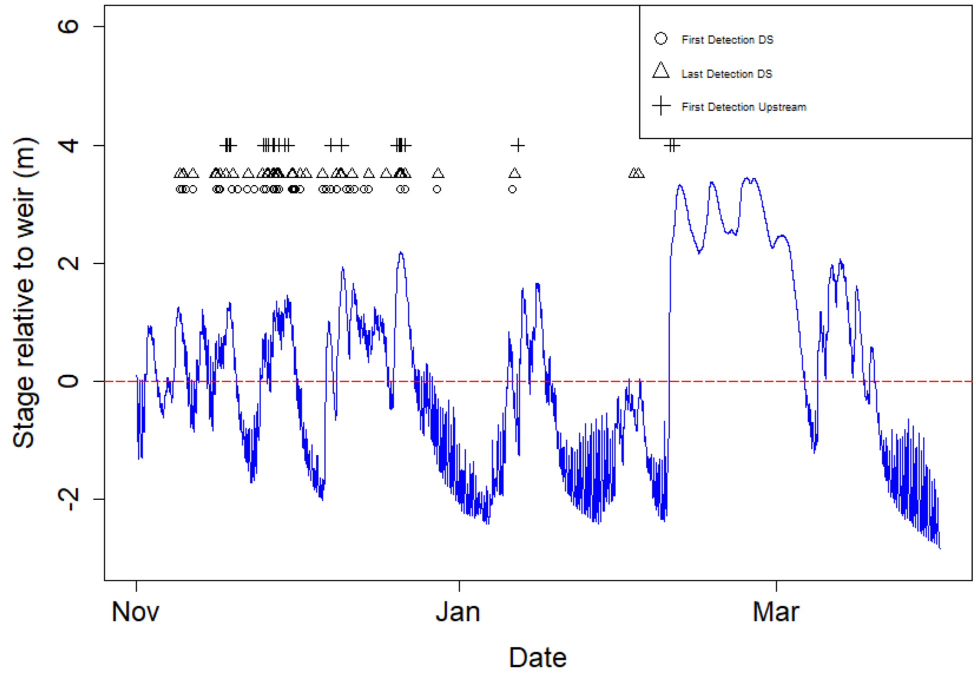



*Figure 2.17: The first and last downstream detections as well as the first upstream detection for each acoustically tagged lamprey detected from November 1st 2019 to March 31st 2020 compared to the downstream river stage relative to Naburn weir crest (m). The horizontal red line shows the stage at which Naburn weir is drowned out (4.91 mAOD).*

A total of 214 attempts to pass the weir were made by downstream lamprey over the course of the 2019-2020 study period. The number of attempts per lamprey ranged from 1 to 20 with an average of 4.5 ± 0.7 attempts per lamprey. Seventy-one percent of attempts (*n*= 152) occurred when the weir was drowned out and 73.8 % (*n*= 158) of attempts occurred after sunset. Significantly more attempts occurred when the weir was drowned out (Pearson's $X^2$ test with Yate's continuity correction applied, $X^2$= 35.4, df= 1, p< 0.01) and after sunset (Pearson's $X^2$ test with Yate's continuity correction applied, $X^2$= 48.6, df= 1, p< 0.001) than expected. A Poisson model containing the factors; the mean stage across attempts, the mean water temperature across attempts, the lamprey's weight, lamprey's length was created as the initial model as these were the factors deemed likely to affect lamprey swimming behaviour. A negative binomial model was selected as the final model as it had a lower ΔAIC when compared to a Poisson model with the same factors. It was initially found that the number of attempts to traverse the weir per lamprey increased as the average temperature across attempts increased (Wald test, $z$= 2.07, $p$= 0.038) (Figure 2.18). However, once the Holm–Bonferroni method was applied, this average temperature across attempts was found to have an insignificant effect under the new significance level of 0.013.

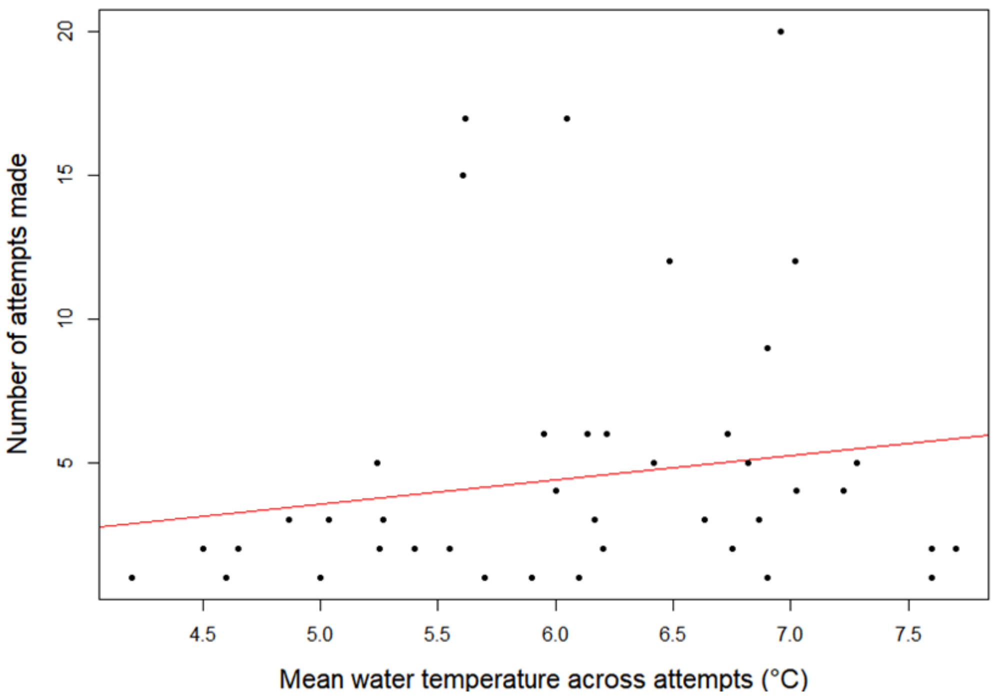



*Figure 2.18: The number of attempts by each acoustically tagged lamprey detected downstream of Naburn weir between November 1st 2019 and March 31st 2020 against the mean water temperature recorded across said lamprey's attempts.*

Forty-two acoustically tagged lamprey (87.5 % of the lamprey who were detected downstream) were recorded as successfully passing the weir (detected on R13/14) during the 2019-2020 study period. A logistic regression containing the factors; downstream stage of last recorded downstream detection, downstream temperature of last recorded downstream detection, lamprey's length, lamprey's weight, if the last recorded downstream detection occurred between sunrise and sunset and if the last recorded downstream detection occurred when the weir was drowned out to investigate what factors affected the chance of a lamprey successfully traversing the weir as these factors were deemed likely to affect lamprey swimming performance. Of these factors, if the last recorded downstream detection occurred between sunrise and sunset and if the last recorded downstream detection occurred when the weir was drowned out were removed from the final model as they both had an insignificant effect and the model was improved by their removal (ΔAIC was reduced).

It was initially found that the chance of a lamprey successfully traversing the weir increased as downstream stage recorded on the last downstream detection increased (Wald test, $z = 2.03$, $p = 0.042$) (Figure 2.19). However, once the Holm–Bonferroni method was applied, the downstream stage was found to have an insignificant effect under the new significance level of 0.013. Thirty-five of the successful attempts started when the weir was drowned out and 36 successful attempts started after sunset. Significantly more successful attempts than expected started when the weir was drowned out (Pearson's $X^2$ test with Yate's continuity correction applied, $X^2 = 17.9$, df= 1, $p < 0.001$) or after sunset (Pearson's $X^2$ test with Yate's continuity correction applied, $X^2 = 21.4$, df= 1, $p < 0.001$). By checking that detections within the navigation lock (R12) were not preceeded by a detection within the river channel (on R11) and that these detections did not occur in periods of low stage (which would be indicative of calm water conditions, increasing detection range), the results indicate that whilst 38 lamprey likely crossed naburn weir directly, three lamprey may have utilised the navigation lock to travel upstream and a single lamprey may have used the bypass to travel upstream.

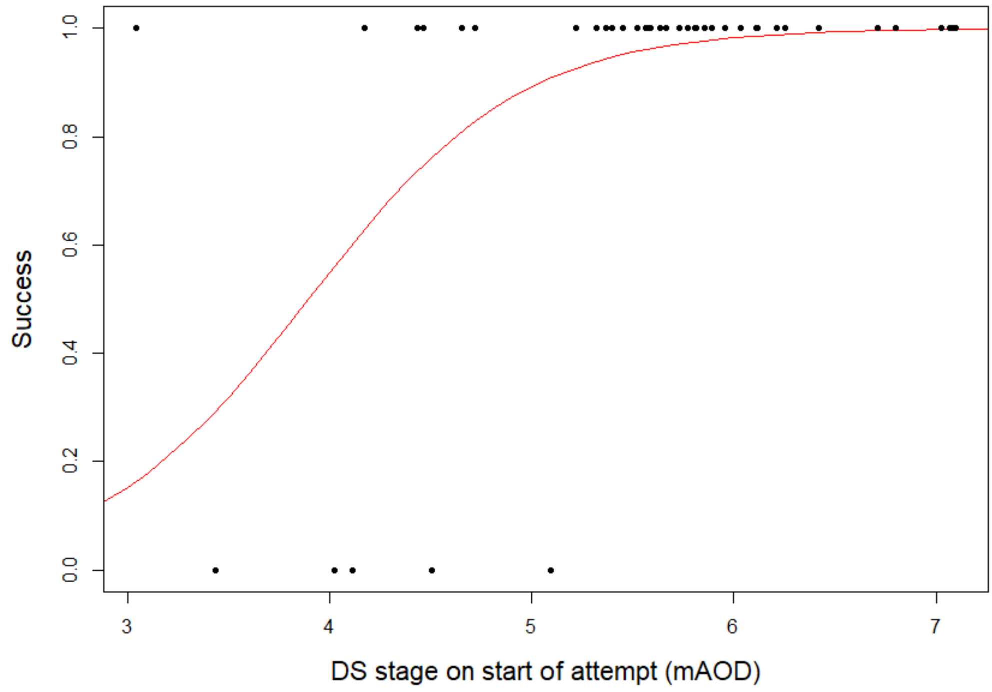



*Figure 2.19: The probability of success or failure of acoustically tagged lamprey that approached Naburn weir to travel upstream between November 1st 2019 and March 31st 2020 against the downstream stage (mAOD) recorded at the start of their last recorded attempt (last downstream detection).*

Passage time over the weir varied between 0.28 and 1385.32 hours with an average of 154.79 ± 37.75 hours. A linear regression containing the factors; lamprey length, lamprey weight, stage recorded at last downstream detection, temperature recorded at last downstream detection, if the last recorded downstream detection occurred when the weir was drowned out and if the last recorded downstream detection occurred between sunset and sunrise was initially created. Of these factors, if the last recorded downstream detection occurred when the weir was drowned out and if the last recorded downstream detection occurred between sunset and sunrise were found to have an insignificant effect and so were removed from the final model. It was initially found that passage time decreased as downstream stage increased (Linear Regression, $F_{1,37}$= 8.00, $p$= 0.007, $R^2$= 0.333) and as water temperature increased (Linear

Regression, $F_{1,37}$= 4.33, $p$= 0.044, $R^2$= 0.333) (Figure 2.20). However, once the Holm–Bonferroni method was applied, downstream stage was found to still have a significant effect whilst water temperature was found to have an insignificant effect under the new significance levels of 0.013 and 0.017 respectively.

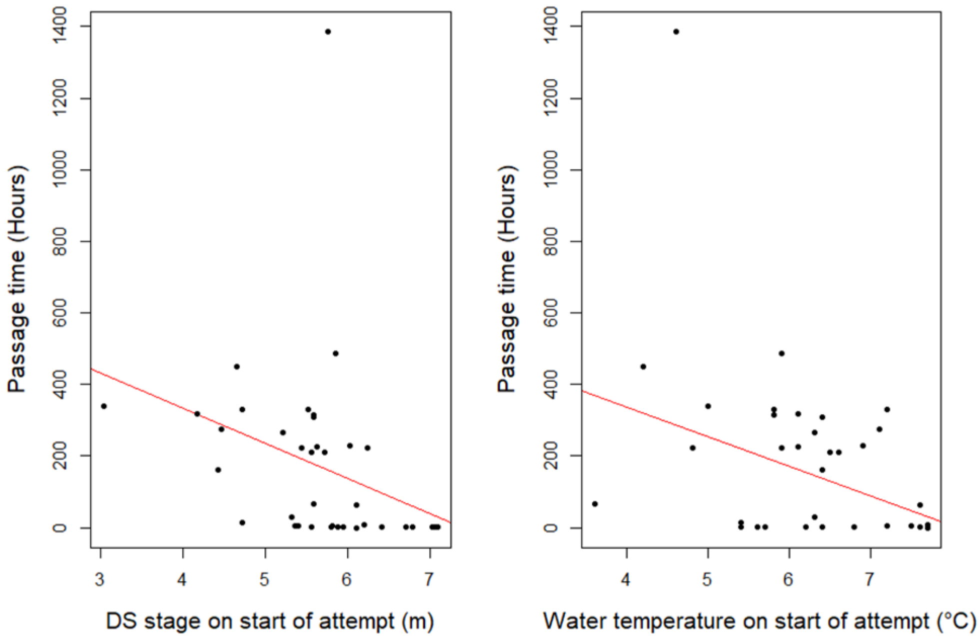



*Figure 2.20: The passage time of successful attempts made by each acoustically tagged lamprey detected upstream of Naburn weir between November 1st 2019 and March 31st 2020 compared against the downstream stage and water temperature recorded at the start of the attempt (last downstream detection prior to upstream detection).*

## 2.5. Discussion

### 2.5.1. Effectiveness of Naburn bypass

This study shows that the semi-formalised nature-like bypass present at Naburn weir is currently unsuitable for providing upstream passage to *Lampetra fluviatilis* undergoing their spawning migration. The bypass in question has been shown to possess a minimum attraction efficiency (MAE) that varied between study period and telemetric method ($MAE_{2018PIT}$= 28.6 %, $MAE_{2019PIT}$= 50.6 %, $MAE_{2018AC}$= 39.5 %, $MAE_{2019AC}$=70.8 %) The bypass's MAE appears higher for acoustically tagged lamprey than PIT tagged lamprey across both years. However, this is due to a difference in the methodologies for calculating attraction efficiency between the two groups. For acoustically tagged lamprey, the bypass's attraction efficiency was calculated using the number of lamprey detected approaching Naburn weir from downstream whilst for PIT telemetry the attraction efficiency was calculated using the number of lamprey released at Cawood. The latter method could not account for factors such as the predation of PIT tagged lamprey or the selection of an alternate river within the Humber River Basin. Consequentially, the MAE estimates for PIT tagged lamprey are probably substantial underestimates. Evidence for this is provided by recalculating minimum attraction efficiency for the acoustically tagged lamprey as the number of lamprey detected within the bypass as a percentage of the number of lamprey released at Cawood, rather than the number of lamprey detected approaching Naburn weir. Under these conditions, the attraction efficiencies of the acoustic tagged lamprey are substantially reduced ($MAE2_{2018AC}$= 27.9 %, $MAE2_{2019AC}$= 57.6 %) and are comparable with the PIT tagged lamprey ($MAE_{2018PIT}$= 28.6 %, $MAE_{2019PIT}$= 50.6 %).

The difference in attraction efficiency estimates between study years is likely the result of the increased river flow during the 2019-2020 study season. *Lampetra fluviatilis* is rheophilic when undergoing its spawning migration (Moser *et al*., 2015). Additionally, during periods of high flow, attraction of many fish species to fishways may increase

(Aarestrup *et al*., 2003; Bunt *et al*., 1999; Foulds & Lucas, 2013), though the relative amounts of flow across different routes can have an effect (Tummers *et al*., 2018). The flow velocity measurements in the bypass indicate that as the river stage increased, the discharge and velocity throughout the bypass increased, subsequently increasing the attractiveness of the bypass to lamprey. This is supported by Figures 2.9 and 2.11 which show that the number of PIT tagged lamprey detected within the bypass roughly correlate with the downstream stage recorded at Naburn. This may explain the significantly higher than expected proportion of attempts to traverse both the bypass and the weir occurring when the weir is drowned out. However, this corelation may not be directly due to attraction from the bypass. If bulk flow at Naburn weir exceeds that of the bypass, lamprey will be drawn to the weir. If lamprey cannot then pass the weir directly, random search patterns could lead lamprey into the bypass. This would increase apparent attraction into the bypass during periods of high stage, independent of the effect of any attraction flows generated by the bypass.

Lamprey are generally negatively phototaxic during spawning migrations (section 1.2.) and *L. fluviatilis* has been shown to be more active in the evening/at night during winter (Foulds & Lucas, 2013; Tummers *et al*., 2016a). This is reflected in the study's results as significantly more attempts to traverse both the bypass and the weir occurred than expected at night.

Unusually, the results suggest the number of attempts to traverse the bypass made by lamprey decreases as stage and flow within the bypass increases. This may be due to increased lamprey activity within the bypass rather than reduced activity. During the 2018-2019 study period, lamprey were observed in the most upstream bypass bend (near BP3) during periods of high stage (A. Lothian, pers comm). Rheophilic lamprey may be increasing their activity within the bypass as stage increases, increasing detection rate. This would extend attempt duration and create an apparent decrease in the number of attempts.

Despite the high attraction efficiency of the bypass, it is still insufficient. Lucas & Baras (2001) estimate that an attraction and passage efficiency of over 90 % is required for diadromous species such as *L. fluviatilis* (Lucas & Baras, 2001). This is even more crucial if suitable spawning habitat is absent below the obstacle in question (Lucas *et al*., 2009) as is the case at Naburn weir. However, the attraction efficiency is only a measure of how easily lamprey could locate the bypass at Naburn and the insufficient attraction efficiency found in this study is irrelevant in the face of the miniscule passage efficiency (a measure of how easily lamprey can successfully traverse the bypass) found in this study. After taking into account the initial malfunction of BP4 (by recalculating passage efficiency whilst only including the lamprey detected within the bypass during BP4's operational period, from December 10$^{th}$ 2019 to February 2$^{nd}$ 2020) and that some lamprey appear to have travelled downstream immediately after detection on BP4, this study calculates a minimum passage efficiency of 5.38 % for the 2019-2020 study period. This is woefully inadequate to provide sufficient passage to lamprey. Moreover, multiple lamprey were detected first on BP4 and subsequently on a downstream antenna within a short period. This implies movement from the river upstream of Naburn weir through the sluice-gate and downstream, into the bypass. This presents the possibility that the bypass forms an additional obstacle to lamprey passage due to the risk of lamprey that have cleared Naburn weir approaching the sluice-gate and being entrained back downstream. Lamprey may exit the bypass in an upstream direction by alternate routes, such as directly over the channel walls when they are overtopped. However, passage through the intended sluice-gate exit was extremely infrequent.

Multiple theoretical explanations for this low passage efficiency exist. Firstly, the bypass channel and sluice gate cross section experience high water velocities of over 2 $ms^{-1}$ at high river stage (Figure 2.8). *Lampetra fluviatilis* has a maximum burst speed of 2.12 $ms^{-1}$ (Russon & Kemp, 2011) but it is important to note that this was documented in 12.6

˚C water. During the PIT telemetry study period, the water temperature ranged between 3.3 ˚C and 7.7 ˚C. As lamprey swimming performance and activity is temperature dependent (Binder *et al*., 2008; Kemp *et al*., 2010), *L. fluviatilis* may have been unable to progress against the water velocities *in-situ* due to the low water temperatures. Furthermore, lamprey attempting to pass a single vertical slot at a navigation lock, were shown to display increased passage duration at velocities > 0.7 $ms^{-1}$ through the slot when exposed to temperatures similar to those recorded in this study (Silva *et al*., 2017). This indicates that the typical velocity constraint to passage *in-situ* may be much lower than Russon & Kemp's (2011) peak measurement in laboratory conditions. The structure of the sluice-gate exit itself may also be an impediment to lamprey passage. *Lampetra fluviatilis* is known to prefer swimming in close proximity to the side walls of weirs and other obstacles when travelling upstream (Russon *et al*., 2011; Tummers *et al*., 2018). This pattern of behaviour was observed within the bypass channel (A. Albright, Personal observation). However, the upstream sluice-gate presented no exit at the sides of the channel, only via swimming directly through the opening or in close proximity to a densely bristled ramp situated within the middle of the sluice-gate's bottom edge. This ramp was designed to allow upstream passage of elvers, not lamprey (see section 2.3.2.). *Lampetra fluviatilis* is known to have difficulty in crossing less densely bristled passes (Kerr *et al*., 2015). It could be that the densely bristled elver ramp prevents lamprey from exiting the bypass by preventing attachment to the exit ramp. This forces lamprey to burst swim across the entire ramp in high velocity conditions, leading to fatigue and failure to exit.

### 2.5.2. Lamprey passage over Naburn weir

It is clear that *L. fluviatilis* is not utilising the sluice-gate exit of the bypass present at Naburn weir to travel upstream in any great capacity. Multiple lamprey ($n$= 18, $n_{2018}$=6, $n_{2019}$= 12) were detected on the acoustic receiver situated within the navigation lock present on site. However, careful examination of the order of detection and time intervals of detection on the first receiver upstream of the weir (R11) and in the navigation lock (R12) suggests that very few (*n*= 4, $n_{2018}$=1, $n_{2019}$= 3) appeared to use the navigation lock to travel upstream. Thus, indicating that most lamprey were detected within the lock during exploratory behaviour after traversing the weir. A previous study has shown that navigation locks operated as a vertical slot fishway can produce very low attraction efficiency but high passage efficiency for *L. fluviatilis* (Silva *et al*., 2017). However, Naburn's navigation lock is usually closed except to allow boat traffic through (a rare event in autumn/winter) and is not used as a fishway. Hence, upstream passage through the navigation lock seems unlikely unless the lock gates were wedged open unintentionally, were opened more frequently than planned operating regimes or were in such poor condition that lamprey can fit through the resulting gaps.

The majority of tagged lamprey reached Naburn weir quickly (likely due to the high attraction flow created by the weir) but were delayed for a highly variable amount of time before successful passage. The majority of successful passage attempts occurred during periods of high river stage, when the weir was drowned out. This suggests that although migrating lamprey quickly reach the downstream face of Naburn weir, upon arrival, lamprey remain there until the river stage is high enough to provide suitable depth, velocity and turbulence for passage over, or around, the weir. This is supported by the finding that passage time generally decreases as stage increases (which would tend to correlate with high water temperatures as high flows tend to occur during mild frontal weather conditions), indicative of more favourable conditions for lamprey passage. Additionally, *L. fluviatilis* increased passage efficiency and reduced delay times over an experimental weir when under flooded conditions (Kerr *et al*., 2015). These delays could prove detrimental to the Humber River Basin's population of *L. fluviatilis* as pre-adult *L. fluviatilis* do not feed during the spawning migration and therefore have a fixed energy budget (see section 1.2.). Therefore, any delays in reaching spawning grounds, in addition to increasing the risk of missing the spawning period altogether, will result in additional energy expenditure, reducing the potential fecundity of the individual lamprey (Docker *et al*., 2019). Moreover, delay below Naburn weir may increase predation rates as weir pools can provide suitable conditions for a variety of predators (Baumgartner, 2007; Garcia de Leaniz, 2008). *Mergus merganser* and *Larus* spp were recorded gathering in Naburn weir pool during the study period (A. Albright, Personal observation).

The dependence on high river stage for passage over Naburn weir explains why the 2018-2019 study period (which experienced fewer periods of high river stage) had considerably lower passage efficiency for acoustically tagged lamprey than the 2019-2020 study period. This is concerning as Naburn weir is the first anthropogenic barrier that migrating lamprey will encounter on the main Ouse (see section 2.2.). This means that most lamprey cross additional barriers in order to find suitable spawning habitat. The impact of successive barriers has been shown to dramatically restrict the in-river distribution of *L. fluviatilis* spawners (Lucas *et al*., 2009). This study suggests that, during low river stage years, the impacts of barriers on spawning migrations could be dramatically increased, with potentially severe impacts on population recruitment. Evidence for crashes in population recruitment within the Humber River Basin can be found in Nunn *et al*. (2008) where the absence of the 2003-year class of larval lamprey from the River Ure was attributed to low river levels during the associated spawning migration period. Considering the increased variability in UK winter river flow predicted under climate change models (Arnell, 2003), a series of low river stage years could result in a crash in the *L. fluviatilis* population within the Ouse. As the Ouse catchment, upstream of Naburn, supports the majority of the Humber River Basin's population of *L. fluviatilis* (Jang & Lucas, 2005; Bracken *et al*., 2015) this could have serious ramifications for the Humber River Basin river lamprey population. However, the exact effects of low river levels on population recruitment within the Ouse catchment are unclear. Surveys comparing the abundance of different year classes of larval lamprey against the respective river levels are recommended to determine if a link between low river levels and low larval abundance exists within the Ouse catchment.

### 2.5.3. Potential improvements to passage

Improved passage efficiency across Naburn weir and elsewhere within the Humber River Basin is vitally important in light of the resurgence of the commercial lamprey fishery (see section 1.6.3.3.) to increase the long-term viability of the present lamprey population. Although this study has shown the bypass at Naburn weir is currently unsuitable for lamprey passage it is important to remember that it is not a true nature-like bypass. Rather, it is a semi-formalised nature-like bypass (see section 2.3.2.) and so the results from this study are not indicative of *L. fluviatilis* passage performance across true nature-like bypasses, a form of fishway that is often effective for weaker swimming species (Santos *et al*., 2005; Aronsuu *et al*., 2015; Kim *et al*., 2016). Consequently, subsequent research towards the suitability of true nature-like bypasses for upstream lamprey passage is recommended. It is important to note that the bypass at Naburn weir had to conform to requirements such as a tight land footprint and minimising erosion risk as well as a restricted budget implemented by the Environment Agency. Therefore, a true nature-like bypass could not have been realistically provided under the aforementioned restrictions. To convert the current bypass at Naburn into a true nature-like bypass, it would need to be completely re-modelled with changes such as increased total length, reduced gradient and the removal of sharp bends.

As the bypass present at Naburn is insufficient, methods to optimise lamprey passage directly over Naburn weir or through the navigation lock warrant investigation. Low-cost retrofit solutions to lamprey passage over anthropogenic obstacles have recently risen in popularity. However, techniques such as vertically or horizontally mounted studded tiles result in minimal to mediocre improvements in *L. fluviatilis* passage (Tummers *et al*., 2016a; Vowles *et al*., 2017; Lothian *et al*., 2020) and so will require additional supplementary methods. As previously mentioned, navigation locks used as vertical slot fishways have been shown to be very effective for lamprey passage but suffer from poor attraction (Silva *et al*., 2017). Therefore, methods to increase attraction into the navigation lock during open periods could increase success.

Multiple lamprey attractant/repellent technologies have been discovered and could increase lamprey passage at Naburn. Some, such as electric currents (Johnson *et al*., 2014), guiding lights (Söberg, 2011), and bubble screens (Miehls *et al*., 2017) are likely to be either too expensive, too dangerous or simply ineffective within a frequently navigated, turbid waterway such as Naburn weir. However, the use of pheromones could prove fruitful. Sea lamprey produce several pheromones (Li *et al*., 2003; Fine & Sorensen, 2010; Yun, 2012). Of these, sex pheromones (produced by males when spawning) and alarm pheromones, are commonly used in efforts to control *P. marinus* populations in the North American Great Lakes. The application of sex pheromones as a lure has increased the trapping efficacy of *P. marinus*, an effect that is further improved if chemical alarm cues are present downstream of the trap to push lamprey towards it (Wagner *et al*., 2006; Johnson *et al*., 2009; Hume *et al*., 2015; Dawson *et al*., 2016; Hume *et al*., 2020).

These pheromones can be synthesised in laboratory conditions but are not as effective as natural pheromones (Sorensen *et al*., 2005; Luehring *et al*., 2011). Additionally, the current costs of producing these pheromones naturally or synthetically are exorbitant (Sorensen & Hoye, 2007; Burns *et al*., 2011). Nonetheless, pheromones could be applied to guide lamprey to suitable upstream migration routes such as through the navigation lock at Naburn weir. As the response to lamprey pheromones diminishes with phylogenetic distance (Hume & Wagner, 2018), compounds available for *P. marinus* will likely be ineffective for attracting *L. fluviatilis*. *Petromyzon marinus* produces bile acids such as 3-keto petromyzonol sulfate (3kPZS) which serves as its male mating (female attractant) pheromone whilst *L. fluviatilis* produces the bile acid petromyzonol sulfate (PZS) (Yun, 2012). It is unknown if this compound serves a similar role to 3kPZS (Yun, 2012). Therefore, research into the role of PZS and the presence of chemical alarm cues produced by *L. fluviatilis* is advised as well as methods to synthesize these chemicals (or chemical analogues) in a cost-effective manner for application in the field.

However, a more immediate solution may also be required. The commercial lamprey fishery present within the Humber River Basin could be utilised to enhance upstream lamprey passage across the Ouse catchment by operating a Trap and Transport operation. Fishers could be incentivized to transport a subset of trapped lamprey above anthropogenic barriers present within the Humber River Basin and into regions of suitable spawning habitat. Some sites have already been identified by Nunn *et al*. (2008) and Jang and Lucas (2005) but a comprehensive survey across the entire Humber River Basin is required. Transportation of lamprey above anthropogenic barriers has been tried before to variable success (Ward *et al*., 2012; Clemens *et al*., 2017; Aronsuu *et al*., 2019). Jang and Lucas (2005) indicate that the vast majority of potential spawning sites within the Derwent sub-catchment are under-utilised by spawning lamprey. This is also the case in much of the Nidd and Ure (M. Lucas, pers comm). Direct transportation could more evenly spread spawning events across available sites, thus reducing vulnerability to stochastic events or anthropogenic disturbance. Of course, this process would rely on the commercial lamprey fishery voluntarily releasing a portion of their trapped lamprey. Careful management would be necessary with incentives such as increased quotas potentially offered as rewards for quantified increases in Humber River Basin lamprey populations.

Consideration regarding Trap and Transport must be given to the distribution of distinct *L. planeri* populations within the tributaries of the Yorkshire Ouse tributaries that have been generated partly as a result of multiple barriers partially segregating populations (Bracken et al., 2015). It is known that *L. planeri* and *L. fluviatilis* can hybridize (Hume et al., 2013;

Bracken et al., 2015). Consequently, largescale transport of *L. fluviatilis* to the middle Nidd, middle Ure and upper Derwent, for example, would risk introgression with known genetically discrete, locally evolved *L. planeri* populations. By contrast, Trap and Transport beyond the first two Ouse barriers (Naburn and Linton weirs) would be entirely reasonable and is being tested as part of the current MMO-funded project.

A point that must be considered is the future of Naburn weir. A small-scale hydropower scheme has recently been approved on site (H20 Power Limited, https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/789024/Decision_Statement.pdf). The proposed turbines comprise of two Archimedes screw turbines, a design that downstream migrating juvenile lamprey have been shown to be minimally affected by (Bracken & Lucas, 2013). The planned trash screen however, is worrying. If the screen spacings are between 3-10 mm it could impinge a considerable proportion of downstream migrating metamorphosing lamprey (Moser *et al*., 2015). Any trash screens should be designed to reduce the risk of impingement, injury and mortality to metamorphosing lamprey. This could be done by using vertical or interlocking bar screens (Rose & Mesa, 2012). Most Archimedes screw turbines have widely spaced bar screens (5-10 cm) so impingement may not be an issue with this station. An important caveat to the hydropower station proposal is the requirement to install an additional multispecies fish pass for salmon, lamprey and eel (H20 Power Limited, https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/789024/Decision_Statement.pdf). This presents an opportunity to establish an effective bypass for *L. fluviatilis* at Naburn weir at no cost to governing bodies. Consultation with scientific bodies is of utmost importance when designing said bypass in order to maximise attraction and passage efficacy for lamprey and other non-salmonid passage at Naburn weir.

# CHAPTER 3: An investigation into the use of European river lamprey as bait by the UK coarse predator angling community

The rationale and design of this study were conceived by A. Albright and M. Lucas; data collection, analysis, interpretation and writing were carried out by AA with comments by ML.

## 3.1. Abstract

Recreational fishing (otherwise known as angling) is a commonplace leisure activity within the developed world. Anglers are often supportive of conservation efforts, providing funding, voluntary actions and even small-scale protected areas. However, the catch-orientated attitude of many anglers can push managers into supporting deleterious practices whilst the use of natural baits can form vectors for the transmission of diseases and spread of non-native species. This often turns recreational fisheries into hotspots of both inter and intrasectional conflict. It is thus important to understand stakeholder opinions surrounding potential issues within angling. One such issue is the use of *Lampetra fluviatilis*, a protected species, as angling bait. Previous studies have revealed the scale of *L. fluviatilis* exploitation and the structure of the lamprey bait market within the UK but overlooked the attitudes of the consumers, an important stakeholder group. Consequently, this chapter aimed to assess the proportion of UK coarse (non-salmonid) predator anglers using lamprey as bait as well as gauge their knowledge and opinions regarding this practice via telephone questionnaires.

It was found that 67.8 % of participants used lamprey as bait to some degree and 39.1 % of participants would prefer lamprey to be sourced from the UK. Participants generally agreed that lamprey should be conserved and that, if threatened by exploitation, a ban on their use as angling bait should be implemented. However, ordinal regression analysis indicated the existence of a subset of anglers who value lamprey as bait

more than others and so may oppose conservation efforts. It appears that the preference for UK sourced lamprey could allow the UK commercial lamprey fishery to persist. The benefits of the potential establishment of bait certification schemes and farming of lamprey larvae for bait supplements are also considered.

## 3.2. Introduction

Recreational fishing is defined as activities that capture and potentially harvest aquatic animals for reasons other than to meet primary physiological needs (Arlinghaus & Cooke, 2009). Recreational fishing is widespread, with an estimated 10 % of the global population partaking in the activity but is concentrated in more developed regions (Arlinghaus & Cooke, 2009). Although a diverse assortment of gear is used in recreational fishing this chapter is concerned with recreational fishing using rod and line (otherwise known as angling) which is the most common form of recreational fishing (Arlinghaus *et al*., 2002).

Anglers are an example of cognitive dissonance (whereby an individual hold two conflicting beliefs, values or attitudes (Thøgersen, 2004)) regarding conservation as although anglers generally appreciate the value of the natural environment (Holland & Ditton, 1992; Williams & Moss, 2001), they can also inflict damage to it. One example is the introduction of non-native species for sport, with Gozlan (2008) estimating that 12 % of all freshwater fish introductions were due to angling. These introductions are not restricted to fish. Angling has been identified as a vector for the spread of invasive invertebrates and novel pathogens (Keller *et al*., 2007; Rodgers *et al*., 2011; Kilian *et al*., 2012; Kalous *et al*., 2013). Angling can also create strong exploitative pressure on fish populations, especially within highly catch orientated forms of fishing (Almodóvar & Nicola, 2004; Dorow *et al*., 2010; McClenachan, 2013). More troublesome is the tendency of anglers to under-estimate their impact on natural ecosystems with around 49 % of anglers believing that their fishing behaviour has no effect on the ecosystems they fish (Gray & Jordan, 2010). This may be due to aspects such as lack of education, shifting baseline syndrome (whereby anglers would lose track of the scale of environmental damage inflicted to aquatic ecosystems due to the timescale of that damage exceeding their lifespan (Soga & Gaston, 2018)) or cognitive dissonance leading them to blame other factors such as commercial fishermen (Arlinghaus & Mehner, 2005; Dorow & Arlinghaus, 2012; McClenachan, 2013; Gallagher *et al*., 2015; Rees *et al*., 2017). Indeed, anglers can even view their practices as beneficial in spite of the potential negative effects (Reed & Parsons, 1999; Arlinghaus & Mehner, 2005).

However, the wider effects of angling can benefit aquatic conservation. Anglers incur large expenditures through factors such as bait, equipment and licencing fees that has led to, for example, the English freshwater angling community contributing an estimated £1.46 billion to the economy in 2015 (EA, 2018). Consequently, anglers are economically invested in the natural fish resources that they utilise. This can be harnessed to fund conservation efforts and aquatic ecosystem management (Arlinghaus *et al*., 2002). Angling clubs even provide a direct source of conservation as, under UK law, they are urged to manage the freshwater ecosystems they own (Arlinghaus *et al*., 2002). Additionally, anglers are often a highly motivated group of stakeholders and possess considerable political power. This can power lobbying for conservation goals, especially those concerning issues of water quality, where anglers may act as watchdogs and take direct legal action to prevent pollution (Bate, 2001). This motivation also leads them to participate in citizen science projects, providing a valuable asset to the scientific community (Schuett *et al*., 2014; Williams *et al*., 2016). As previously mentioned, anglers often appreciate the value of natural surroundings and believe that biodiversity should be conserved (Holland & Ditton, 1992; Dorow & Arlinghaus, 2012). Thus, they are often open to education and comply with guidelines as long as it benefits their interests to do so (Gray & Jordan 2010; Nguyen *et al*., 2013).

Recreational fisheries are hotspots of conflict over common pool resources between stakeholders as their management requires the consideration of ecological, economic and social aspects (Arlinghaus, 2005; Arlinghaus & Cooke, 2009). Anglers are consumptive users, using fish populations for both food and recreational pleasure (Duffus & Dearden, 1990), so it is unsurprising that anglers and angling groups frequently conflict with other stakeholders on matters of resource use and management (Arlinghaus *et al*., 2002; Arlinghaus, 2005). Anglers may have a lower tolerance for crowding and so perceive more conflicts with other recreational users such as boaters and divers (Arlinghaus, 2005; Kainzinger *et al*., 2015) which has led to physical harassment in extreme cases (Lynch *et al*., 2004). Anglers have been shown to have different perceptions and preferences regarding the management of aquatic ecosystems than researchers, fishery managers or conservation groups (Connelly *et al*., 2000; Gozlan *et al*., 2013). These disparities can prove problematic as anglers prioritize the conservation of their target fish species and so may favour the population control of fish-eating animals such as cormorants (Phalacrocoracidae), conflicting with conservation and animal welfare groups (Dorow & Arlinghaus, 2012; Marzano & Cheyne, 2013; Schakner *et al*., 2019).

Moreover, the catch orientated attitudes and minimal ecological awareness of some anglers can push fishery managers, who must satisfy angler demands and conservation objective simultaneously, into deleterious management practices such as intensive stocking or the deliberate introduction of non-native species to satisfy expectations (Arlinghaus & Mehner, 2003; Arlinghaus & Mehner, 2005; Dorow & Arlinghaus, 2012; Garlock & Lorenzen, 2017; Rees *et al*., 2017; Nolan *et al*., 2019). Many anglers oppose actions that restrict their own activities such as size restrictions and bag limits (Renyard & Hilborn, 1986; Reed & Parsons, 1999). In extreme circumstances, angling associations may oppose conservation actions to establish protected areas out of fear that it will negatively impact recreational fishing (Lynch *et al*., 2004). One example would be “Right to Fish” legislation. Such legislation prohibits the closure of any area to anglers and has been successfully established in Maryland and Rhode Island due to extensive lobbying by national sportfishing groups (McClenachan, 2013). Furthermore, if tight restrictions are implemented, non-compliance is commonplace among harvest orientated anglers (Sullivan, 2002; Näslund *et al*., 2010).

Anglers and commercial fisheries frequently conflict when they target similar species, each group blaming the other for issues such as overexploitation or illegal harvesting (Kearney, 2002). However, anglers are a heterogenous group and so commonly experience intrasectional conflict (Bear & Eden, 2011). This can occur through place attachment whereby resident anglers come into conflict with non-residents (Arlinghaus, 2005). Specialized anglers are more likely to conflict with other anglers due to disparities in both motivation and expectations (Arlinghaus, 2005). A good example are German carp anglers who practice voluntary catch and release (VC&R) whereby they release the fish alive after capture (Arlinghaus, 2007). However, VC&R can cause post hooking mortality and sub-lethal effects (Bartholomew & Bohnsack, 2005; Campbell *et al*., 2010). In addition to animal welfare groups who believe that VC&R causes unnecessary suffering (Aas, 2002; Arlinghaus *et al*., 2009), carp anglers who practice VC&R in Germany have conflicted with the, more harvest orientated, wider German angling community who may view them as a scapegoat to divert attention away from other problematic aspects of angling (Arlinghaus, 2007).

However, the blame for these disparities must be shared across stakeholder groups. Anglers do appreciate the value of natural ecosystems and are often eager to learn about best practices regarding ecosystem conservation (Williams & Moss, 2001; Gray & Jordan 2010). However, they are not always involved in the management decisions of recreational fisheries (Cowx *et al*., 2010). Hasler & Colotello (2011) show that although 68 % of anglers want to be involved in fisheries management decisions, only 20 % of researchers share the same view. Barriers to communication are common in recreational fisheries and are considered to be one of their major limiting factors (Arlinghaus *et al.,* 2002).

These communication barriers are worrisome as they may restrict the effectiveness of future conservation actions. It is widely considered that clear and effective communication between stakeholders as well as cooperation between stakeholders is vital for successful conservation of ecosystems (Meffe, 2002; Vogler *et al*., 2017). Effective communication between stakeholders enables conservationists to gauge; the knowledge of stakeholders, the impacts stakeholders may have and how amicable stakeholders are to change in addition to incorporating stakeholder's local to improve the process of managing natural resources (Neilsen & Mathisen, 2006; Cowx *et al*., 2010; Danylchuk & Cooke, 2010; Dorow *et al*., 2010). Without communication there is a risk of social discrimination between groups and failure to include the opinions or participation of all stakeholders during planning (Arlinghaus, 2005). This could cause the failure of conservation efforts as neglected groups may not comply with regulations (Gibson & Marks, 1995). Non-compliance may be more likely within the angling community as they can be sceptical of government agencies and researchers (Smith *et al*., 1997). Moreover, the diffuse nature of angling can restrict enforcement efforts, therefore, communication and cooperation between stakeholders in recreational fisheries management is crucial to increase voluntary compliance (Arlinghaus *et al*., 2002; Arlinghaus, 2005).

The use of lamprey as angling bait is one example of a conservation issue regarding angling. Lamprey, a taxonomic group in which over half the species are threatened (Renaud, 1997) are threatened by numerous factors such as pollution, anthropogenic barriers and commercial exploitation (see section 1.3.). Reasons for exploiting lamprey are widespread, including research into curing motor neuron disease (see section 1.4.), but human consumption and fishing bait (recreational and commercial) are major components. Anadromous sea lamprey (*Petromyzon marinus*) and European river lamprey (*Lampetra fluviatilis*) are an economically important food resource across the Baltic (Tuunain *et al*., 1980; Birzaks & Abersons, 2011). Both of these species are listed under appendix three of the Bern Convention (1979) and annexes two and five of the Habitat and Species Directive (92/43/EEC). This means that exploitation is allowed, subject to management measures, but protection is required by member states of the European Union through methods such as the establishment of Special Areas of Conservation (SACs).

As previously mentioned, lamprey have been long recognised as angling bait (Figure 3.1). Pacific lamprey (*Entosphenus tridentatus*), a species that has massively declined across North America (Ward *et al*., 2012), has had its larvae used as sport fishing bait (Close *et al*., 2002). Izaak Walton (1653) notes that larval lamprey (most likely *L. fluviatilis* and *P. marinus*) make for good eel bait. Although the use of Pacific lamprey larvae as bait has been banned in numerous states in the US (Luzier *et al*., 2011) sub-adult *L. fluviatilis* have become commonly used as angling bait in the UK for coarse predator species such as northern pike (*Esox lucius*) (Masters *et al*., 2006). Most angling for coarse predatory species across the globe occurs with artificial lures. However, in Britain and Ireland there is a history of using live and more recently dead (since the 1950's) fish baits to capture coarse predatory species, especially *E. lucius*. In the mid 1990's, commercial fishermen and a few influential anglers popularized the use of dead (frozen and thawed) *L. fluviatilis* as coarse predator angling bait (Foulds & Lucas, 2014). Commercial operators prepare and package lamprey and supply them to angling bait and tackle shops. These lamprey are sourced from England and abroad. Within England, *L. fluviatilis* are captured in the tidal Ouse and Trent, within the Humber River basin (see section 1.6.), Masters *et al.,* (2006) estimated a minimum relative exploitation level of 9.9 % when looking at a single fisher within the Humber River basin. However, a second fisher was identified and Foulds & Lucas (2014) later estimated an exploitation level of >20 %. This rate is considerably lower than other fisheries in Europe (see section 1.3.) and *P. marinus* populations in the American Great Lakes have been demonstrably unaffected by the annual removal of an estimated 40 % of the spawning population (Mardsen & Siefkes, 2019). Nevertheless, it was still cause for concern in the Humber, which is an SAC for which *L. fluviatilis* is a designated feature. This is because *L. fluviatilis* is an anadromous, semelparous species and so is vulnerable to unsustainable harvest by nature of its' life history (McDowall, 1988; Reynolds *et al*., 2002). *Lampetra fluviatilis* is also considerably less fecund than *P. marinus* with a mean fecundity of 20,000 compared to *P. marinus*' 165,000 (Docker *et al*., 2019).

*Figure 3.1: Example of frozen lamprey sections sold as angling bait for coarse predator fishing. Reproduced from www.baitbox.com.*

English regulatory agencies previously felt they lacked the direct legal instruments to restrict taking of lamprey bycatch from eel fisheries in tidal waters (Masters *et al*., 2006; Foulds & Lucas, 2014), but this was solved in the Marine and Coastal Access Act (2009) which incorporated *L. fluviatilis* into the Salmon and Freshwater Fisheries Act (1975). Since then, strict numbers of licences, quotas and fishing seasons have been enforced (Foulds & Lucas, 2014). Considering that exploitation of *L. fluviatilis* is likely to continue (for example, it currently provides the only annual metric of *L. fluviatilis* relative abundance within the Humber to management agencies) it is vital to understand the opinions of the key stakeholders involved in the sale of lamprey for angling bait; the fishers who catch river lamprey, river lamprey wholesale suppliers, fishing tackle shops and coarse predator anglers who use lamprey as bait. Foulds (2013) and Foulds & Lucas (2014) have already covered the knowledge and attitudes of wholesale suppliers and fishing tackle shops. Consequently, this chapter is concerned with the consumers; coarse predator anglers who drive the demand for lamprey in the UK.

Consumers have recently increased their environmental awareness regarding the impact of the goods they buy (Saunders *et al*., 2011; Lundblad & Davies, 2016). Many consumers now prefer ecologically sustainable or locally sourced products and are willing to pay a premium to ensure these standards are kept (Forbes *et al*., 2009; McClenachan *et al*., 2016; Shao & Ünal, 2019). Consumers may even resort to boycotting products or companies due to environmental concerns (Hoffmann *et al*., 2018) and so anglers may prefer their baits to be produced in a responsible fashion. However, this rise in environmental concern may not apply to specialist predator anglers who, as a catch orientated group, may oppose restrictions that affect their chances of catching fish (Arlinghaus & Mehner, 2005; Nolan *et al*., 2019). Additionally, anglers may hold a misconception that parasitic lampreys are damaging to the ecosystem (due to the media attention directed to invasive *P. marinus* in the American Great Lakes) and so are less inclined to support their protection (Lucas *et al*., 2020). Consequently, it is important to recognise both the scale of lamprey use by anglers and their knowledge and opinions regarding natural and artificial angling baits in order to properly manage exploitation of *L. fluviatilis*.

This investigation into the knowledge and attitudes of coarse predator anglers towards baits had several aims. These are;

1) Understand the general fishing behaviour and attitudes of coarse predator anglers
2) Determine the proportion of anglers using lamprey as bait and for what purpose
3) Establish the knowledge and opinions of anglers regarding lamprey as bait
4) Determine how willing anglers are to replace lamprey with alternative baits

## 3.3. Methodology

### 3.3.1. Questionnaire design

Questionnaires are a growing form of data collection in ecology. They are particularly useful in the study of public or stakeholder opinions regarding human-nature interactions and ecological management strategies (White *et al*., 2005). Consequently, a questionnaire was deemed to be a suitable method to collect data on the opinions of anglers towards using lamprey as bait. A telephone questionnaire was specifically chosen despite potential issues such as a response bias towards socially desirable answers and a greater cost than postal surveys (White *et al*., 2005; Kreuter *et al*., 2008). This is because telephone questionnaires can; produce a higher response rate, reduce the likelihood of missing data, allow for participants to express opinions in detail and easily cover a large geographical area (Bourque & Fielder, 2003; White *et al*., 2005; Lungenhausen *et al*., 2007).

A questionnaire comprising of up to 29 questions was created for the study and organised into four separate sections. The first section concerned aspects of the participants' fishing behaviour e.g., environmental attitudes and opinions towards natural and artificial baits in general. The second covered the participants' knowledge and opinions regarding the use of lamprey as bait. This section specifically asked if participants used lamprey as bait and if they agreed that, if lamprey were threatened by exploitation, a ban on their use as angling bait should be implemented. The third was an open question where participants could comment on their previous answers and the wider subject of angling. The final section determined the demographics of the participant, asking for age, gender, nationality and highest education level achieved. A copy of the questionnaire can be found under Appendix I.

The questionnaire was designed to obtain extra information from anglers that use lamprey as bait. This was achieved through question 13: 'When using natural dead baits, how regularly do you use lamprey; Always, Often, Sometimes, Rarely or Never?' Participants that responded with 'Never' were not asked questions 14 to 21 as these investigated the participants' knowledge and opinions of using lamprey as bait. Participants that gave any other answer than 'Never' were asked the full set of questions.

Closed questions were the predominant form of question asked as these are quick for participants to complete and easier to analyse (Rowley, 2014). Many of these were seven-point Likert scales where the responses ranged from Strongly Agree to Strongly Disagree. As an example, respondents were asked to rate their opinion towards the statement "Lamprey are responsibly sourced for bait" according to the scale of; Strongly Agree, Agree, Slightly Agree, Neutral, Slightly Disagree, Disagree, Strongly Disagree. As recommended by Frary (1996), the 'Neutral' response was not explicitly offered to participants. However, some participants could not choose a non-neutral response to questions and thus a neutral response was recorded.

Section three consisted of an open question asking participants to expand upon any answers they previously gave if they so wished. This was included to further engage participants in the questionnaire and reveal any issues or novel aspects with the use of lamprey as bait that were missed by the questionnaire (O'Cathain & Thomas, 2004). Answers given to this section were transcribed, statements that appeared multiple times across responses were identified and their frequency recorded.

The exact phrasing of questions or statements can affect both the validity of the responses given and the willingness of participants to provide an answer (Petrinovich & O'Niell, 1996; DiFranceisco *et al.*, 1998; Minson *et al.,* 2018). Additionally, if asking multiple questions worded to contain positive assumptions, there is a risk of pushing respondents to mindlessly choose positive responses rather than evaluating the question (Frary, 1996). As a result, non-sensitive questions were randomly positively or negatively worded when the questionnaire was designed.

In order to ascertain participants' attitudes towards certain aspects of using lamprey as bait it was necessary to ask sensitive questions. These are defined by Tourangeau & Yan (2007) to be questions that potentially stimulate a socially undesirable response. One such example would be "Please describe your opinion on the statement 'If lampreys were threatened by exploitation a ban on their use as angling bait should not be implemented' under the scale of Strongly agree to Strongly disagree". Sensitive questions were situated at the end of section two of the questionnaire in order to minimise the risk of participants terminating the questionnaire before completion (Marshall, 2005). Additionally, Foulds (2013) demonstrated that when asking fishing tackle shop managers sensitive questions about using lamprey as bait, positive or negative wording significantly affected the response. Consequently, such sensitive questions about using lamprey as bait were split into two versions; one positively worded (e.g. lamprey should be conserved) and one negatively worded (e.g. lamprey should not be conserved). Before starting a questionnaire, it was randomly decided which set of questions the participant would receive. All responses were then converted to the positively worded phrasing for use in analysis. For example, respondents who strongly disagreed that "lamprey should not be conserved" were recorded as strongly agreeing that "lamprey should be conserved". Finally, a short pilot test (*n*=3) was conducted to ensure the wording of questions was easy to understand before data collection began.

### **3.3.2. Data collection**

Dead or sectioned lamprey is used as a bait for coarse predatory fish across the UK, although more in some regions than others (Foulds, 2013; Foulds & Lucas, 2014). Therefore, at the outset of this study it was decided that questionnaire sampling should be stratified across the UK as far as was practicable. For this purpose, the UK was split into five regions, comprising of Northern England, Southern England, Wales, Scotland and Northern Ireland. It was decided to directly contact angling clubs in order to gather responses as it was assumed that members of angling clubs, both local and national, would be committed anglers and so willing to participate in the study. An online directory (https://fishbuddy.directory) was used to randomly select up to five angling clubs per county. Unfortunately, this produced a slight sampling bias towards Southern England, a region of the UK that contains the greatest number of counties. This mean that more angling clubs from Southern England were contacted than from any other region, potentially resulting in a disproportionate number of respondents originating from Southern England. Therefore, additional angling networks were contacted to provide more even coverage across the entire UK. Such networks ranged from associations of predator anglers (such as the Pike Anglers' Club of Great Britain - PAC) to advertising within broader forms of angling media (for example, an interview on Talksports' Fisherman's Blues radio show).

These networks were sent an introductory paragraph explaining the brief aims of the research. However, any specific mention of obtaining anglers' opinions on the use of lamprey as bait was excluded to avoid potential respondent bias or antagonising the networks. Networks were then requested to inform their members of the research so that interested individuals could get in contact so that the questionnaire could be conducted at a suitable time and date. However, additional methods of obtaining participants were required as Watson *et al.* (2014) estimates that the majority of sea anglers are not associated with any angling association. It should be noted that the behaviour and attitudes of sea anglers likely differs from coarse anglers due to aspects such as not requiring to purchase a licence to practice sea fishing in the UK. This creates a lower economic investment and so, potentially, a lower chance of joining an angling association than coarse anglers. Nonetheless, it is not unreasonable to assume that a considerable proportion of UK coarse anglers are not members of angling associations. Initially, it was planned to visit large angling events, such as the Big One Fishing Show, to conduct questionnaires in person with anglers. Unfortunately, these events were cancelled as a result of the UK being put into Coronavirus lockdown on March 16$^{th}$, 2020. Consequently, it was decided to utilise ‘snowball sampling’, a non-probability sampling procedure which benefits from known members of a population being able to identify ‘hidden’ members of a population (Biernacki & Waldorf, 1981). This was done by asking participants to recommend the questionnaire to fellow anglers after the questionnaire was completed.

Some individuals requested to be given a copy of the questionnaire to complete by themselves. No questionnaires were allowed to be completed in such fashion as it may have allowed participants to independently research the use of lamprey as bait, thus affecting their response. Additionally, comparing telephone questionnaires to self-administered questionnaires could prove problematic (Dillman *et al.*, 1996). A total of 152 clubs and other networks were contacted. It is impossible to calculate the response rate as networks did not disclose how many anglers they notified of the questionnaire. As all questionnaires were conducted by the same individual, interviewer bias was avoided.

After scheduling a suitable time to conduct the questionnaire, all participants were then reminded of the research’s basic aims and were informed that; the questionnaire would be recorded, that all data obtained would be kept confidential and anonymous, that the data may be used in a scientific paper, that data would be retained for a period of two years and that answering the questionnaire was completely voluntary. Consent to record was then requested, if not clearly given the questionnaire was terminated. Participants were first asked if they fished for freshwater predatory fish such as *E. lucius*, if they responded negatively the questionnaire was terminated. Questionnaires took between 10 and 15 minutes to complete. Afterwards, participants were reminded that they could withdraw their consent up until the point that the data was used in a thesis or scientific publication. Data was collected from March 2020 to July 2020.

After data collection, additional variables were added to the questionnaires derived from the collected data. Firstly, a binary variable was added describing whether or not the participant used lamprey as bait to any degree. Secondly, during the questionnaire, participants were asked to report what species of fish they commonly used as bait. This list was then compared to the ICUN Red list (https://www.iucnredlist.org) and another binary variable was added to determine if the participant used a species of fish rated as vulnerable or at greater risk for bait.

### 3.3.3. Analysis

Mann-Whitney tests were conducted to reveal any significant differences in opinions or likelihoods between participants who used lamprey as bait to some degree and participants that did not.

A series of logistic regressions were performed to determine what factors affected the likelihood of participants using lamprey as bait and the likelihood of a participant preferring lamprey for bait to be sourced from the UK. For each of these response variables the data was subset into numerous global models; demographics, general fishing behaviour, environmental attitude and bait attitudes. Each of these models were then dredged with the MuMIn package (Barton, 2009) to select subset models with an $\Delta$AIC <2. These subset models then underwent a model averaging procedure to create the final models. Final models were tested with an ANOVA function utilising a $chi^2$ test. To investigate pairwise differences in non-binary variables, tukey post hoc tests were performed.

A series of ordinal regressions were conducted to investigate what factors affected the opinions of participants regarding the use of lamprey as bait. To do this, the data was subset into numerous global models; demographics, general fishing behaviour, environmental attitude and bait attitudes. In cases where ordinal factors (Likert scales) would have been included in the model it was replaced by a binary factor to represent if the participant agreed or did not agree with the statement in question. Each of these models were then dredged with the MuMIn package (Barton, 2009) to select subset models with an $\Delta AIC < 2$. These subset models then underwent a model averaging procedure to create the final models which were then investigated. All analysis was conducted in R (Version 3.6.2).

## 3.4. Results

### 3.4.1. Demographics

A total of 69 questionnaires were conducted and completed. All participants gave consent to be recorded and all confirmed that they fished for coarse predatory species. No individuals terminated the questionnaire early or withdrew permission after completion of the questionnaire. 100 % of participants were both male and British. A majority of participants were members of a specialist angling club but far fewer were members of an environmental organization. The most frequent age range was 55-64 and a university degree was the most frequently achieved highest level of education. Table 3.1 shows other aspects of participant's demographic data. A full breakdown of completed anonymised questionnaires can be found in Appendix II.

*Table 3.1: The demographic data collected from the questionnaire participants. Values are presented as percentages. Table continues on following page.*

| | | Non-lamprey users (*n*= 25) | Lamprey users (*n*= 44) | Total (*n*= 69) |
|---|---|---|---|---|
| Location | Southern England | 76.0 | 40.8 | 53.6 |
| | Northern England | 12.0 | 20.5 | 17.4 |
| | Wales | 8.0 | 11.4 | 10.1 |
| | Scotland | 0.0 | 22.7 | 14.5 |
| | Northern Ireland | 4.0 | 4.5 | 4.3 |
| Age | 18-24 | 16.0 | 2.3 | 7.2 |
| | 25-34 | 12.0 | 11.4 | 11.6 |
| | 35-44 | 12.0 | 22.7 | 18.8 |
| | 45-54 | 8.0 | 18.2 | 14.5 |
| | 55-64 | 28.0 | 34.1 | 31.8 |
| | 65-74 | 20.0 | 11.4 | 14.5 |
| | ≥75 | 4.0 | 0.0 | 1.4 |

*Table 3.1: The demographic data collected from the questionnaire participants (continued).*

| | | | | |
|---|---|---|---|---|
| Highest education level achieved | Pre-16 | 0.0 | 6.8 | 4.3 |
| | Post-16 | 12.0 | 20.5 | 17.4 |
| | College diploma | 16.0 | 22.7 | 20.3 |
| | University degree | 56.0 | 31.8 | 40.6 |
| | Specialist professional qualification | 16.0 | 18.2 | 17.4 |
| Member of specialist angling club | Yes | 32.0 | 31.8 | 55.1 |
| | No | 68.0 | 68.2 | 44.9 |
| Member of environmental organisation | Yes | 60.0 | 25.0 | 30.4 |
| | No | 40.0 | 75.0 | 69.6 |

### 3.4.2. Fishing behaviour and bait choice

Over half of participants (59.4 %, *n*= 41) went coarse predator fishing at least once a week in the year prior to the study and only three (4.3 %) had not gone coarse predator fishing at any point during the previous year. The majority of participants (47.8 %) most commonly used natural dead fish baits when fishing for coarse predatory species (Figure 3.2). Artificial lures and flies were second most popular, being the most commonly used fishing method of 44.9 % of participants. Non fish baits (such as annelid worms) and live fish baits were infrequently preferred, being the most common fishing method of 5.8 % and 1.4 % of participants respectively. However, it is important to note that the majority of participants (65.2 %) tended to use several bait methods when coarse predator fishing according to place and conditions. In addition to this, only 39.1 % of participants explicitly stated that they do not use live bait whilst 5.8 % stated that they do not use any form of fish dead bait. This indicates that 60.9 % and 94.2 % of respondents respectively use live fish bait or dead fish bait to some degree. Catch and release (C&R) was prevalent across participants with 87.0 % (*n*= 60) claiming to always practice C&R

across all forms of fishing.

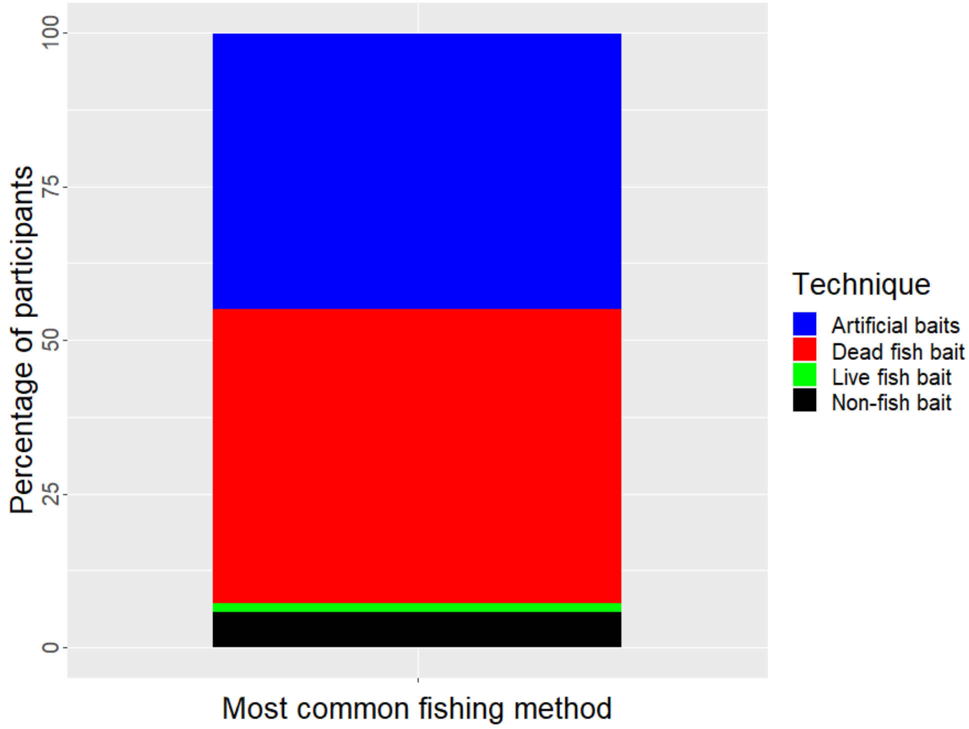



*Figure 3.2: The percentage who respondents who stated that their most common freshwater predator fishing method was artificial baits, dead fish baits, live fish baits and non-fish baits respectively.*

A total of 21 species of fish were identified as being commonly used for natural fish bait by participants (Figure 3.3). Participants used an average of 3.4 species of fish for bait (±0.2 SE). Three species were identified to be of conservation concern at a global scale by the IUCN; Atlantic horse mackerel (*Trachurus trachurus*), pollan (*Coregonus pollan*) and European eel (*Anguilla anguilla*) (Freyhof & Kottelat, 2008; Smith-Vaniz *et al*., 2015; Pike *et al*., 2020) and 17.4 % (*n*= 12) of respondents stated that they commonly used these species for natural fish bait. The most frequently identfied fish used for bait was the Atlantic mackerel (*Scomber scombrus*).

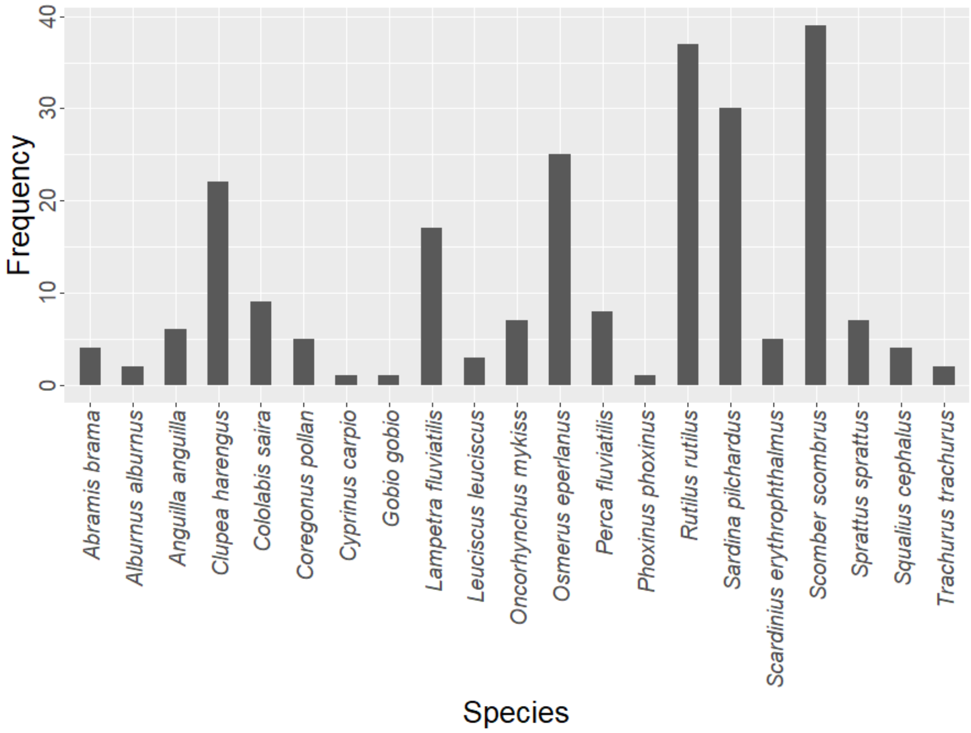



*Figure 3.3: The species of fish (excluding lamprey) that participants claimed to frequently use as bait whilst fishing for predatory freshwater fish and the frequency of participants that used each species.*

Overall, anglers slightly agreed that; artificial baits were more expensive than natural baits, natural dead baits tended to catch bigger fish than artificial baits and that predatory fish were more likely to be deep hooked by natural live and dead baits than artificial baits but they slightly disagreed with the statement that that natural dead baits resulted in fewer takes compared to artificial baits (Table 3.2). Opinions regarding natural and artificial baits between lamprey users and non-lamprey users did not significantly differ (Mann-Whitney tests, $p$>0.05). Eight participants added that there were notable differences between the fishing methods of natural and artificial baits.

*Table 3.2: The mean scores and standard errors of participants responses towards statements comparing natural and artificial baits. Scores are calculated for all participants, participants that used lamprey as bait and participants that did not use lamprey as bait. Measures are based on a 7-point Likert scale where; 1= Strongly disagree, 2= Disagree, 3= Slightly disagree, 4= Neutral, 5= Slightly Agree, 6= Agree and 7= Strongly agree.*

| Statement | Non-lamprey users (*n*= 25; Mean ± SE) | Lamprey users (*n*= 44; Mean ± SE) | Total (*n*= 69; Mean ± SE) |
|---|---|---|---|
| Artificial baits are more expensive than Natural baits | 5.0 ± 0.4 | 4.9 ± 0.3 | 4.9 ± 0.2 |
| Natural dead baits result in fewer takes than artificial baits | 3.6 ± 0.4 | 3.0 ± 0.3 | 3.2 ± 0.2 |
| Natural dead baits tend to catch bigger fish than artificial baits | 5.2 ± 0.3 | 4.7 ± 0.3 | 4.9 ± 0.2 |
| Predators are more likely to be deep hooked by natural live and dead baits than artificial baits | 5.4 ± 0.4 | 5.1 ± 0.3 | 5.3 ± 0.2 |

### 3.4.3. Use of lamprey and knowledge regarding use of lamprey

The vast majority of participants (95.6 %, $n$= 66) were aware that lampreys are currently used for coarse predator bait and lamprey was also widely used among participants. 67.8 % ($n$= 44) stated that they used lamprey as dead bait for predators to some degree. Fishing location significantly affected the likelihood of a participant using lamprey as bait (ANOVA, $F_{(3,64)}$ = 13.398, $p$<0.01) although post hoc analysis could not find any significant differences between groups (Tukey tests, $p$> 0.05), Figure 3.4 showing that all participants who fished most frequently in Scotland used lamprey as bait. Specialist angling club membership significantly affected the likelihood of a participant using lamprey as bait (ANOVA, $F_{(1,63)}$= 4.696, $p$= 0.0302), with the odds of members of such clubs using lamprey as bait being 3.384 times higher than non-members (β= 1.219, SE= 0.580, d.f.=1, $Z$= 2.102, $p$= 0.0355). The use of threatened species (excluding lamprey) as bait significantly affected the likelihood of a participant using lamprey as bait (ANOVA, $F_{(1,67)}$= 5.878, $p$= 0.0153), with 91.7 % ($n$= 11) of participants that used threatened species (excluding lamprey) also using lamprey compared to 57.9 % (n= 33) of participants that did not use threatened species (excluding lamprey) using lamprey as bait. Although a χ2 test shows that a significant difference in the probability of using lamprey as bait between anglers that used other threatened species and those that did not existed (χ2= 4.894, $p$= 0.270), it was found that this factor had an insignificant effect in the multifactor model output (β= 2.030, SE= 1.104, d.f.= 1, $Z$= 1.839, $p$= 0.066). Forty-eight (69.6 %) of respondents claimed to be unaware of lamprey's conservation status.

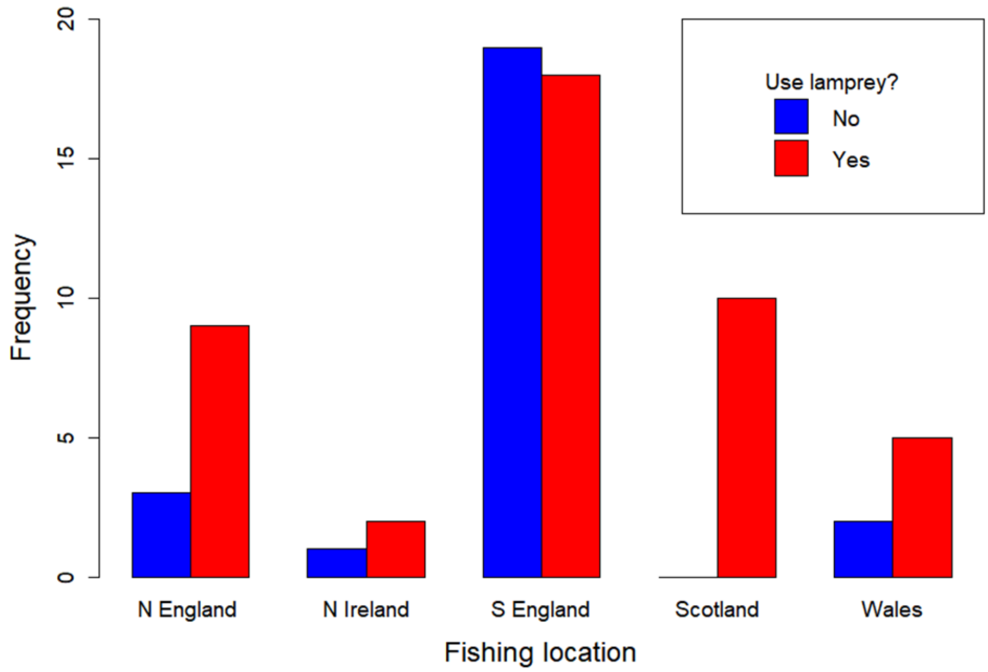



*Figure 3.4: The frequency of participants that did not/did use lamprey as bait respectively according to their most frequent fishing location.*

Of the participants that used lamprey as bait, *E. lucius* was the major target species with 97.7 % (*n*= 43) of participants stating that they targeted this species whilst using lamprey as bait (Figure 3.5). Uses for lamprey asides from predator fishing were rare with a single participant stating that they used it as bait for the common barbel (*Barbus barbus*). Participants generally used lamprey for bait within their local area, with only 29.5 % (*n*= 13) taking lamprey with them on angling trips outside their home region (within the UK). Unfortunately, participants did not specify what region they took lamprey as bait to. Knowledge of lamprey was sparse (Figure 3.6) with only 11.4 % (*n*= 5) of respondents who used lamprey as bait claiming to know what species of lamprey they used. Moreover, only two of these respondents identified the species of lamprey they used to be river lamprey (i.e., *Lampetra fluviatilis)*. In a similar vein, only 13.6 % (*n*= 6) of respondents who used lamprey as bait claimed to know the source of their lamprey. One participant believed that lampreys were farmed to provide bait.

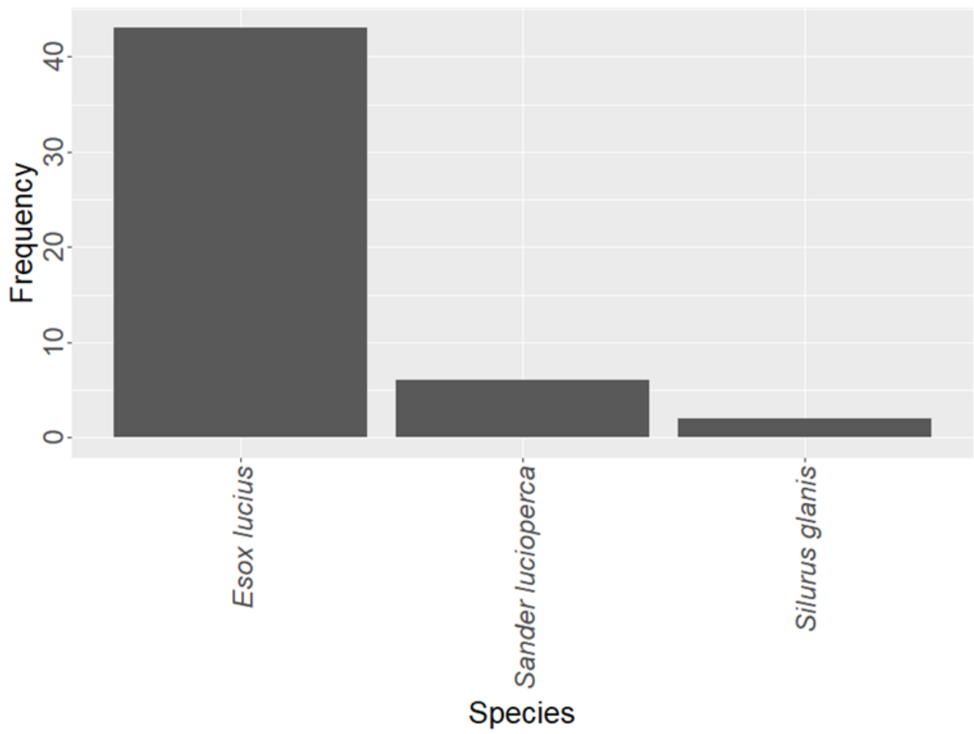



*Figure 3.5: The frequency of which predatory fish species were targeted by participants whilst using lamprey as bait.*

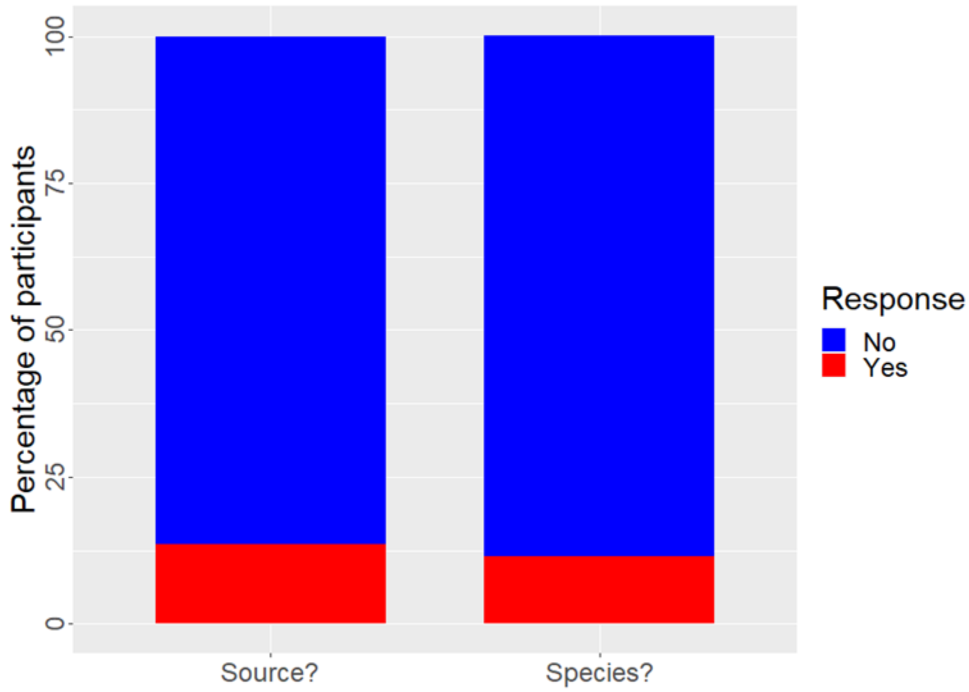



*Figure 3.6: The percentage of participants who claimed to know or not know the source of the lamprey they used as bait and the species of lamprey they used as bait respectively.*

When comparing lamprey to other natural dead baits participants that used lamprey disagreed that; lamprey is cheaper, more difficult to use or tends to catch smaller sized predatory fish than other natural baits. Participants were neutral towards the statement that using lamprey as bait results in more takes than other natural baits (Table 3.3).

*Table 3.3: The mean scores and standard errors of participants responses towards statements comparing lamprey to other natural baits. Scores are only calculated for participants who used lamprey as bait. Measures are based on a 7-point Likert scale where; 1= Strongly disagree, 2= Disagree, 3= Slightly disagree, 4= Neutral, 5= Slightly Agree, 6= Agree and 7= Strongly agree.*

| Statement | Lamprey users (*n*= 44; Mean ± SE) |
|---|---|
| Lamprey is cheaper than other natural baits | 2.0 ± 0.2 |
| Lamprey is more difficult to use than other natural baits | 1.9 ± 0.2 |
| Using lamprey as bait results in more takes when fishing for predators than other natural baits | 3.6 ± 0.3 |
| Using lamprey tends to catch smaller-sized predator fish than other natural baits | 2.8 ± 0.3 |

### 3.4.3. Opinions regarding lamprey

Most participants (56.5 %, *n*= 39) had no opinion on where they would prefer their lamprey to be sourced from, 39.1 % (*n*= 27) of participants stated that they would prefer lamprey to be sourced from the

UK for bait and 4.35 % ($n$= 3) stated that they would prefer lamprey to be sourced from the EU for bait. The participant's fishing frequency and how much they agreed that natural dead baits result in fewer takes than artificial baits when fishing, controlling for factors such as geographic location, significantly affected the likelihood of preferring lamprey sourced from the UK (ANOVA, $F_{(4,62)}$= 9.950, $p$= 0.0413; ANOVA, $F_{(6,62)}$= 17.023, $p$< 0.01 respectively) although post hoc analysis could not find any significant differences between groups (Tukey tests, $p$> 0.05) (Figures 3.7 and 3.8 respectively).

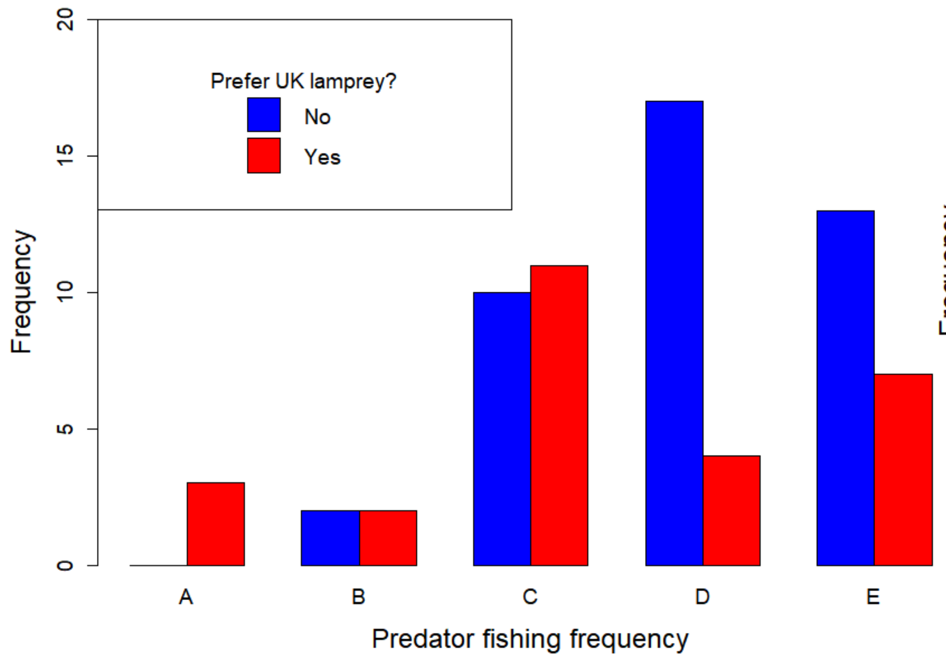



*Figure 3.7: The frequency of participants that preferred/did not prefer lamprey to be sourced from the UK for bait respectively split by their fishing frequency during the last year where; A= Never, B= Less than once a month, C= Once a month, D= Once a week and E= More than once a week.*

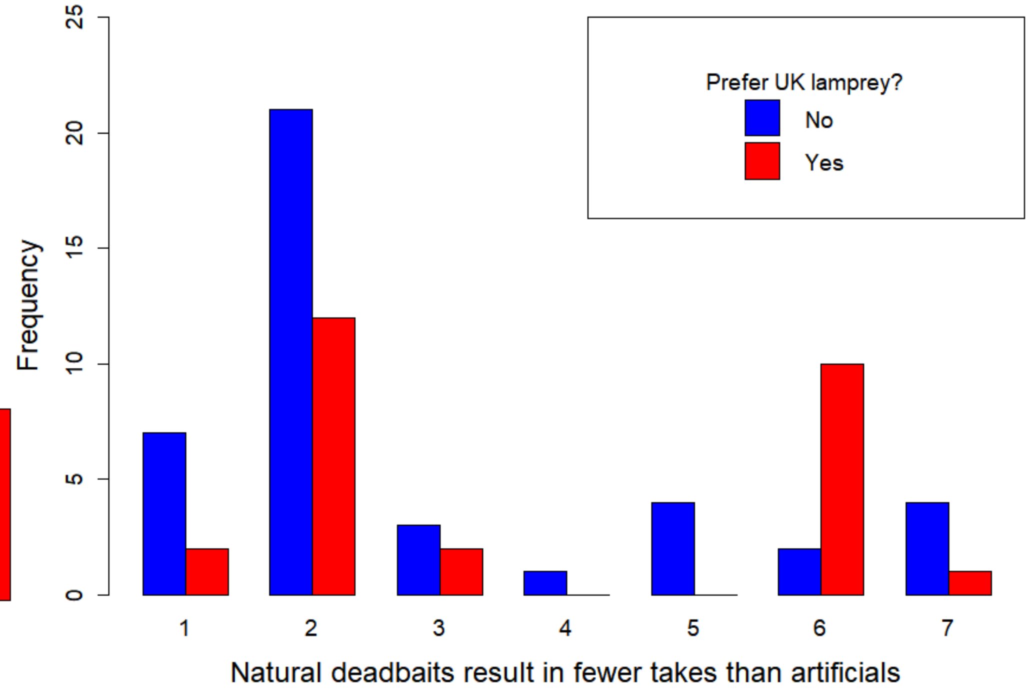



*Figure 3.8: The frequency of participants that preferred/did not prefer lamprey to be sourced from the UK for bait respectively split by their opinion towards the statement "Natural dead baits result in fewer takes than artificial baits" under a 7-point Likert scale where; 1= Strongly disagree, 2= Disagree, 3= Slightly disagree, 4= Neutral, 5= Slightly Agree, 6= Agree and 7= Strongly agree.*

Participants strongly agreed that bait companies should source their bait in an environmentally sustainable fashion (Table 3.3) with five respondents explicitly stating that they trusted suppliers to source sustainable bait. Respondents also agreed that lamprey should be conserved and, if threatened by exploitation, a ban on their use as angling bait should be implemented. Although participants were, overall, neutral towards the statement that lamprey are responsibly sourced for bait, participants that did not use lamprey for bait disagreed significantly more than participants that did (Mann-Whitney test, $W= 343$, $p= 0.004$). Seventeen participants explicitly stated that they would prefer lamprey to be from a sustainable source and six expressed a preference towards farmed lamprey.

Participants disagreed that lamprey could not be replaced with other natural baits. Thirteen respondents explicitly stated that there was little difference between natural fish baits. However, participants only slightly disagreed that lamprey could not be replaced with artificial baits. Twenty-two participants noted that they thought lamprey are a good bait for predatory fish.

*Table 3.4: The mean scores and standard errors of participants responses towards statements regarding the use of lamprey as bait, scores are calculated for all participants, participants that used lamprey as bait and participants that did not use lamprey as bait. Measures are based on a 7-point Likert scale where; 1= Strongly disagree, 2= Disagree, 3= Slightly disagree, 4= Neutral, 5= Slightly Agree, 6= Agree and 7= Strongly agree.* *Table continues on following page.*

| Statement | Non-lamprey users (*n*= 25; Mean ± SE) | Lamprey users (*n*= 44; Mean ± SE) | Total (*n*= 69; Mean ± SE) |
|---|---|---|---|
| Bait companies should source their bait in an environmentally sustainable fashion | 6.5 ± 0.2 | 6.7 ± 0.1 | 6.6 ± 0.1 |
| Lamprey are responsibly sourced for bait | 3.4 ± 0.2 | 4.5 ± 0.2 | 4.1 ± 0.2 |
| You could not replace lampreys with other natural baits | 2.4 ± 0.3 | 2.2 ± 0.2 | 2.3 ± 0.2 |
| You could not replace lampreys with artificial baits | 3.4 ± 0.4 | 3.2 ± 0.3 | 3.2 ± 0.3 |
| Lampreys should be conserved | 6.3 ± 0.2 | 6.0 ± 0.2 | 6.1 ± 0.1 |

*Table 3.4: The mean scores and standard errors of participants responses towards statements regarding the use of lamprey as bait (continued).*

| | | | |
|---|---|---|---|
| Lampreys have been sufficiently protected in the UK | 3.2 ± 0.3 | 3.3 ± 0.2 | 3.3 ± 0.2 |
| If lampreys were threatened by exploitation a ban on their use as angling bait should be implemented | 6.0 ± 0.3 | 6.3 ± 0.1 | 6.2 ± 0.1 |

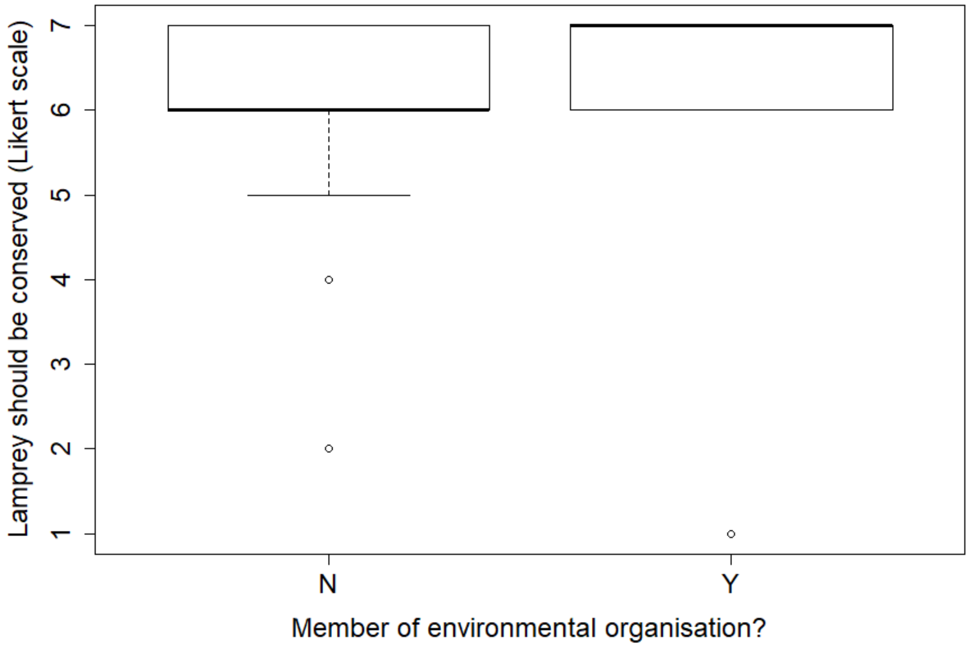
Table 3.5 shows the significant factors affecting participants opinions towards the use of lamprey as bait. For example, members of environmental organisations had odds of agreeing more that lamprey should be conserved 2.95 times that of non-members. On the other hand, participants who agreed (to some degree) that you could not replace lampreys with other natural baits had odds of agreeing more that lamprey should be conserved 89.9 % lower than that of participants who disagreed that you could not replace lampreys with other natural baits. Figures 3.9 to 3.16 are box plots showing these significant effects.

*Table 3.5: Factors that had a significant effect on participant's opinions towards the use of lamprey as bait. The statement in question, the significant factor, the odds ratio, β, standard error,* t *value and* p *value are included. Table continues on following page.*

| Response | Factor | Odds ratio | β | SE | *t* value | *p* |
|---|---|---|---|---|---|---|
| Lamprey should be conserved | Member of environmental organisation | 2.95 | 1.08 | 0.466 | 2 | 0.0456 |
| | Agree that you could not replace lampreys with other natural baits to some degree | 0.101 | -2.3 | 0.868 | -2.64 | <0.01 |
| Lamprey are responsibly sourced for bait | Member of specialist angling club | 3.78 | 1.331 | 0.466 | 2.85 | <0.01 |
| | Age (45 to 54 against 18 to 24) | 21.5 | 3.07 | 1.03 | 2.98 | <0.01 |
| | Age (55 to 64 against 18 to 24) | 15.9 | 2.77 | 0.886 | 3.12 | <0.01 |
| | Member of environmental organisation | 0.196 | -1.63 | 0.512 | -3.19 | <0.01 |
| | Use lamprey as bait | 3.29 | 1.19 | 0.455 | 2.62 | <0.01 |

*Table 3.5: Factors that had a significant effect on participant's opinions towards the use of lamprey as bait (continued).*

| | | | | | | |
|---|---|---|---|---|---|---|
| If lampreys were threatened by exploitation a ban on their use as angling bait should be implemented | Agree that you could not replace lampreys with artificial baits to some degree | 0.303 | -1.2 | 0.568 | -2.11 | 0.0352 |
| You could not replace lampreys with artificial baits | Mostly use lures (against mostly use dead bait) | 0.328 | -1.11 | 0.486 | -2.3 | 0.0217 |



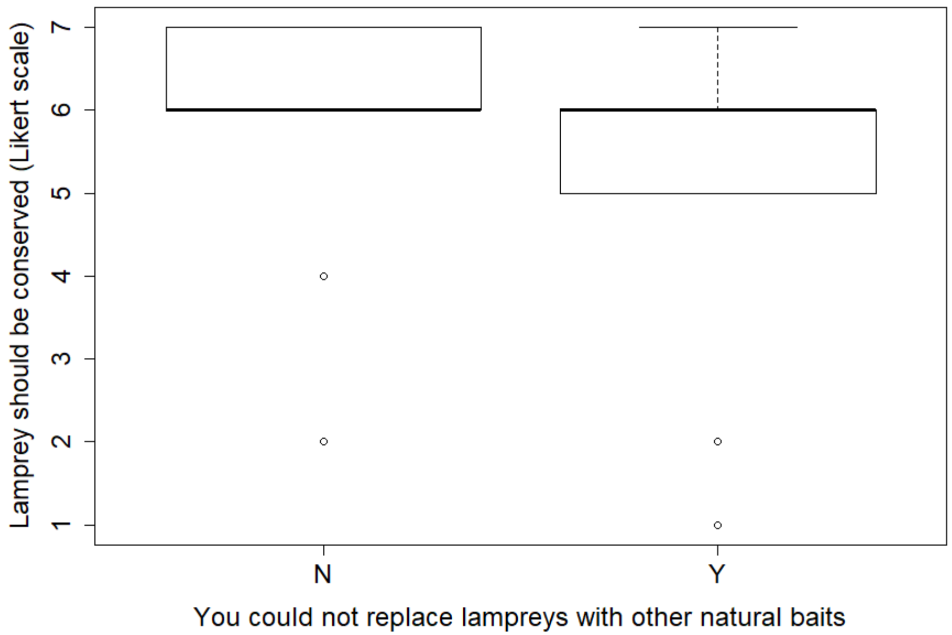




*Figure 3.9: Participants' opinion towards the statement "Lampreys should be conserved" (under a 7-point Likert scale where; 1= Strongly disagree, 2= Disagree, 3= Slightly disagree, 4= Neutral, 5= Slightly Agree, 6= Agree and 7= Strongly agree) split by if they were/were not members of an environmental organisation.*

*Figure 3.10: Participants' opinion towards the statement "Lampreys should be conserved" (under a 7-point Likert scale where; 1= Strongly disagree, 2= Disagree, 3= Slightly disagree, 4= Neutral, 5= Slightly Agree, 6= Agree and 7= Strongly agree) split by if they did/did not agree that lamprey could not be replaced with other natural baits to some degree.*

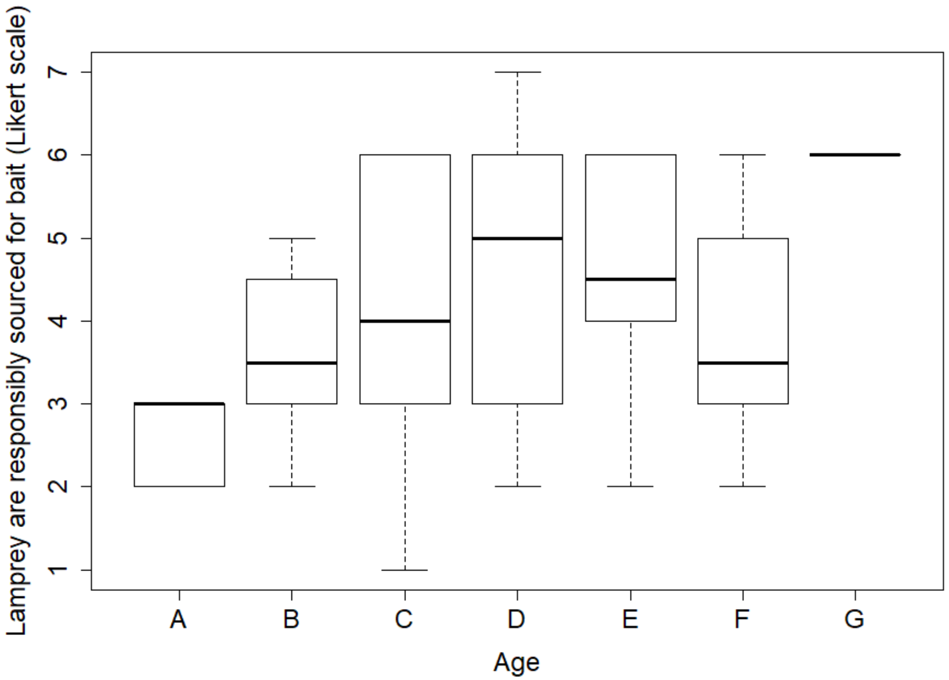



*Figure 3.11: Participants' opinion towards the statement "Lampreys are responsibly sourced for bait" (under a 7-point Likert scale where; 1= Strongly disagree, 2= Disagree, 3= Slightly disagree, 4= Neutral, 5= Slightly Agree, 6= Agree and 7= Strongly agree) split by their age (where; A= 18-24, B= 25-34, C= 35-44, D= 45-54, E= 55-64, F= 65-74, G= ≥75).*

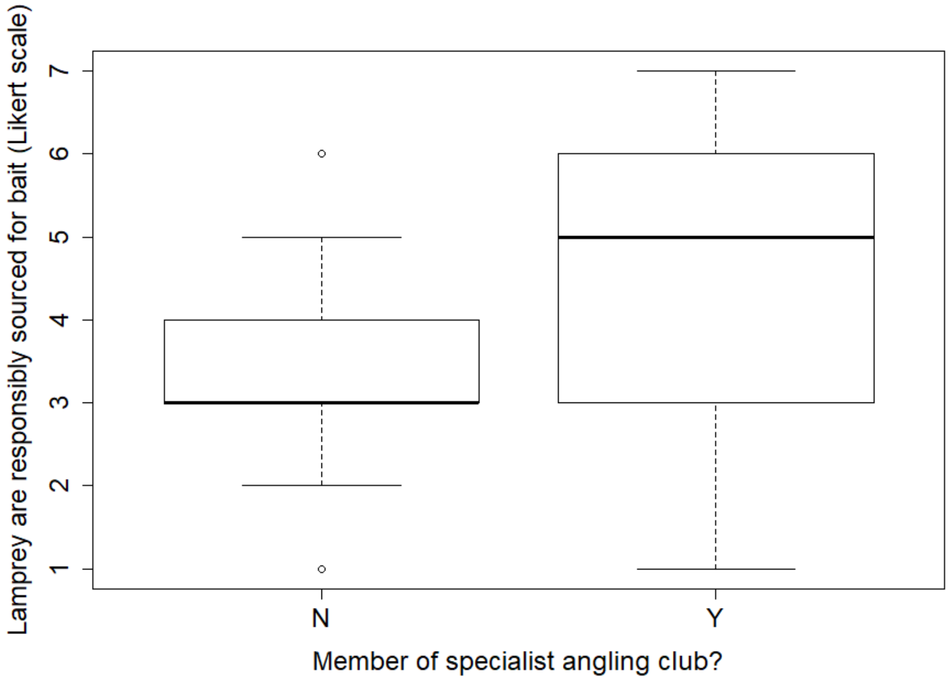
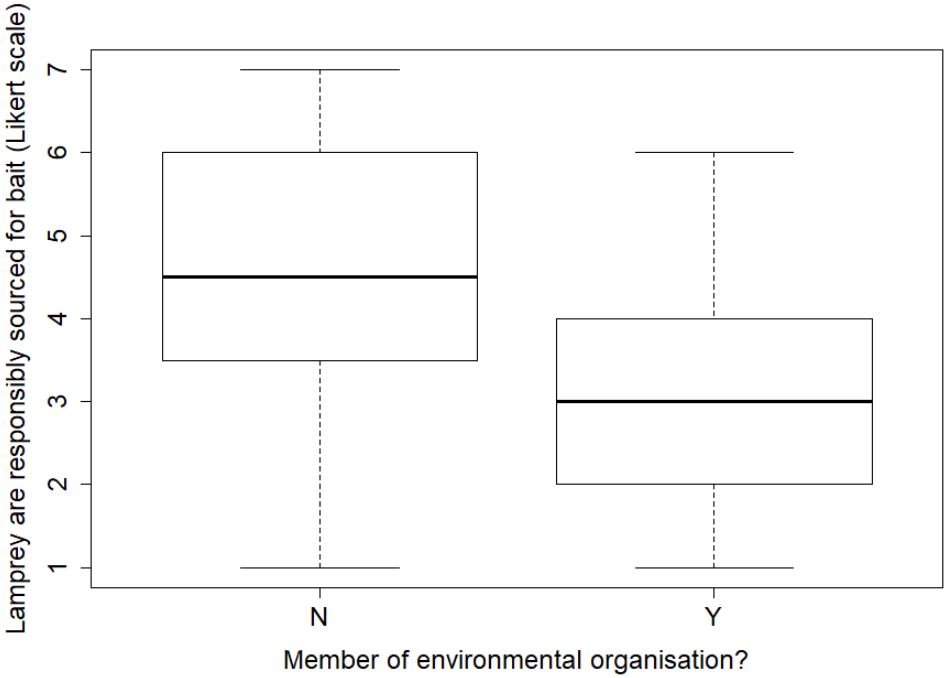



*Figure 3.12: Participants' opinion towards the statement "Lampreys are responsibly sourced for bait" (under a 7-point Likert scale where; 1= Strongly disagree, 2= Disagree, 3= Slightly disagree, 4= Neutral, 5= Slightly Agree, 6= Agree and 7= Strongly agree) split by if they were/were not members of a specialist angling club.*



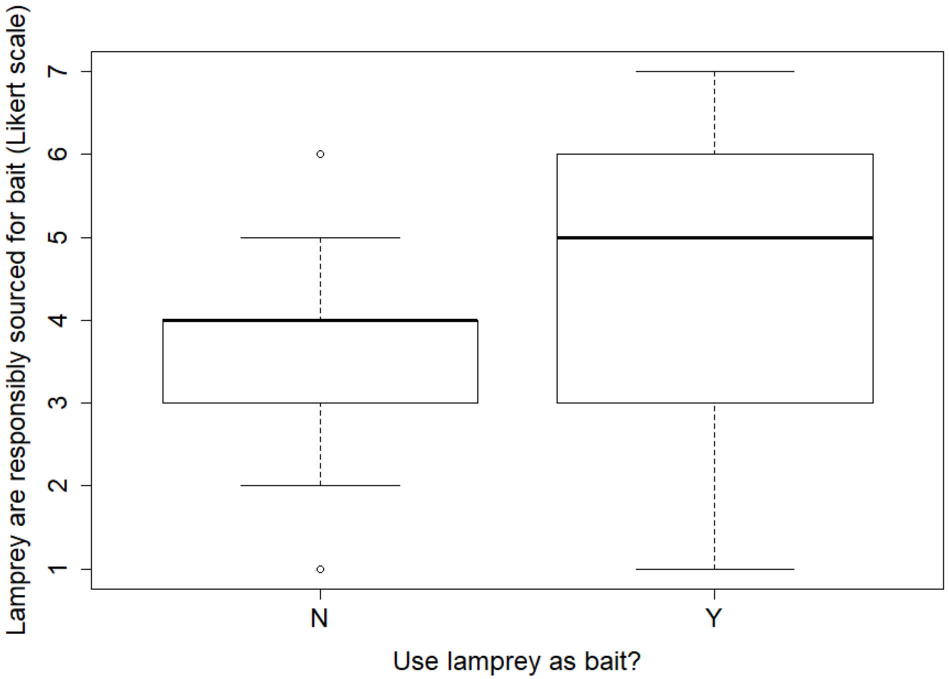
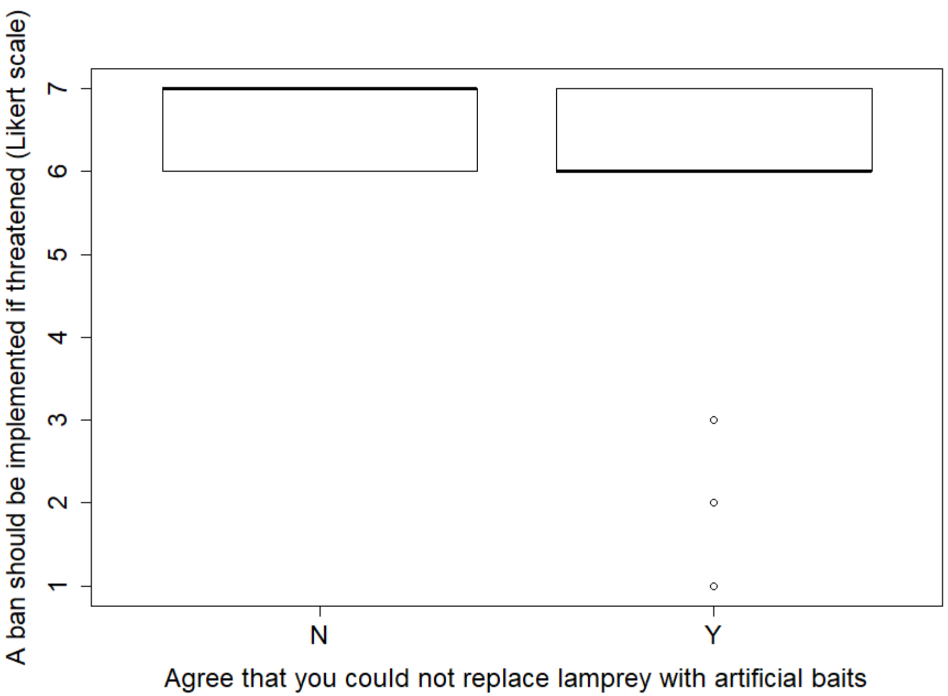




*Figure 3.13: Participants' opinion towards the statement "Lampreys are responsibly sourced for bait" (under a 7-point Likert scale where; 1= Strongly disagree, 2= Disagree, 3= Slightly disagree, 4= Neutral, 5= Slightly Agree, 6= Agree and 7= Strongly agree) split by if they were/were not members of an environmental organisation.*

*Figure 3.14: Participants' opinion towards the statement "Lampreys are responsibly sourced for bait" (under a 7-point Likert scale where; 1= Strongly disagree, 2= Disagree, 3= Slightly disagree, 4= Neutral, 5= Slightly Agree, 6= Agree and 7= Strongly agree) split by if they did/did not use lamprey for bait.*



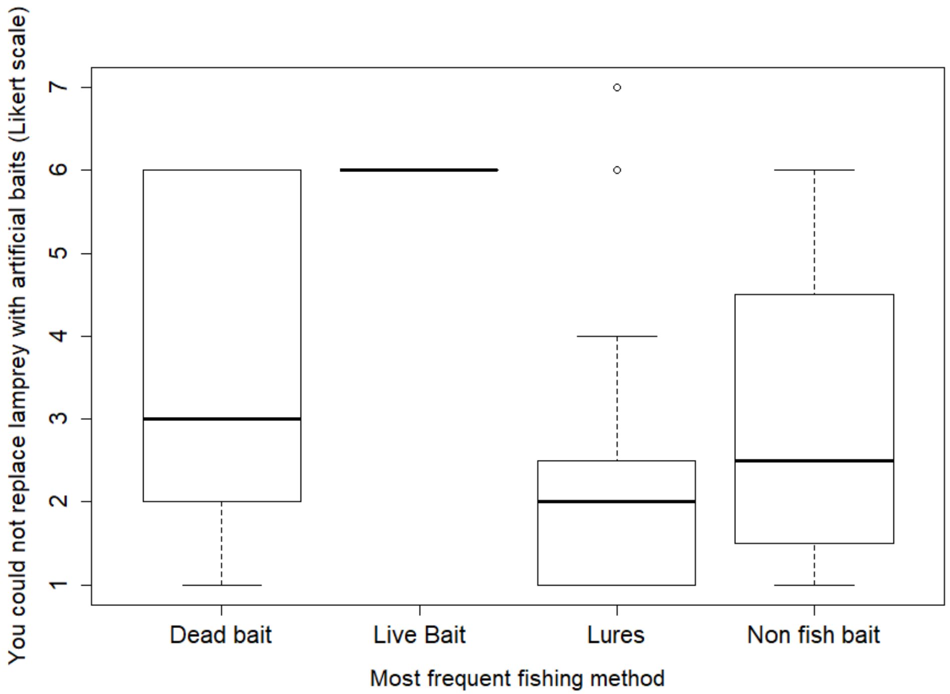




*Figure 3.15: Participants' opinion towards the statement "If lampreys were threatened by exploitation a ban on their use as angling bait should be implemented" under a 7-point Likert scale where; 1= Strongly disagree, 2= Disagree, 3= Slightly disagree, 4= Neutral, 5= Slightly Agree, 6= Agree and 7= Strongly agree) split by if they did/did not agree that lamprey could not be replaced with artificial baits to some degree.*

*Figure 3.16: Participants' opinion towards the statement "You could not replace lampreys with artificial baits for predator fishing and still catch as effectively" (under a 7-point Likert scale where; 1= Strongly disagree, 2= Disagree, 3= Slightly disagree, 4= Neutral, 5= Slightly Agree, 6= Agree and 7= Strongly agree) split by their most frequent fishing method.*

## 3.5. Discussion

### 3.5.1. Fishing behaviour

This study indicates that dead fish baits are the most common coarse predator fishing method in the UK. This is consistent with wider freshwater fishing behaviour across the UK and parts of Europe where natural baits are popular. This is in stark comparison to the USA where artificial lures are the predominant method (Radomski *et al*., 2005). Nonetheless, artificial lures are still commonplace in the UK. As the majority of participants commonly employ a variety of fishing methods, according to environmental conditions, it is likely that most anglers surveyed use artificial lures to some degree. Moreover, multiple participants said that their choice of fishing method was mood dependent, selecting artificial lures for a more active fishing experience and natural baits for a more passive one. This indicates that the angler's choice of bait varies due to personal factors aside from perceived effectiveness of baits.

Almost all coarse predator anglers surveyed practiced catch and release (C&R) near exclusively across all forms of fishing. This may be partly due to the implementation of mandatory C&R in waters owned by angling organisations. However, it is likely that the majority of this C&R is voluntary, as this is the prevalent attitude towards freshwater fishing within the UK (Smith, 2002). This is in contrast to continental Europe and the US where voluntary C&R is less frequent and is even illegal in Germany, where it is considered animal cruelty (Sutton, 2003; Arlinghaus, 2007). One reason for this could be a difference in angling motivations. Whilst American and European anglers are often motivated for consumption related reasons (Dorow *et al*., 2010; Schroeder & Fulton, 2013) UK anglers may be motivated for catch-oriented reasons such as the desire to catch large "trophy" fish (Arlinghaus & Cooke, 2009; Rees *et al*., 2017) or non-catch reasons such as the appreciation of nature (Holland & Ditton, 1992; Rees *et al*., 2017).

It appears that live bait is still frequently used within the UK coarse predator fishing community. This is alarming as the practice of live-baiting, more specifically the release of bait after angling sessions, has led to the global introduction of invasive species and novel pathogens into waterways (see section 3.2.). Within the UK specifically, live-baiting has resulted in the introduction of species such as roach (*Rutilus rutilus)* and ruffe (*Gymnocephalus cernua*) outside of their native range, with subsequent declines of indigenous fish populations or changes in the fish community structure (Winfield *et al*., 2011). Animal welfare issues regarding the practice have also been raised (Holmes, 2020). Consequently, legislation was introduced to control the use of live-bait, banning its use in Scotland and certain Cumbrian lakes as well as specifying that, although allowed within England and Wales, bait fish must be retained at and used only in the water from which they were taken (www.gov.scot; www.gov.uk). Thankfully, the majority of participants in this study claimed to be abiding by the current legislation.

In a similar vein, the use of species of conservation concern as angling bait is worrying. *Anguilla anguilla* has been subjected to high levels of exploitation from both recreational and commercial sources which has contributed to recorded declines in recruitment of over 90 % in recent decades (Dekker, 2003; Starkie, 2003). Despite its critically endangered status and protection in the UK, *A. anguilla* has been recorded as being used for bait in this study and can be brought frozen from retailers (Figure 3.17). The source of these eels is unclear and warrants investigation. *Anguilla anguilla* is listed on appendix II of CITES, therefore trade to or from the EU is faces legislative hurdles (Nijman, 2017). Now that the UK has left the EU, there is a pressing need to understand the origin of *A. anguilla* sold for bait in the UK.

A lesser known species that has been identified as being used for bait by a number of participants in this study is the pollan (*Coregonus pollan*). The exact taxonomic status of *Coregonus pollan* is unclear with many sources identifying the species to be a sub species of the Arctic cisco, *Coregonus autumnalis* (Behnke, 1972; Ferguson *et al*., 1978). However, in this study it is treated as a distinct species as this is how it is classified by both the ICUN and Fishbase (www.fishbase.in; www.iucnredlist.org). *Coregonus pollan* belongs to the Coregonidae and is endemic to Ireland where its distribution is limited to a mere five lakes (Harrison *et al*., 2012). Of these five populations only one, Lough Neagh (within Northern Ireland), still contains an abundance of *C. pollan* with all other sites displaying a marked decline of biomass in recent decades (Harrod *et al*., 2002; Rosell *et al*., 2004). *Coregonus pollan* has declined due to factors such as lake eutrophication and the introduction, potentially as a result of anglers releasing live baits, of *R. rutilus* that competes with *C. pollan* for food (Rosell *et al*., 2004; Winfield *et al*., 2011). *Coregonus pollan* is still commercially exploited, with a small fishery persisting at Lough Neagh (Rosell *et al*., 2004). This fishery is managed through regulations such as a gill net mesh size and minimum legal-size limit of 20.5 cm (Rosell *et al*., 2004; Fisheries Regulations (Northern Ireland), 2014). Most of the captured pollan are exported to Switzerland (BBC, 2018).

However, this study has revealed that *C. pollan* are also used as recreational angling bait with 7.25 % of participants stating that they used it as dead bait. Pollan is available from online bait retailers (Figure 3.18). Some of these retailers were contacted to enquire about the origin of this bait and whilst some stated that they came from Ireland, others refused to disclose their source. More alarming is that one site advertises pollan 17.8 to 22.9 cm in length. This minimum size is below the 20.5 cm minimum legal-size limit for both recreational and commercial fishing set by the Northern Ireland Fisheries Regulations (2014). If these pollan are sourced from Lough Neagh (the only known commercial fishery) then this is in violation of said regulations. With the continued survival of *C. pollan* populations in question (Rosell *et al*., 2004) it is vital to closely examine the source and scale of this exploitation. It should also be investigated whether or not fish labelled as pollan are indeed *C. pollan* rather than other members of the Coregonidae such as vendace (*Coregonus vandesius* and *C.*

*albula*). This may be problematic as members of this family display complex phenotypic plasticity, rendering morphological identification unreliable (Etheridge *et al*., 2012). Electrophoretic analysis of tissue proteins can provide crude results (Ferguson, 1974). However, genetic analysis with nuclear or mtDNA is preferred as it can clearly distinguish between species of the Coregonidae although the power to distinguish subspecies is often weaker (Horreo, 2017).

*Figure 3.17: Example of European eel* (Anguilla anguilla*) frozen and sold as angling bait. Image reproduced from http://www.baitbox.com/*

*Figure 3.18: Example of fish labelled as pollan (*Coregonus pollan*?), frozen and sold as angling bait Image reproduced from http://www.baitbox.com/*

Participants' opinions regarding the comparison of natural and artificial baits may explain the preference towards dead fish baits. Overall, they slightly agreed that natural baits caught larger fish than artificial baits, consistent with a previous study of American anglers (Hunt & Ditton, 1998). Fish size has been shown to be a significant factor affecting the motivations of UK predator anglers (Rees *et al*., 2017). This may explain the prevalence of dead fish baits because catch orientated trophy anglers select natural dead baits to maximize their perceived chances of catching larger fish. This opinion is partially supported in the literature with Arlinghaus *et al*. (2008) showing that natural dead baits caught significantly larger *E. lucius* than artificial lures. However, this may be due to the large size of the natural baits used, as bait size was also found to affect the size of fish caught (Arlinghaus *et al*., 2008). Anglers also only slightly agreed that natural baits resulted in a higher chance of deep hooking than artificial baits. This is in contrast to the scientific literature which consistently agrees that natural baits result in greater rates of deep hooking and post release mortality than artificial baits (Siewert & Cave, 1990; Arlinghaus *et al*., 2008; Weltersbach *et al*., 2019). This may be a result of anglers' tendency to de-amplify risks associated with activities that they enjoy, provided that acute effects are not immediately visible (Burger, 2000). Therefore, anglers may downplay the risk of deep hooking presented by natural baits in order to accept their use in the pursuit of catching larger fish.

An interesting point is that anglers slightly disagreed that natural dead baits result in fewer takes than artificial baits. Whilst Hunt & Ditton (1998) found that most anglers believed that natural baits caught more fish than artificial baits, Heerman *et al*. (2013) found that, for Eurasian perch (*Perca fluviatilis*), artificial baits result in a higher CPUE than natural baits. It could be that anglers are ignoring or discrediting the lower catch rates associated with natural baits. However, it is important to note that the majority of participants targeted *E. lucius*, a species known to demonstrate short term learned avoidance to artificial lures, but not natural baits, when intensively fished (Beukemaj, 1970; Arlinghaus *et al*., 2017). Consequently, this opinion may result from participants visiting already intensively fished sites, where the effectiveness of artificial baits may be limited.

### 3.5.2. Use and opinions of lamprey as bait

It is clear that the use of lamprey as bait is widespread within the UK coarse predator angling community, being used to some degree by 67.8 % of participants and known by the vast majority. The participants mainly used lamprey as bait for *E. lucius.* This is in line with a recent report on UK freshwater angling that shows *E. lucius* to be the 2$^{nd}$ most popular coarse predatory species targeted in the UK (the most popular coarse predatory species targeted was *P. fluviatilis*). In 2015 an estimated total of 1,720,000 days were spent fishing for *E. lucius* in 2015 (EA, 2018). However, anglers are a heterogenous group (see section 3.2.). Therefore, as this study explicitly questioned coarse predator anglers, it is possible that uses for lamprey outside of coarse predator fishing were not detected. For instance, lamprey is sporadically mentioned as bait for Atlantic cod (*Gadus morhua*) and Conger eels (*Conger conger*) across online UK sea angling media (see https://britishseafishing.co.uk). It is likely that a small market for lamprey as a sea bait exists.

Regardless, it appears that very few anglers would prefer lamprey bait to be sourced from outside of the UK. Over 39 % would explicitly prefer lamprey to be sourced from within the UK. Although studies comparing preference towards domestic or imported angling baits are lacking, these results do broadly compare with the wider view of UK consumers. They have been shown to prefer domestic goods, especially food items of which a British source was selected as a first choice 74.9 % of the time (Knight, 1999; Balabanis & Diamantopoulos, 2004). Coarse predator angling is popular in the UK, the Pike Anglers Club of Great Britain (PAC) has up to 2,500 members (PAC, pers comms). Coarse angling in the UK is even more so, with over 920,000 rod licences issued between 2018 to

2019 in England (EA, 2020) and a recent surge in angling interest due to the relaxation of lockdown restrictions (https://www.gov.uk). Therefore, it seems that this preference for UK sourced lamprey will support the operation of the current lamprey fishery present within the Humber River Basin (see section 1.6.3.3.).

A point to discuss is the mediocre view of lamprey's effectiveness as a bait held by most anglers that used lamprey. Participants disagreed that lamprey was cheaper than other natural baits (frozen lamprey retail for roughly £5 for a pack of two to three lamprey online) but were neutral towards the statement that lamprey resulted in more takes when angling for predatory fish. Although *E. lucius* are known to predate on *Lampetra* (Sandlund *et al*., 2016) this occurred in riverine habitat. Therefore, coarse predator anglers using *L. fluviatilis* as bait in enclosed waters would be using a bait that could not be naturally encountered by *E. lucius* in said area since the waters were enclosed. Despite this, many participants explicitly stated that they thought lamprey were a good angling bait. This belief in lamprey's effectiveness may be the result of influence from angling media. Lamprey are widely promoted as a good bait for *E. lucius* by various facets of angling media who claim that its "high blood content" creates a scent trail to attract predator fish (https://www.anglingtimes.co.uk) whilst Fickling (2012) regards lamprey to be a common prey item of *E. lucius* stating: "we were catching pike with them [lamprey] down their throats in 1973". This media influence may affect the purchasing decisions of anglers, leading them to purchase lamprey over other baits (Cao *et al*., 2014; Byrum, 2019). Discussions regarding the most effective method of catching fish are unsurprisingly commonplace in angling media but studies comparing the actual effectiveness of natural baits in angling are scarce (but see Arlinghaus *et al*. (2017) for a comparison of various artificial baits). As a result, a study into the effectiveness of different dead baits may be warranted to verify claims made by angling media.

Anglers may also view lamprey as a good bait as a result of their wider perspective of bait effectiveness. Eight participants, six of whom used lamprey as bait, believed bait effectiveness varied across fishing locations and sessions. Although no studies comparing the effectiveness of natural angling baits across multiple locations or conditions exist, it has been shown that the CPUE of *E. lucius* by anglers is significantly affected by behavioural and abiotic factors such as angling site, temperature and wind speed (Kuparinen *et al*., 2010; Arlinghaus *et al*., 2017). It could be speculated that participants' views that bait effectiveness varies across location and session actually result from abiotic factors affecting catch rates. These are then attributed to the bait by the angler. Consequently, to compensate for this perceived variability in bait effectiveness, anglers purchase lamprey to create a wide array of baits for use across numerous angling locations.

A concerning point uncovered by this study is that participants that used globally threatened species of fish for bait were more likely to use lamprey as bait. The continued use of species like *A. anguilla* for bait could indicate limited effectiveness of prior efforts to raise awareness to declines in abundance. On the other hand, the perceived value of scarcity (Hall *et al*., 2008) associated with declining species could promote the use of said species as bait. The illegal harvest of *A. anguilla* to meet demand has been well documented (Garcia & Sónia, 2014; Richards *et al*., 2020). This could in turn promote the use of *L. fluviatilis* as bait given its recent declines in commercial catches (Söberg, 2011). However, as most participants were unaware of lampreys' conservation status this scenario is unlikely. Rather, it is more likely that this use of threatened species (and associated use of lamprey) stems from anglers underestimating their environmental impacts (Gray & Jordan, 2010) and unintentional ignorance towards the status of fish populations across Europe. Increasing public awareness of bait fish declines within the angling community in addition to investigating the motivations of anglers using threatened species could reduce the use of threatened species for angling bait (Easman *et al*., 2018).

### 3.5.3. Knowledge regarding the origin of bait

Few participants knew the species of lamprey they used as bait. Only two participants correctly identified the species they used as river lamprey (*Lampetra fluviatilis*); the only species of lamprey currently known to be used as angling bait in the UK (Foulds & Lucas, 2014). This ignorance could be problematic given the widespread media attention on invasive *P. marinus* in the North American Great Lakes (Lucas *et al*., 2020). Media coverage plays a significant factor in raising public awareness and interest regarding non-native and invasive species (Gozlan *et al*., 2013). Thus, there is a risk that anglers are mis-informed about lamprey in the UK and use *L. fluviatilis* as bait under the misconception they are an invasive species. Improved public awareness of the lamprey native to the UK should reduce this risk.

Very few participants claimed to know the geographic source of the lamprey they used as bait. Foulds and Lucas (2014) estimated that, in 2001, the majority of lamprey for angling bait in the UK were sourced from the Netherlands and Estonia, but in 2012 the Netherlands implemented stringent regulations on lamprey bycatch landings from the Dutch eel fishery, effectively closing that source. Since there has been a moratorium in place on lamprey fishing in the Humber in recent years, at least one major wholesale bait supplier (Baitbox) was forced to exclusively import lamprey from Estonia (P. Bird, Baitbox, pers. comm). The opaqueness of the angling bait industry complicates locating the origin of dead fish baits as bait packaging lacks features that informs consumers of the baits' source. If the majority of lamprey are imported into the UK, there is a potential risk of disease transfer.

Lampreys are infected by a wide array of pathogens but appear quite disease resistant, possibly due to the replacement of their lymph nodes with lymphoid tissue regions (Jackson *et al*., 2019). Viral pathogens likely present the largest threat of disease transmission in angling bait. Finnish *L. fluviatilis* have been found to carry a strain of the negative strand RNA virus Viral Haemorrhagic Septicaemia (VHSV) and it is theorised that lamprey may act as a mechanical vector of VSHV into host fish (Gadd *et al*., 2010). Viral Haemorrhagic Septicaemia is known to cause mortality in salmonids and *E. lucius*, the latter of which can contract it through the ingestion of infected prey items (Ahne, 1985; Cabon *et al*., 2020). Moreover, industry standard for the preparation of angling dead baits is blast freezing to -21 ˚C, (BaitBox, pers comms). This is often insufficient to reduce viral loads of infected fish below the critical threshold (Pheles *et al*., 2013). Unfortunately, other treatment methods (such as injection of mineral oil or dehydration) will increase costs or reduce the suitability of bait (Herve-Claude *et al*., 2008; Pheles *et al*., 2013). As a result, the lack of knowledge regarding the origin of lamprey as bait creates a risk of anglers acting as vectors of disease through infected and insufficiently treated lamprey. Those that carry lamprey long distances and into other regions of the UK when angling pose the greatest risk of introducing disease into numerous waterways. The degree of disease transmission risk that previously frozen dead fish to UK waters poses relative to other angler-related sources such as on damp nets and un-sanitized equipment is open to question and has not been assessed.

### 3.5.4. Attitudes regarding lamprey conservation

Anglers are often a highly environmentally minded group, generally appreciating the value of the natural surroundings that they are surrounded by and commonly participate in citizen science programs or volunteer for conservation efforts (see section 3.2.). This mindset is reflected in the findings of this study as anglers overwhelmingly agreed that lamprey should be conserved and that, if threatened by exploitation, a ban towards the use of lamprey as angling bait should be implemented. Combined with the overall disagreement that lamprey could not be replaced with other natural or artificial baits, it seems that UK freshwater predator anglers will support conservation actions to protect UK stocks of lamprey if given sufficient evidence of their conservation status. However, the overall view is flawed by the heterogenous nature of angling groups.

The presence of a subset of anglers that value lamprey as angling bait more than others is indicated by aspects such as lamprey users agreeing that lampreys were responsibly sourced more than non-lamprey users, and that participants who thought lampreys could not be replaced with artificial baits were less likely to agree to a ban.

Coarse predator anglers who highly value lamprey as bait can be considered analogous to the highly eel-centric anglers identified by Dorow & Arlinghaus (2012). Such anglers were likely to dismiss their own impact on fish stocks (e.g., in the case of the current study, believing that lampreys are responsibly sourced) and less willing to accept restrictions (such as a ban) on their angling. In addition to this, even though the majority of participants practice voluntary C&R, the use of lamprey as dead bait ensures that these anglers are an inherently consumptive group and so are likely less accepting of regulation (Aas, 1995; Dorow *et al*., 2010). Therefore, it is likely that the subset of lamprey-centric anglers will oppose legislative restrictions to the use of lamprey as bait out of fear that it will negatively impact their fishing experience. When one considers that anglers generally oppose gear restrictions more than harvest-based restrictions such as length limits (Wilde & Ditton, 1991; Hunt & Ditton, 1998) and that anglers constitute a powerful lobbying force (Bate, 2001), this opposition could be sizable. Non-legislative methods may present a more desirable alternative to both environmental and angling groups.

One such technique could be voluntary restrictions by anglers. Education is often utilised to increase public awareness of conservation issues (Novacek, 2008) and provide a guide towards sustainable practice. An example would be the Marine Conservation Society's "Good Fish Guide" which recommends more sustainable sources of seafood to consumers (www.mcsuk.org). Meanwhile, anglers are often aware of, adapt to and comply with the best C&R practices available (Nguyen *et al*., 2013; Delle-Palme *et al*., 2016) and have been shown to be ready to socially sanction fellow anglers who do not follow best practices (Guckian *et al*., 2018). A speculative "Good Bait Guide" could be created and circulated throughout angling networks to install a voluntary set of “best bait practices” into the angling community, potentially reducing the use of threatened species such as *L. fluviatilis* as bait. Furthermore, participants expressed a strong desire that bait companies should source their bait sustainably. To my knowledge, no methods to validate the origin or sustainability of baits currently exist. This could be used to the economic benefit of bait suppliers as consumers often prefer certified sustainable or local goods (Jaffry *et al*., 2004; Forbes *et al*., 2009; Shao & Unal, 2019). In the case of seafood, consumers were willing to pay 14 % more for certified sustainable products and 12.6 % more for locally produced products (Zander & Feucht, 2018). The installation of certification schemes into the angling bait supply chain could improve transparency and increase revenue as long as it is supported by the angling community. Therefore, studies into anglers’ preference for and willingness to pay for certified sustainable baits are crucial to test the viability of this scheme.

However, a strategy focused solely on ensuring the sustainability of *L. fluviatilis* may be desired. Multiple participants expressed a preference towards purchasing hypothetical farmed lamprey. Multiple species of lamprey are currently artificially propagated for research and conservation needs (Feng *et al*., 2018; Kujawa *et al*., 2019; Moser *et al*., 2019). *Lampetra fluviatilis* is one such species, being reared in laboratory conditions to provide larvae for restoration attempts in Finland (Abersons, 2019; Aronsuu *et al*., 2019). Unfortunately, the obligatory parasitic flesh-feeding lifestyle of juvenile *L. fluviatilis* (see section 1.5.) prevents them from being reared to the adult stage in artificial conditions. However, artificial propagation could still provide larval/metamorphosing *L. fluviatilis*, which grow up to approximately 120 mm long (Hardisty & Huggins, 1970), as angling bait. Careful planning of propagation technique could reduce production time significantly. Barron *et al*. (2020) found that larval *E. tridentatus* fed with effluent waste water from the culture of salmonids (*Oncorhynchus mykiss*) combined with conventional diets of dry yeast and commercial fish feed grew faster than larvae subjected to conventional, pulse-based feeding regimes. They estimate that, under this combined feeding regime, the larval feeding period could be reduced from three to seven years to under two years even in high density conditions (680 larvae per $m^2$) (Barron *et al*., 2020).

Production of lamprey for bait within the controlled conditions of fish farms could provide two additional benefits. Firstly, through sequestering waste nutrients, larval lamprey can act as a biological filter to improve the quality of effluent water. Secondly, the rearing of lamprey within controlled conditions allows for efficient testing for contaminants or pathogens such as VSHV. This could allow bait suppliers to certify lamprey as virus free, a bait certification that has been shown to increase angler likelihood of purchase and willingness to pay (Vollmar *et al*., 2014). Although larval lamprey would be too small to use directly as bait for *E. lucius*, they may be suitable as bait for other coarse fish such as perch (*P. fluviatilis*) or chub (*Squalius cephalus*). Moreover, as lamprey are promoted in angling media for its “high blood content” which produces a large scent trail (https://www.anglingtimes.co.uk) these larval lamprey could be processed to create a bait supplement, products that are already widespread in the coarse angling community. This supplement could be applied to other baits in order to substitute the use of frozen pre-adult lamprey. Studies into the willingness to accept and pay for artificially propagated larval lamprey as bait or as a bait supplement to replace frozen pre-adult lamprey should be conducted.

# CHAPTER 4: General discussion

This thesis addressed two potential conservation issues affecting the exploited population of *Lampetra fluviatilis* within the Humber River Basin; passage effectiveness over an anthropogenic barrier through a fishway and customer demand for the exploitation of *L. fluviatilis* within the UK. This chapter summarises key findings of this thesis, sets them in a wider context and presents recommendations for future research.

## 4.1. Suitability of Naburn's semi-formalised nature-like bypass for *Lampetra fluviatilis*

Chapter two utilised PIT and acoustic telemetry to evaluate the attraction and passage efficacy of a semi-formalised nature-like bypass that had been designed with the intention of allowing adult lamprey and juvenile eel upstream passage at Naburn weir. As the first study of its type, it provided the opportunity to determine the more general suitability of this design for application elsewhere. It was found that although attraction efficiency was high, up to a minimum estimate of 70.8 % (calculated by the number of acoustically tagged lamprey that entered the bypass as a percentage of those who were detected downstream of the weir), passage efficiency was very low, at a minimum estimate of 5.38 % (calculated by the number of PIT tagged lamprey determined to have successfully used the bypass to travel upstream of Naburn weir as a percentage of the number of lamprey that were detected within the bypass during the period of time that the most upstream PIT antennas was operational). Unfortunately, the accuracy of these values is questionable due to equipment failure at the early stages of the study. As a result, both estimates, particularly passage efficiency, are likely underestimates. Furthermore, due to the change in PIT antennae setup across the study years and the damage inflicted to PIT antennas within the salmon ladder, confidence limits cannot be estimated for either estimate across the entire study nor can the bypass be compared with the on-site salmon ladder. Although this is an undesirable situation, it is important to note that the PIT antennas (particularly BP4 and those within the salmon ladder) could not have backups installed on site due to both the environmental conditions at Naburn quickly rendering the installation of new PIT antennas impossible and the fear of placing PIT antennas in close proximity to each other which would cause interference and thus affect the validity of results gathered.

Regardless of the likely underestimate of the passage efficiency, it is still far too low to recommend wider application of this bypass design. The bypass's low passage efficiency could result from unsuitable water velocities across the sluice-gate exit during periods of high stage, the same periods at which lamprey are most attracted within the bypass. However, it is possible that tagged lamprey exited the bypass through alternate routes such as directly over the bypass walls when they are inundated. As this thesis examined a semi-formalised nature-like bypass it is not representative of *L. fluviatilis*' performance across true nature-like bypasses, a form of fishway known to be suitable for weaker swimming species (Santos *et al*., 2005: Kim *et al*., 2016). No other existing bypasses intended for lamprey currently known in the UK.

Furthermore, chapter two indicates that although lamprey can pass Naburn weir directly, they appear to be reliant on periods of high river levels, when the weir is drowned out, to do so. This is problematic as Naburn weir is the tidal limit of the River Ouse and so is the first major anthropogenic barrier encountered by adult lamprey migrating upstream through the Ouse. Consequently, low river levels producing poor passage at Naburn weir could impact population recruitment within the River Ouse. with potential ramifications for the lamprey population of the Humber River Basin as a whole (Jang & Lucas, 2005; Masters *et al*., 2006). Previous studies have indicated that most lamprey species perform poorly across a variety of technical fishways (see section 2.2.). However, there are exceptions. Low gradient, high discharge vertical slot fishways have been demonstrated to provide suitable passage to a range of lamprey species. For instance, a 1:38 slope vertical slot fishway was found to provide a passage efficiency of 78-100 % for pouched lamprey (*Geotria australis*)

(Lucas *et al*., 2020) whilst *P. marinus* was recorded to show a passage efficiency of 31 % across a vertical slot fishway installed at the Coimbra dam, Portugal, with 50,000 lamprey recorded using said fishway to successfully traverse the dam over a four year period (Pereira *et al*., 2017; Pereira *et al*., 2019). *Lampetra fluviatilis* also seems to have little trouble passing vertical slot fishways with Adam (2012) showing that 88 % of *L. fluviatilis* successfully utilised such a fishway situated on the River Elbe, Germany. Vertical slot fishways could provide sufficient passage to lamprey across anthropogenic barriers. However, the low gradients required increases the total length of the fishway, subsequently increasing construction costs (Mallen-Cooper *et al*., 2008). Consequently, cheaper solutions to poor passage may be desired by governing bodies.

Methods such as the translocation of migrating adult/sub-adult lamprey directly to suitable spawning grounds may present a temporary stopgap. However, they are unlikely to ensure long-term sustainability of lamprey populations within the Humber River Basin or other river basins. Additionally, research into retro-fitting anthropogenic barriers to increase lamprey passage or designing lamprey-suitable fishways results in remarkably low-tech, low-cost solutions when compared to the options available to aid salmonid passage such as the “Salmon Cannon” (Garavelli *et al*., 2019). In the case of the retrofitting of studded tiles onto weirs it is thought that the tiles will improve passage of both eels and lamprey under the assumption that, as anguilliform fish, they have similar swimming performances (Vowles *et al*., 2017). However, eels and lamprey have been shown to have noticeably different passage performance across low cost retrofit solutions such as studded tiles or bristles (Kerr *et al*., 2015; Vowles *et al*., 2017; Tummers *et al*., 2018; Lothian *et al*., 2020;).

This study advocates for the wide scale evaluation of lamprey swimming performance across current fishways and retrofit modifications in order to design better fish passage solutions. This evaluation of swimming performance must be conducted on as many species of lamprey as possible. This is to combat the current literature focus on *P. marinus* and

*E. tridentatus* because lamprey display species specific differences in both swimming form and behaviour (Moser *et al*., 2015). Once effective bypass or retrofit designs are identified, in order to locate the anthropogenic barriers with the greatest need for improved passage performance, a site-by-site analysis of lamprey ranges should be undertaken in a manner similar to Nunn and Cowx (2012). However, fishway construction may not be required across every barrier. The removal of anthropogenic barriers must always be considered, especially in the case of antiquated or redundant barriers, as this provides optimal passage to all fish species and help restore natural hydrological processes (King & O' Hanley, 2014).

## 4.2. Consumer's view of *Lampetra fluviatilis'* use as angling bait

In chapter three, angling societies and networks were contacted in order to investigate the proportion of predator anglers that use lamprey as bait within the UK through telephone questionnaires. Their knowledge and opinions regarding the use of lamprey as bait were also examined. This study aimed to supplement the findings of Foulds & Lucas (2014) who examined the Humber River Basin lamprey fishery and investigated the structure of the lamprey bait market within the UK. The current study found that 95.6 % of participants were aware that lamprey are used as angling bait and that 67.8 % of participants used lamprey as bait to some degree. Lamprey were overwhelming used as bait for freshwater predatory fish, mostly *E. Lucius.* This is concurrent with the findings of Foulds & Lucas (2014). However, other potential uses for lamprey in the UK may have been missed as a result of targeting predator angling societies and networks, ignoring other aspects of angling such as marine angling societies. In addition to this, the targeting of predator angling societies may affect the validity of the study's findings if members of angling clubs have a significantly different use and opinion of lamprey to the general angling public in the UK. However, it would not be feasible to target anglers who do not belong to angling clubs in order to verify this due to a lack of contact details.

Overall, anglers preferred their lamprey to be sourced from the UK, agreed that lamprey should be conserved and were favourable towards a potential ban of the use of lamprey as angling bait. However, the study also indicated the existence of a subset of anglers who greatly value lamprey as an angling bait and believe that lamprey are sustainably sourced. These anglers may be more opposed to a potential ban on than other groups of anglers.

This preference towards UK sourced lamprey has multiple potential impacts. A preference for UK sourced and for sustainable baits could be used to drive increased sustainability and traceability within the UK bait market through the introduction of certification schemes which increase the willingness to pay of consumers (Jaffry *et al*., 2004; Forbes *et al*., 2009; Zander & Feucht, 2018; Shao & Unal, 2019). Traceability in particular is an issue identified by Foulds & Lucas (2014). In order to assess the potential impact of bait certification schemes onto preference to buy and WTP it is imperative to research the opinions of the UK angling community towards sustainable, local or farmed natural baits.

However, this preference for lamprey sourced from the UK could also have wider impacts on the commercial lamprey fishery present within the Humber River Basin. Foulds and Lucas (2014) found that the majority of lamprey, 76 %, used for angling bait within the UK are imported, mostly from the Netherlands, though following changes in legislation the main exporter is now Estonia (see section 3.5.3.). Under the current situation where the UK has left the EU, the potential impacts on the importation of angling bait into the UK are unknown. If imported lamprey become restricted or more expensive, bait suppliers may source an increased percentage of lamprey from the UK. Lamprey exploitation is currently regulated under the UK Marine and Coastal Access Act (2009) whereby annual quotas of 1044 kg of *L. fluviatilis* can be taken from the tidal River Ouse and 206 kg can be taken from the River Trent between November 1$^{st}$ to December 10$^{th}$. These quotas and restrictions do not apply to other waterways within the UK where lampreys are found such as Loch Lomond

(Maitland *et al*., 1994), although as an SAC for lampreys Lomond also has stringent regulation capability. Therefore, a preference for UK lamprey and restrictions against the importation of lamprey from the EU could push commercial lamprey exploitation out of the Humber River Basin and into other UK waterways, increasing pressure on UK lamprey populations. It is recommended that an assessment of lamprey populations (both *L. fluviatilis* and *P. marinus*) is conducted across the UK to predict what sites could support a commercial fishery (if any) so that pre-emptive management actions can be designed.

In conclusion, the prevalence of lamprey as bait within the freshwater predator angling community and the preference for UK sourced lamprey indicates that the current commercial lamprey fishery will continue and possibly expand. The generally favourable disposition of the angling community towards the conservation of lamprey and sustainability of angling baits could spearhead a movement to increase transparency and sustainability within the UK angling bait market.

## 4.3. Wider perspectives

When considering chapter two's findings in the context of fish passage globally, some conclusions can be drawn. Firstly, that weak-swimming species often suffer from poor upstream passage over anthropogenic barriers (Noonan *et al.*, 2012). This is widely known in the scientific community but there is a continued bias in fishway design towards salmonids (Noonan *et al.*, 2012). Given the multitude of ecological functions non-salmonids can provide, such as invasive species control and nutrient transfer (MacAvoy *et al*., 2009; Syväranta *et al*., 2009; Brönmark *et al*., 2010; Musseau *et al*., 2014), it is vital to improve passage of weaker swimming species. However, making the assumption that sufficient fish passage will be provided by the mere presence of a fishway not specifically designed for salmonids is flawed as species-specific differences in swimming performance affects passage success over fishways or retro-fit modifications to barriers (Noonan *et al.*, 2012; Kerr *et al*., 2015). Therefore, evaluation of weaker swimming species' swimming performance over a wide variety of taxa should be conducted in order to better design and implement fishways to provide multi-species passage.

Chapter two's results also emphasise the importance of environmental variability, specifically high river stage conditions, to successful upstream fish passage. Anthropogenic barriers are often constructed to standardise river levels and reduce the likelihood of flooding events (Entec, 2010; Birnie-Gauvin *et al*., 2017). Unfortunately, flooding events are important to multiple fish species, particularly migratory fish who utilise high stage events to pass anthropogenic barriers and reach suitable habitat (Schmetterling, 2001; Agostinho *et al*., 2004; Baumgartner *et al*., 2014). Migratory species often time migrations to coincide with suitable conditions, such as high river stage, (Enders *et al*., 2009). Thus, it may be advantageous to promote high stage events during migration periods using anthropogenic barriers. This could improve passage of migratory fish species across anthropogenic barriers and also pre-emptively provide a buffer for the effects on river levels predicted from increased climatic variability (Arnell, 2003; Pendergrass *et al*., 2017).

Chapter three's results can be applied to conserving exploited species. Whilst the studies regarding the impacts of exploitation often focus on exploitation for human consumption (see Haas *et al*., 2019), less obvious sources of exploitation, such as recreational fishing, should also be examined. It is clear that the anglers contacted during the study knew little about the lamprey they used as bait (see section 3.4.). This indicates that education could raise awareness of both stakeholders and the general public, a factor that is often crucial in determining the success of conservation efforts (Meffe, 2002; Vogler *et al*., 2017). In turn, this could be applied to other problematic aspects of recreational fishing where anglers may be unintentionally ignorant of the ecological impacts of their actions such as the spread of disease and non-native species from the release of baits (see section 3.2.). The importance of education and awareness is applicable outside of recreational fishing. Raising public awareness and engagement of the effects of exploitation such as commercial fishing should be encouraged as the resulting consumer response can increase industry sustainability (Forbes *et al*., 2009; McClenachan *et al*., 2016; Hoffmann *et al*., 2018; Shao & Ünal, 2019).

# Appendices

## Appendix I: Angler Questionnaire

Prior to beginning questionnaire flip a coin, the results determine which version of potentially socially sensitive questions is used. Heads = **Bold text**, Tails = <u>Underlined text</u>.

**Introduction:** My name is Atticus Albright and I'm from the University of Durham. I am conducting a series of interviews in order to investigate British anglers' views on freshwater predator angling baits. Would you be willing to help me by completing a 20 to 30 minute long telephone questionnaire? Participation in this study is completely voluntary. This conversation will be recorded and a transcript made, however all participants will be kept anonymous and you can withdraw your consent from this questionnaire at any time. Data obtained from this questionnaire will be retained for two years. Do I have your consent to continue?

*Yes*- Thank you very much, I shall begin the recording now (begin recording). This questionnaire will consist of mostly multiple choice options but there will be an open section near the end for you to illustrate any point you wish to raise. For future reference you will be given an personal identity code. Your code is (X), kindly remember it for future contact. Have you made a note of your code? (*Go to 1*)

*No*- Thank you, have a nice day. (*Terminate questionnaire*)

**1)** Please confirm that you fish for predatory freshwater species (such as pike, perch, zander and catfish)
*Yes (go to 2)*
*No (Terminate questionnaire)*

**2)** During last year's season, how often did you go predator fishing on average?
A) Never *(go to 3)*

B) Less than once a month *(go to 3)*

C) Once a month *(go to 3)*

D) Once a week *(go to 3)*

E) More than once a week *(go to 3)*

**3)** In which area of the UK do you fish most frequently?

A) Scotland *(go to 4)*

B) Northern Ireland *(go to 4)*

C) Wales *(go to 4)*

D) Northern England *(go to 4)*

E) Southern England *(go to 4)*

**4)** May I ask if you are a member of a specialist angling club (such as the Pike Anglers Club of Great Britain)?

Yes *(go to 5)*

No *(go to 5)*

**5)** Can I ask if you or any member of your household is a member of one or more environmental/conservation organisations or charities (such as the RSPCB or WWF)?

Yes *(go to 6)*

No *(go to 7)*

**6)** Does that organisation (or one of them) specialise in conservation of waterways (such as the Canal and River trust)?

Yes *(go to 7)*

No *(go to 7)*

**7)** What fishing method do you most often use when predator fishing?

A) Live fish bait *(go to 8)*

B) Dead fish bait *(go to 8)*

C) Lure - including flies *(go to 8)*

D) Non fish bait such as shrimp, worm etc *(go to 8)*

E) Tend to use several of the above according to place/conditions - If so, which? *(go to 8)*

**8)** When using live fish bait, do you obtain your bait at the same water you intend to fish at?

Yes *(go to 9)*

No *(go to 9)*

**9)** Across all forms of fishing, how often do you practice catch and release?

A) Always *(go to 10)*

B) Often *(go to 10)*

C) Sometimes *(go to 10)*

D) Rarely *(go to 10)*

E) Never *(go to 10)*

**10)** Please describe your opinion on the following statements under the scale; Strongly agree, Agree, Slightly agree, Slightly disagree, Disagree, Strongly disagree.

**A)** Artificial baits are more expensive than natural (*go to B*)

**B)** Natural deadbaits result in fewer takes than artificials (*go to C*)

**C)** Natural deadbaits tend to catch bigger fish than artificials (*go to D*)

**D)** Predators are more likely to be deep hooked by natural live and deadbaits than artificials (*go to 11*)

**11)** When using natural baits, what species of fish do you often use for predator bait? *Open question (go to 12)*

**12)** Are you aware that lamprey is used as a predator bait?

Yes *(go to 13)*

No *(go to 13)*

**13)** When using natural deadbaits, how often do you use lamprey?

A) Always *(go to 14)*

B) Often *(go to 14)*

C) Sometimes *(go to 14)*

D) Rarely *(go to 14)*

E) Never *(go to 22)*

**14)** Could you specify what predator species you target whilst using lamprey as bait? *Open question (go to 15)*

**15)** Do you take lampreys with you on fishing trips to other nations within the UK (e.g. from Wales to England), or to Ireland?

Yes *(go to 16)*

No *(go to 16)*

**16)** Do you have other uses for lamprey besides predator fishing?

Yes *(go to 17)*

No *(go to 18)*

**17)** Could you specify what else you use lamprey for? *Open question (go to 18)*

**18)** Do you know what species of lamprey you use as bait?

Yes *(go to 19)*

No *(go to 19)*

**19)** Could you specify what species of lamprey you most commonly use as bait?

A) River lamprey *(go to 20)*

B) Sea lamprey *(go to 20)*

C) Brook lamprey *(go to 20)*

D) Other, please specify *(go to 20)*

**20)** Can I ask for your opinion on the following statements using the scale; Strongly agree, Agree, Slightly agree, Slightly disagree, Disagree, Strongly disagree?

**A)** Lamprey is cheaper than other natural baits *(go to B)*

**B)** Lamprey is more difficult to use than other natural baits *(go to C)*

**C)** Using lamprey as bait results in more takes when fishing for predators than other natural baits *(go to D)*

**D)** Using lamprey tends to catch smaller-sized predator fish than other natural baits *(go to 21)*

**21)** Do you know where the lamprey you use are sourced from?

Yes *(go to 22)*

No *(go to 22)*

**22)** If given the choice, would you prefer that lamprey for bait come from the UK or EU?

UK *(go to 23)*

EU *(go to 23)*

No opinion *(go to 23)*

**23)** Please describe your opinion on the following statements under the scale; Strongly agree, Agree, Slightly agree, Slightly disagree, Disagree, Strongly disagree.

**A)** Bait companies **should not**/<u>should</u> source their bait in an environmentally sustainable fashion *(go to B)*

**B)** The government imposes too strict restrictions on UK anglers *(go to C)*

**C)** Lamprey are responsibly sourced for bait *(go to D)*

**D)** You could not replace lampreys with other natural baits for predator fishing and still catch as effectively *(go to E)*

**E)** You could not replace lampreys with artificial baits for predator fishing and still catch as effectively *(go to F)*

**F)** Lampreys **should**/<u>should not</u> be conserved *(go to G)*

**G)** Lampreys **have not**/<u>have been</u> sufficiently protected in the UK *(go to H)*

**H)** If lampreys were threatened by exploitation a ban on their use as angling bait **should** /<u>should not</u> be implemented *(go to 24)*

**24)** Are you aware of the conservation status of lampreys?

Yes *(go to 25)*

No *(go to 25)*

**25)** If there are any aspects of previous questions and answers that you would like to expand on, please do so now. Let me know if you need a reminder of the questions. *Open question (go to 26)*

**26)** May I ask what your age category is?

18 to 24 *(go to 27)*

25 to 34 *(go to 27)*

35 to 44 *(go to 27)*

45 to 54 *(go to 27)*

55 to 64 *(go to 27)*

65 to 74 *(go to 27)*

Older than 75 *(go to 27)*

**27)** Could you tell me what gender you identify as?

Male *(go to 28)*

Female *(go to 28)*

Other *(go to 28)*

**28)** What is your nationality? *Open question (go to 29)*

**29)** If it's not too much to ask, what is the highest degree of education you have obtained?

A) Pre-16 education with no qualification *(Terminate questionnaire)*

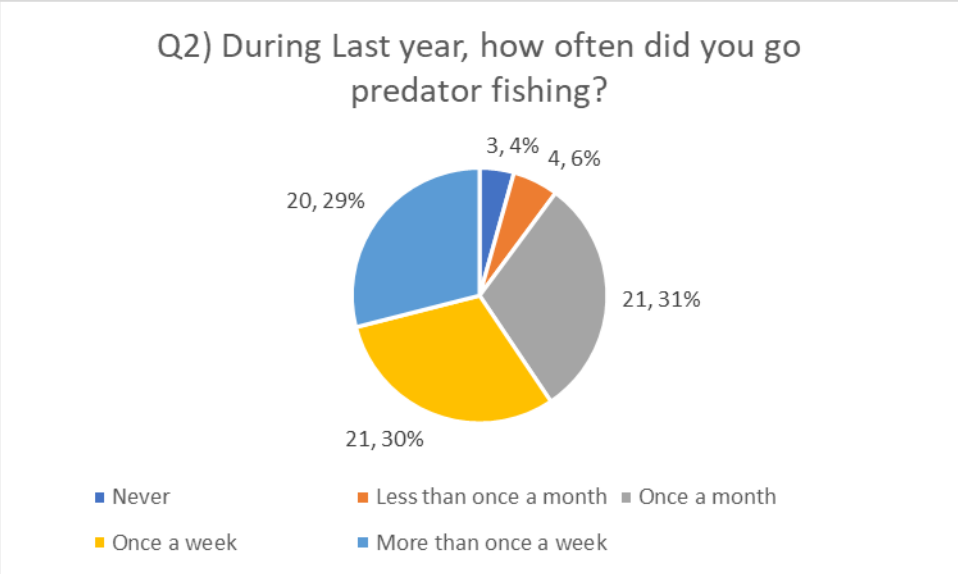
B) Post-16 education with qualification e.g. O'levels, GCSE *(Terminate questionnaire)*

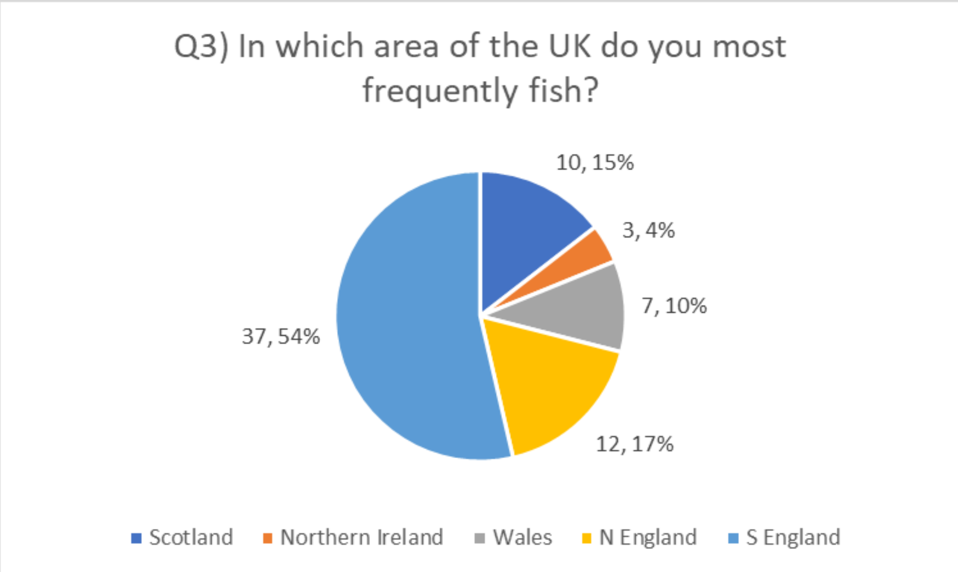
C) College diploma or similar *(NVQ, HND etc) (Terminate questionnaire)*

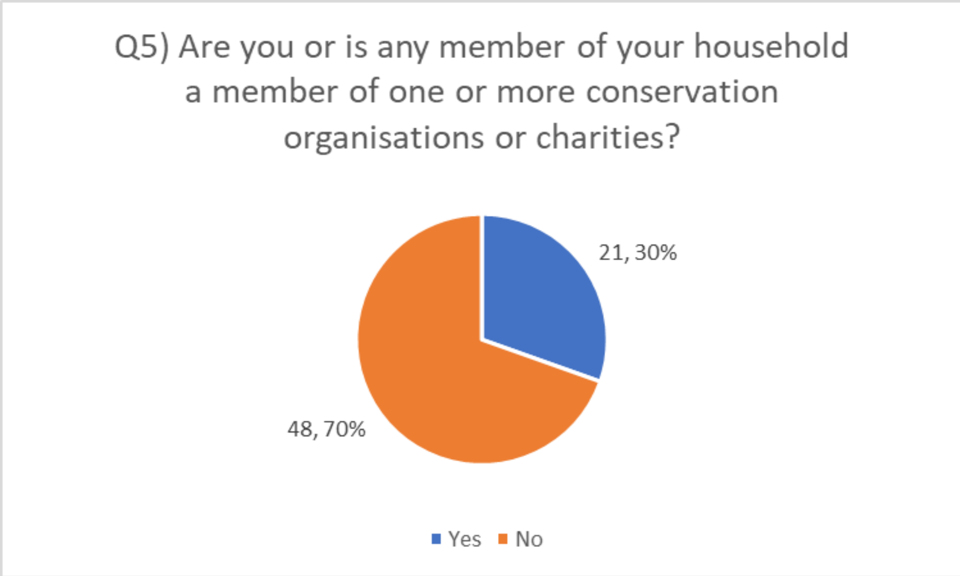
D) University degree *(Terminate questionnaire)*

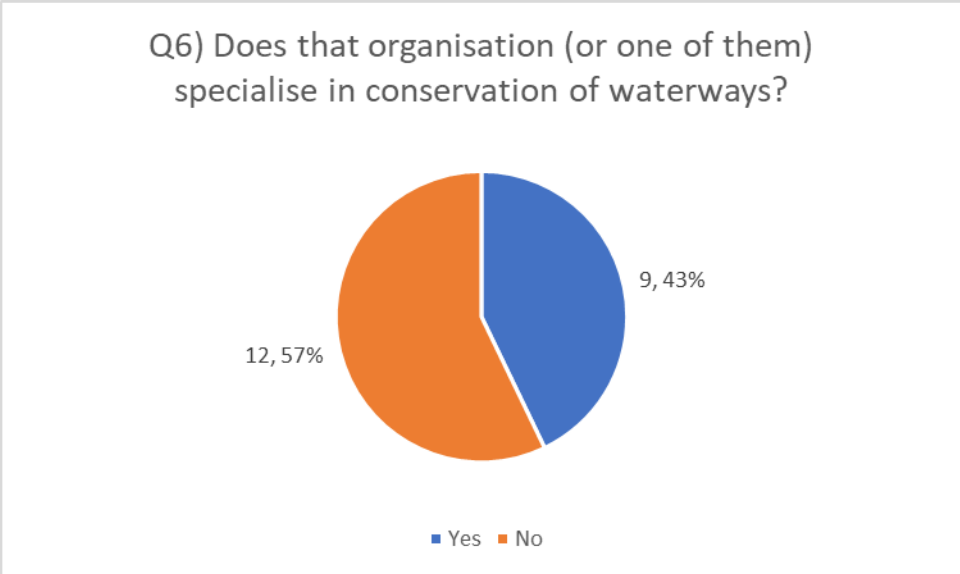
E) Specialist professional (but non-University) qualification *(Terminate questionnaire)*

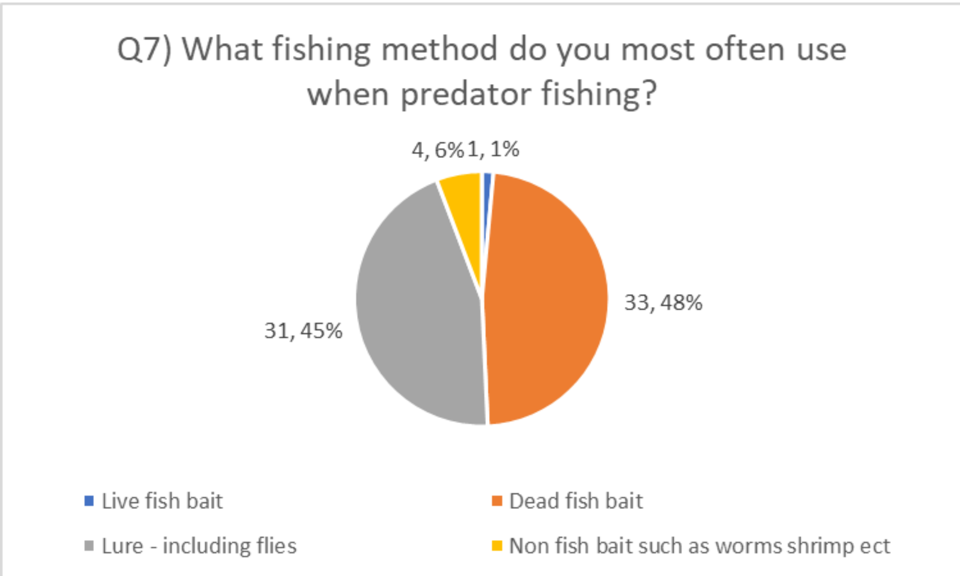
## Appendix II: Responses to Questionnaire

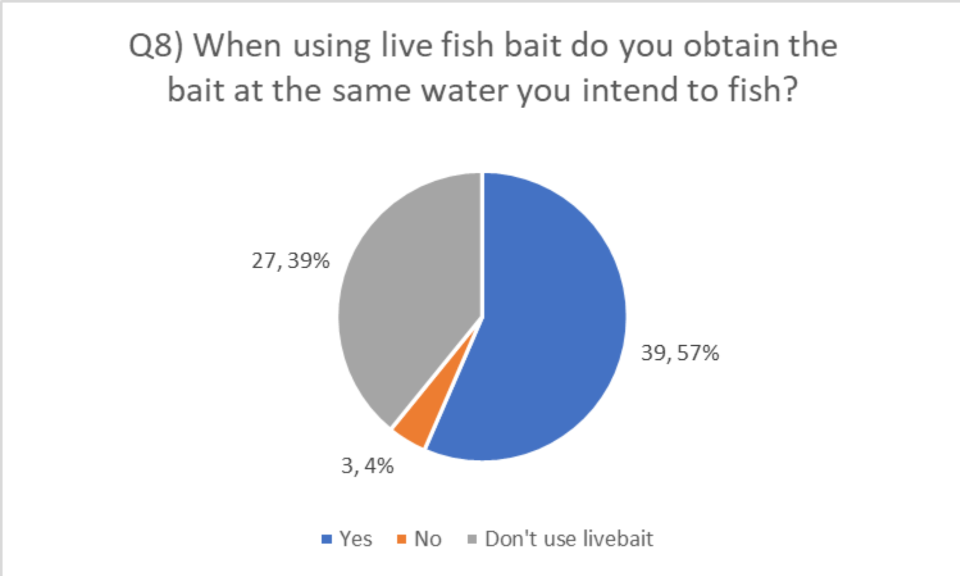


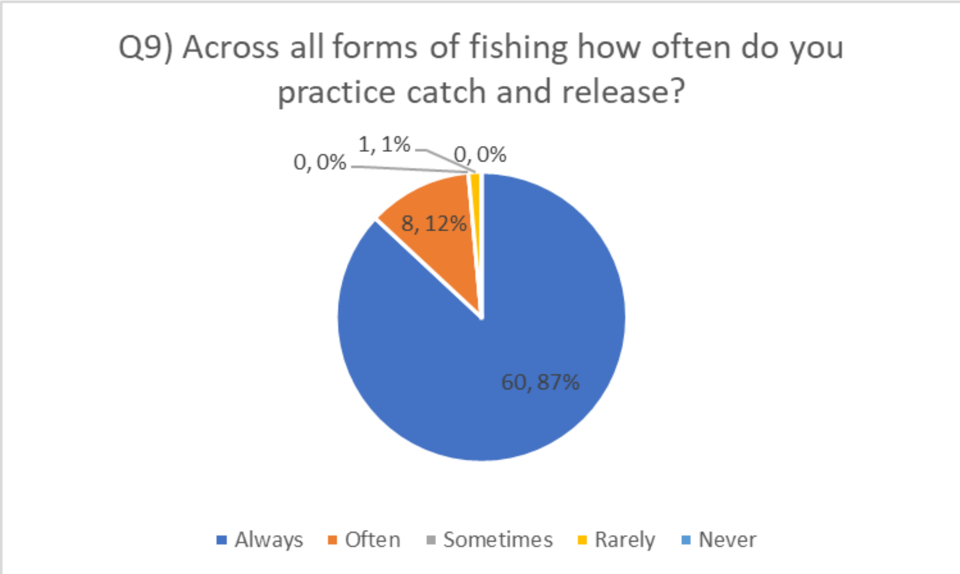



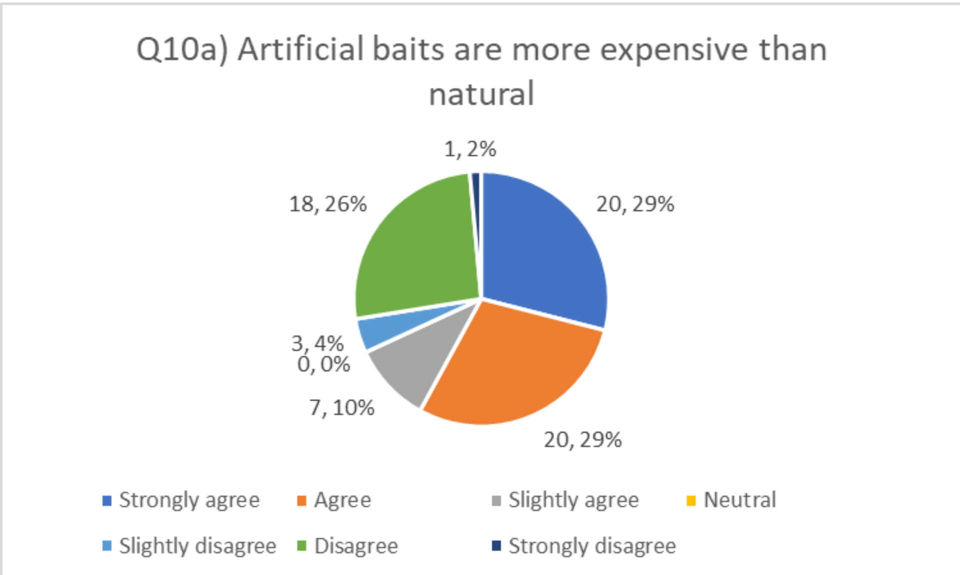


Q5) Are you or is any member of your household a member of one or more conservation organisations or charities?
21, 30%
48, 70%
Yes
No

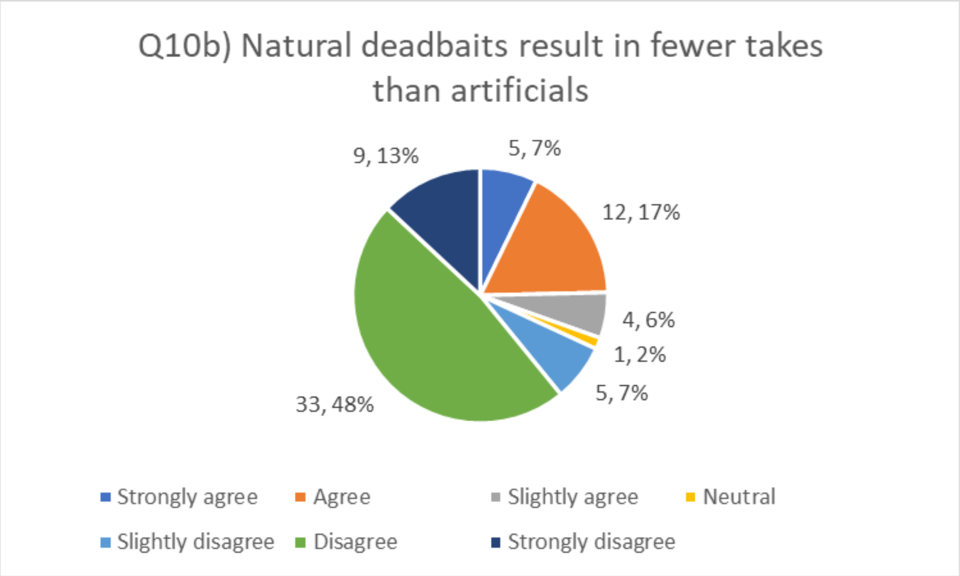

Q6) Does that organisation (or one of them) specialise in conservation of waterways?
9, 43%
12, 57%
Yes
No

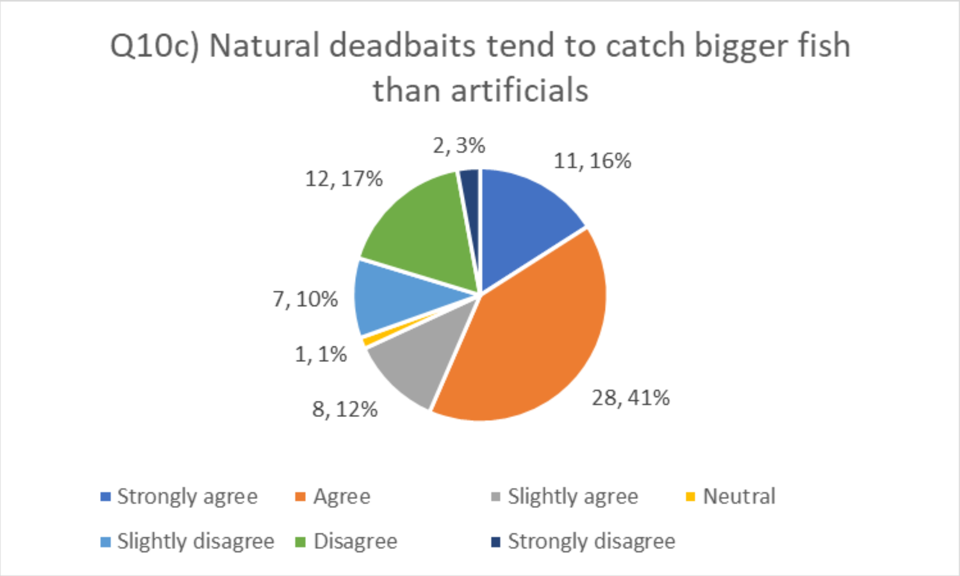

Q7) What fishing method do you most often use when predator fishing?
4, 6%
1, 1%
33, 48%
31, 45%
Live fish bait
Dead fish bait
Lure - including flies
Non fish bait such as worms shrimp ect

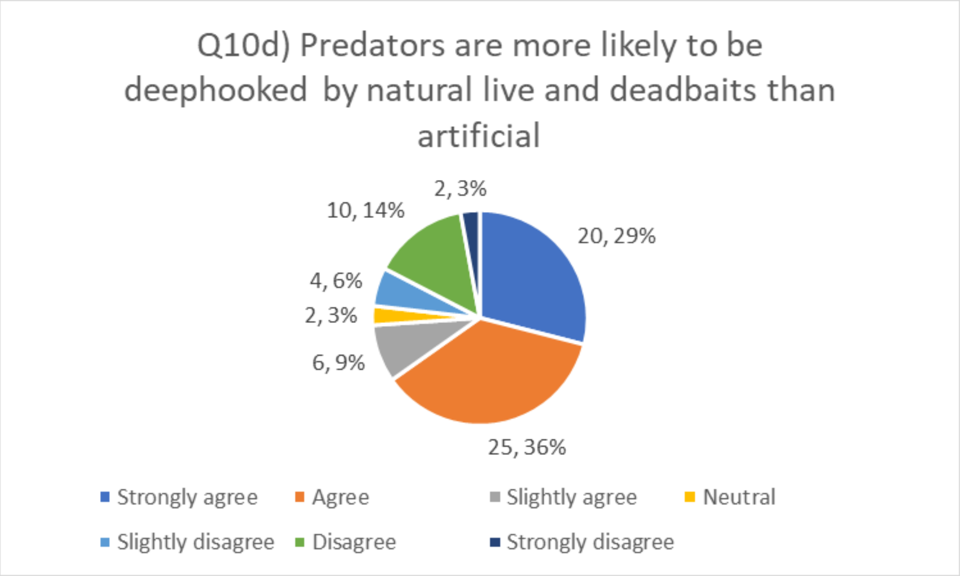

Q8) When using live fish bait do you obtain the bait at the same water you intend to fish?
27, 39%
39, 57%
3, 4%
Yes
No
Don't use livebait

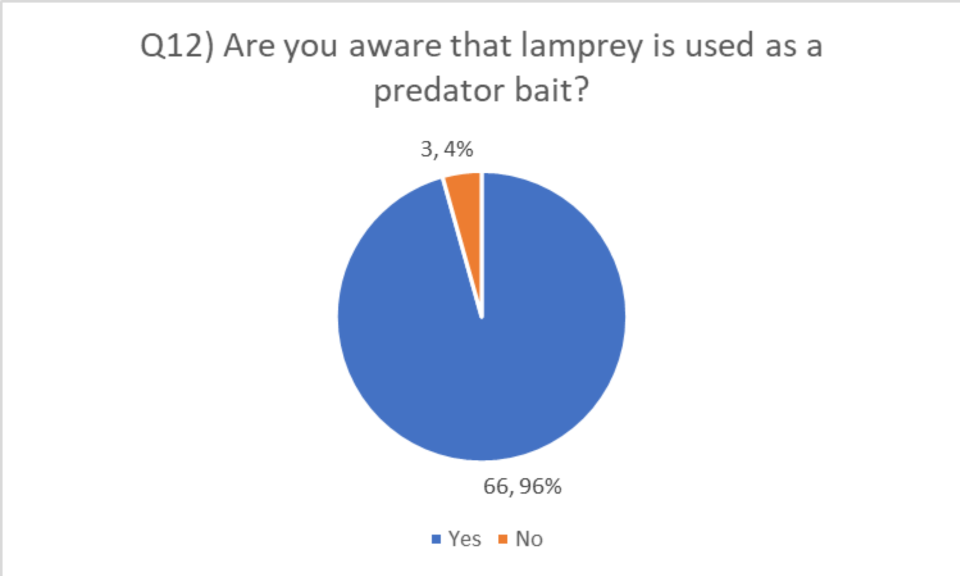

Q9) Across all forms of fishing how often do you practice catch and release?
0, 0%
1, 1%
0, 0%
8, 12%
60, 87%
Always
Often
Sometimes
Rarely
Never

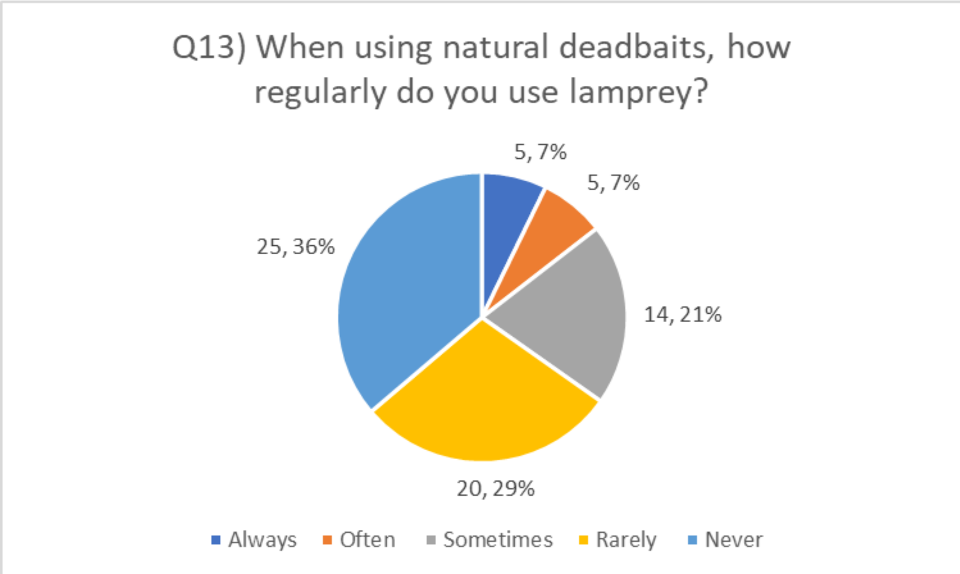

Q10a) Artificial baits are more expensive than natural
1, 2%
18, 26%
20, 29%
3, 4%
0, 0%
7, 10%
20, 29%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree

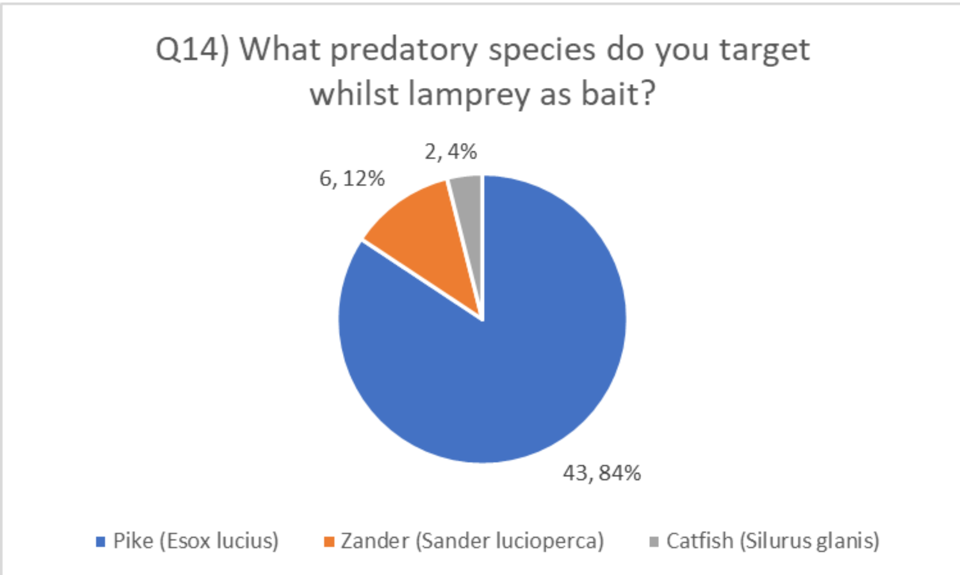

Q10b) Natural deadbaits result in fewer takes than artificials
5, 7%
12, 17%
4, 6%
1, 2%
5, 7%
33, 48%
9, 13%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree

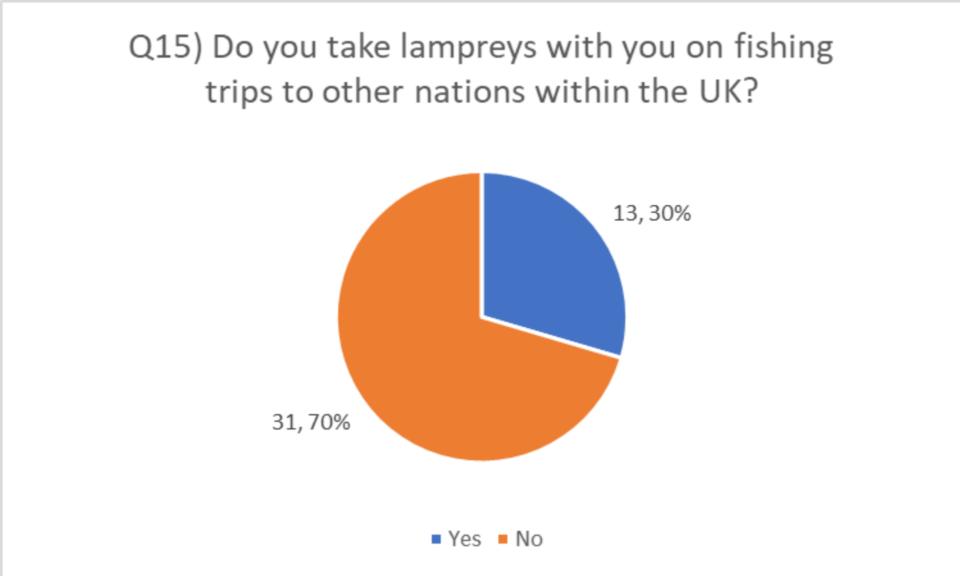

Q10c) Natural deadbaits tend to catch bigger fish than artificials
11, 16%
28, 41%
8, 12%
1, 1%
7, 10%
12, 17%
2, 3%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree


Q10d) Predators are more likely to be deephooked by natural live and deadbaits than artificial
20, 29%
25, 36%
6, 9%
2, 3%
4, 6%
10, 14%
2, 3%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree

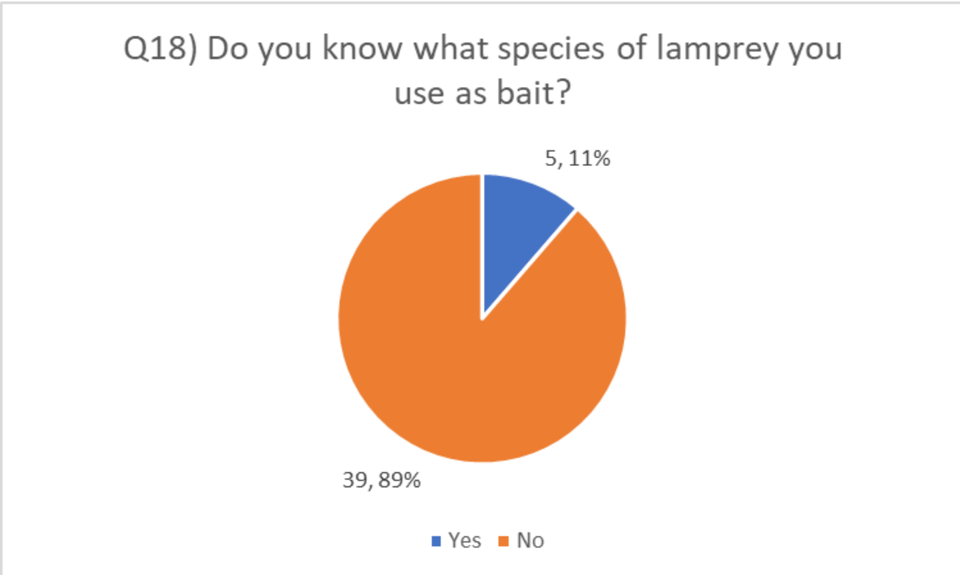

Q12) Are you aware that lamprey is used as a predator bait?
3, 4%
66, 96%
Yes
No

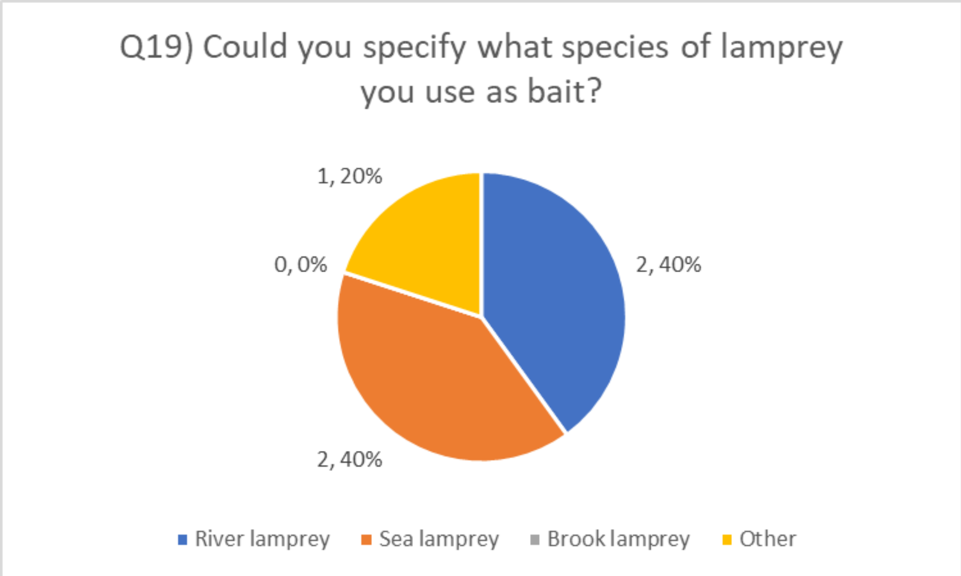

Q13) When using natural deadbaits, how regularly do you use lamprey?
5, 7%
5, 7%
14, 21%
20, 29%
25, 36%
Always
Often
Sometimes
Rarely
Never

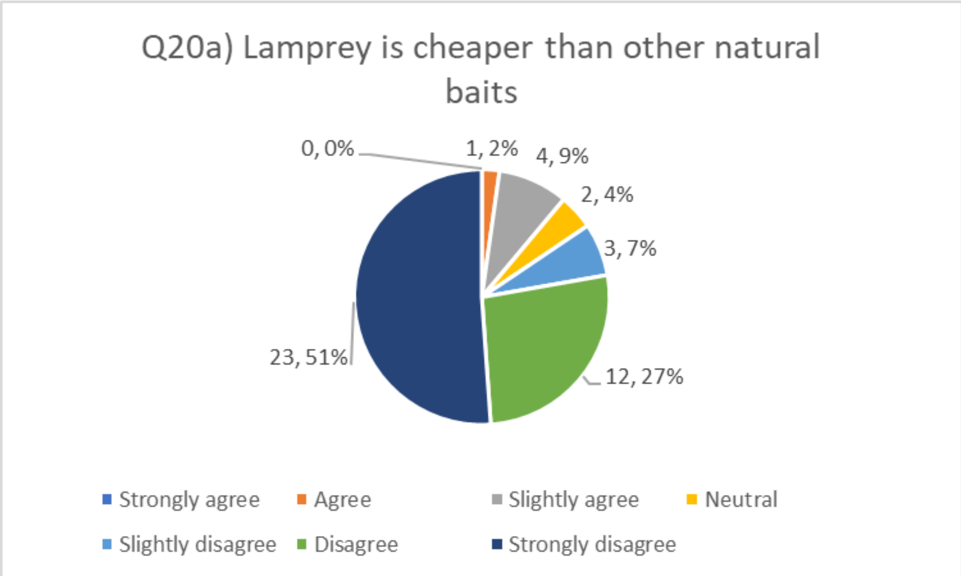

Q14) What predatory species do you target whilst lamprey as bait?
2, 4%
6, 12%
43, 84%
Pike (Esox lucius)
Zander (Sander lucioperca)
Catfish (Silurus glanis)

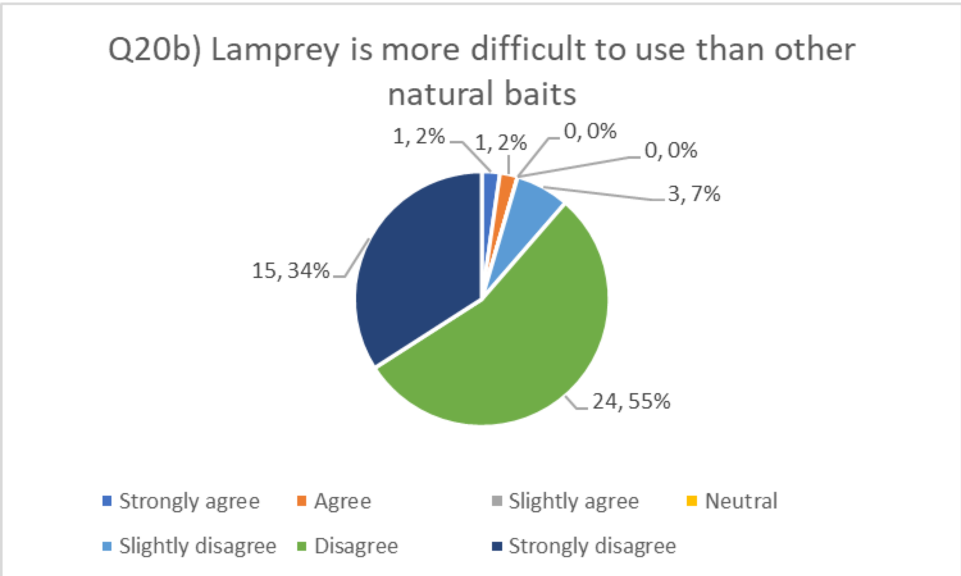

Q15) Do you take lampreys with you on fishing trips to other nations within the UK?
13, 30%
31, 70%
Yes
No

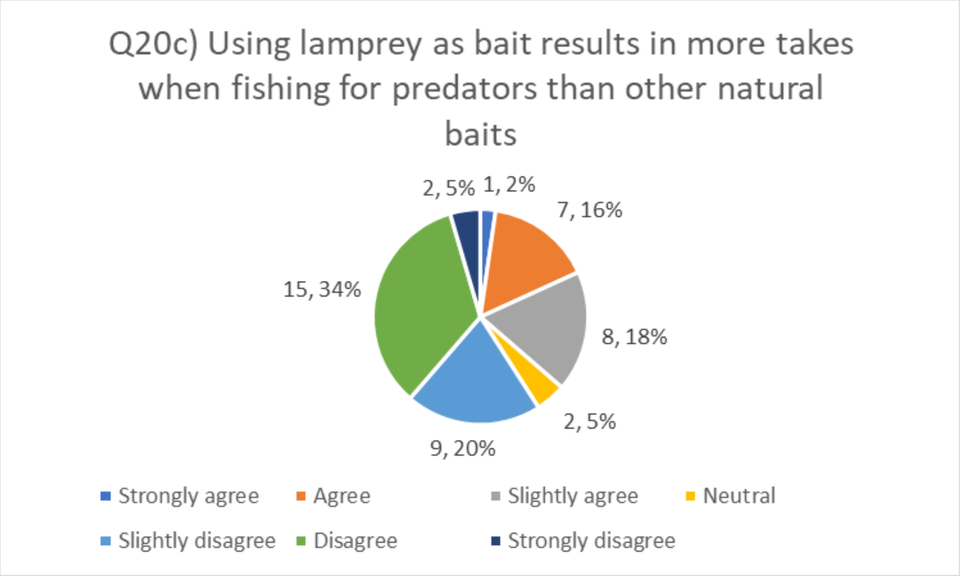

Q16) Do you have other uses for lamprey besides predator fishing?
1, 2%
43, 98%
Yes
No

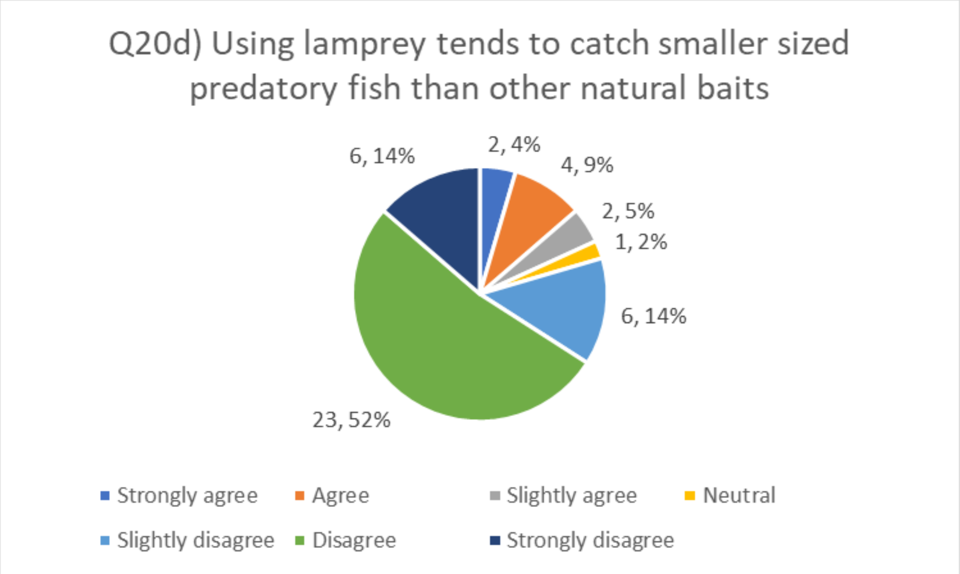

Q18) Do you know what species of lamprey you use as bait?
5, 11%
39, 89%
Yes
No

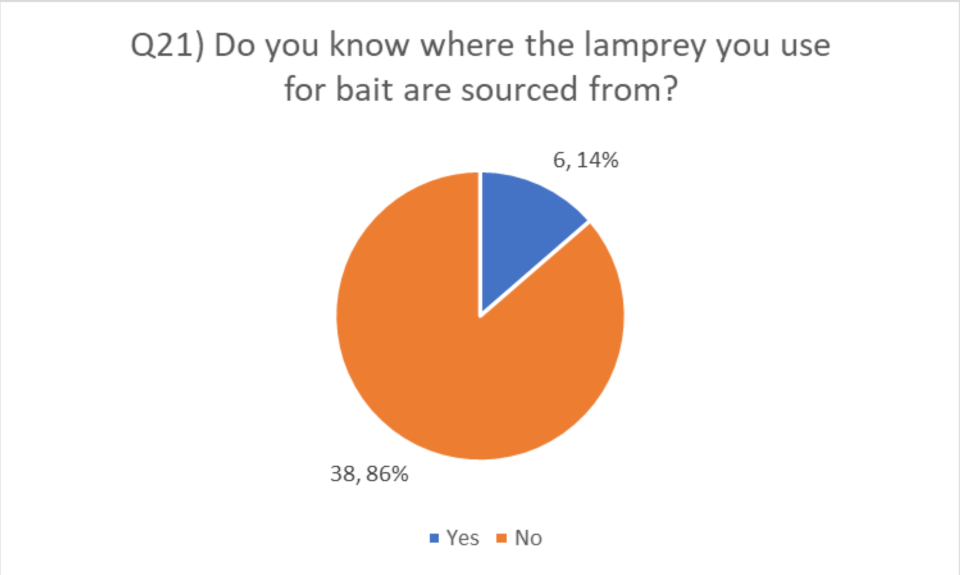

Q19) Could you specify what species of lamprey you use as bait?
1, 20%
0, 0%
2, 40%
2, 40%
River lamprey
Sea lamprey
Brook lamprey
Other

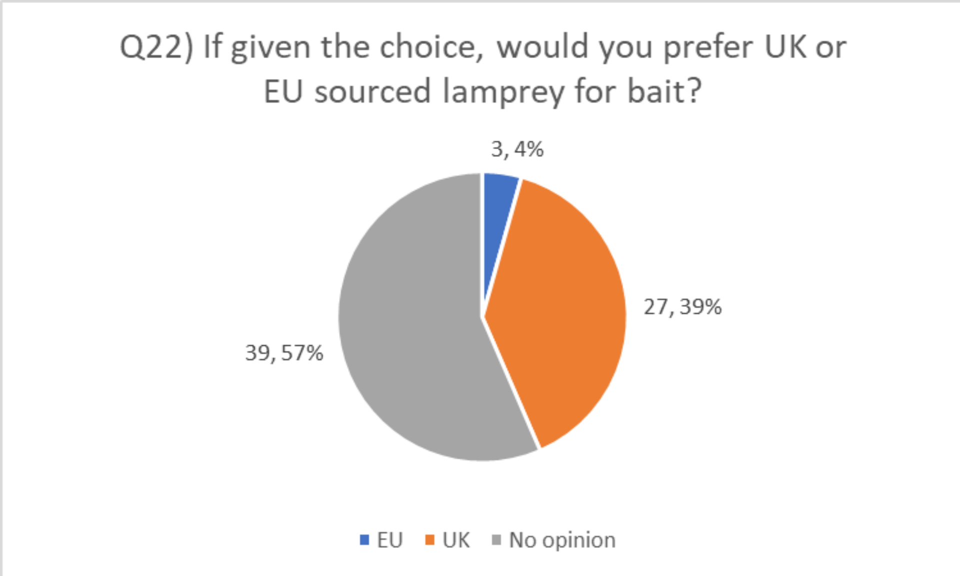

Q20a) Lamprey is cheaper than other natural baits
0, 0%
1, 2%
4, 9%
2, 4%
3, 7%
23, 51%
12, 27%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree

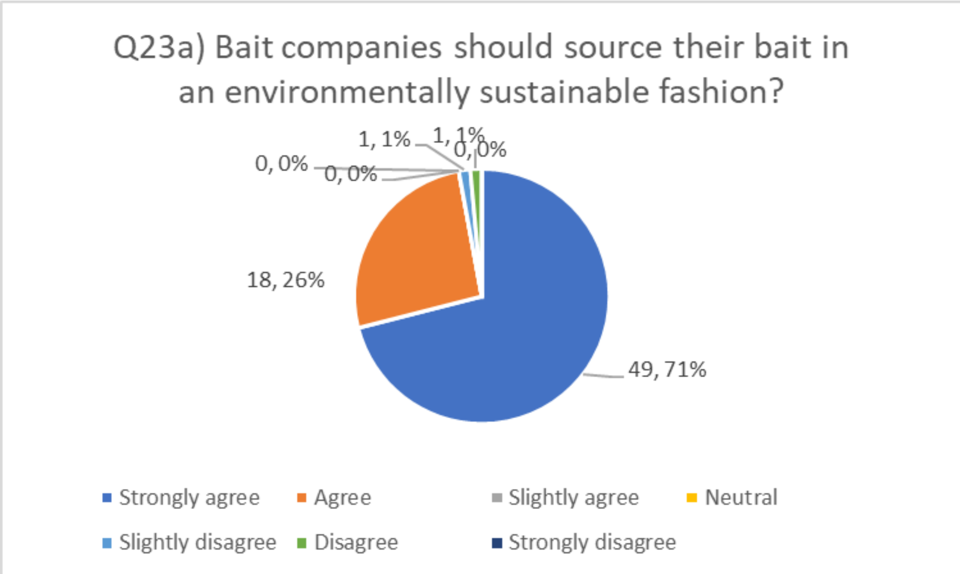

Q20b) Lamprey is more difficult to use than other natural baits
1, 2%
1, 2%
0, 0%
0, 0%
3, 7%
15, 34%
24, 55%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree

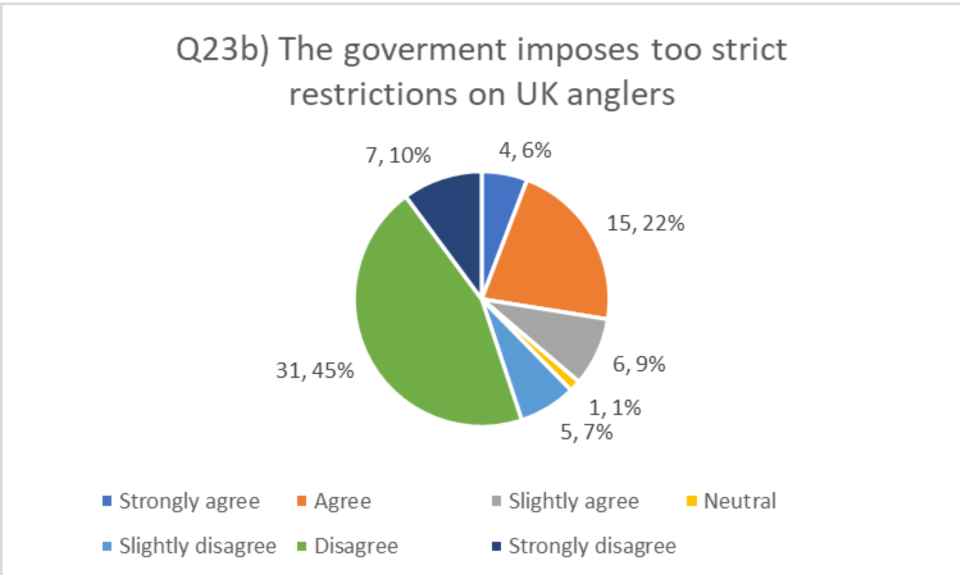

Q20c) Using lamprey as bait results in more takes when fishing for predators than other natural baits
2, 5%
1, 2%
7, 16%
15, 34%
8, 18%
2, 5%
9, 20%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree

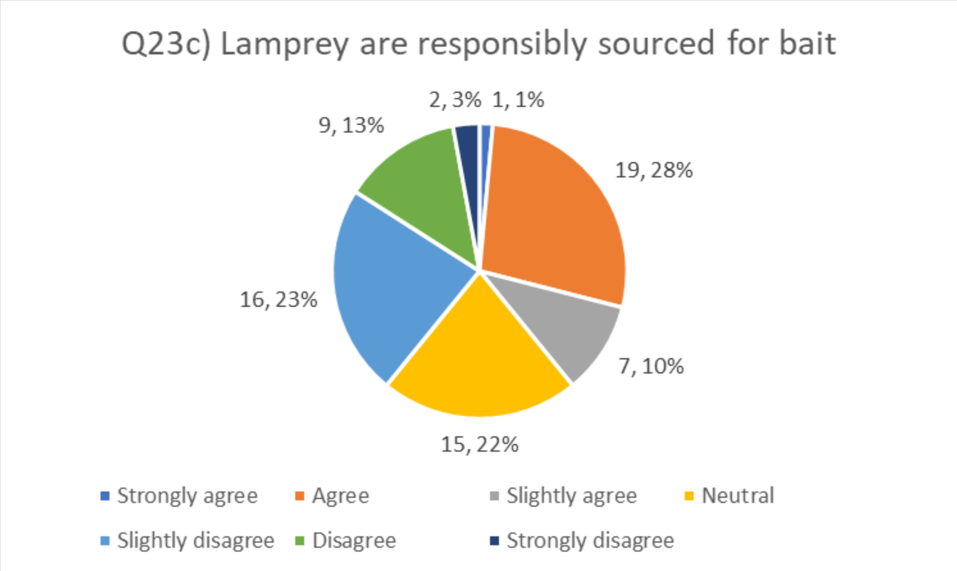

Q20d) Using lamprey tends to catch smaller sized predatory fish than other natural baits
6, 14%
2, 4%
4, 9%
2, 5%
1, 2%
6, 14%
23, 52%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree


Q21) Do you know where the lamprey you use for bait are sourced from?
6, 14%
38, 86%
Yes
No

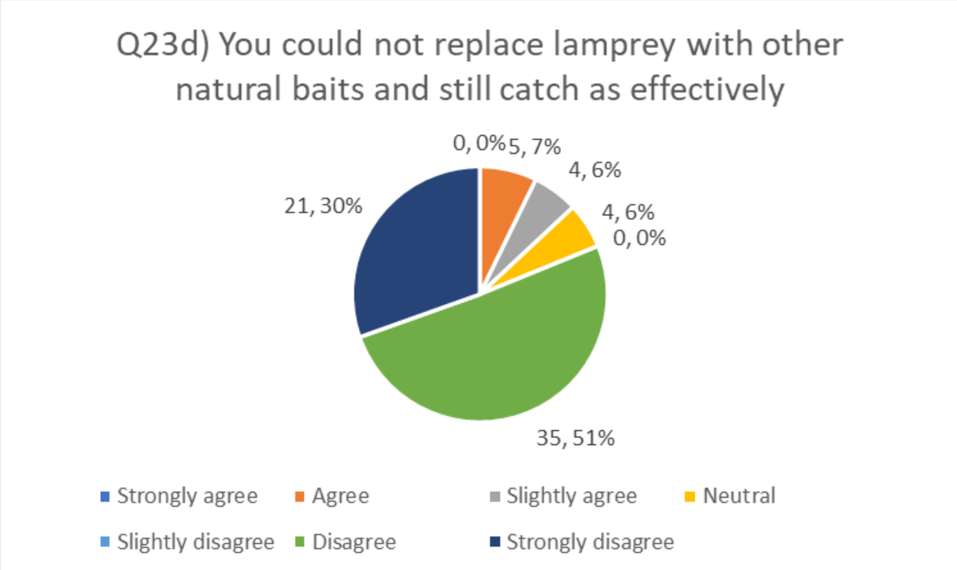

Q22) If given the choice, would you prefer UK or EU sourced lamprey for bait?
3, 4%
27, 39%
39, 57%
EU
UK
No opinion


Q23a) Bait companies should source their bait in an environmentally sustainable fashion?
1, 1%
1, 1%
0, 0%
0, 0%
0, 0%
18, 26%
49, 71%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree

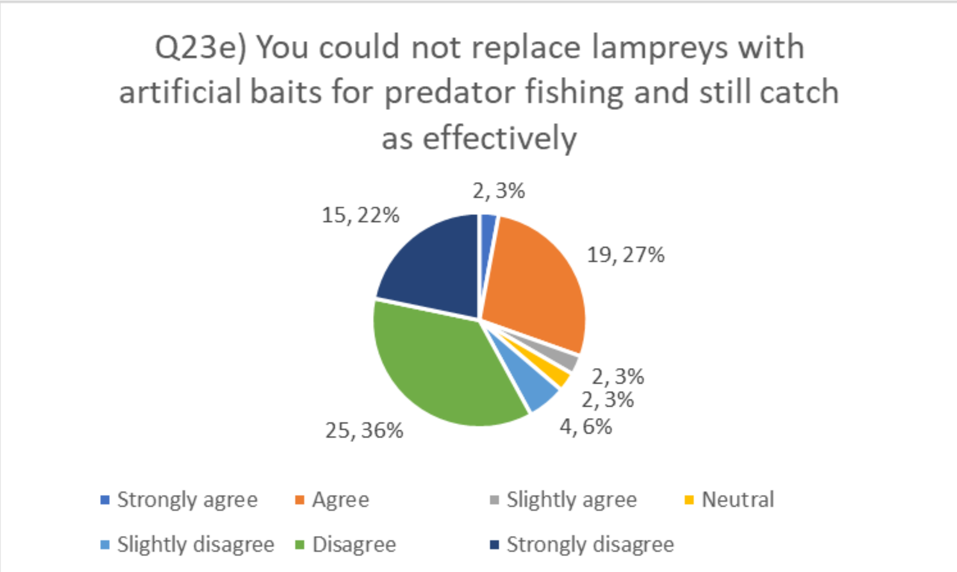

Q23b) The goverment imposes too strict restrictions on UK anglers
7, 10%
4, 6%
15, 22%
6, 9%
1, 1%
5, 7%
31, 45%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree



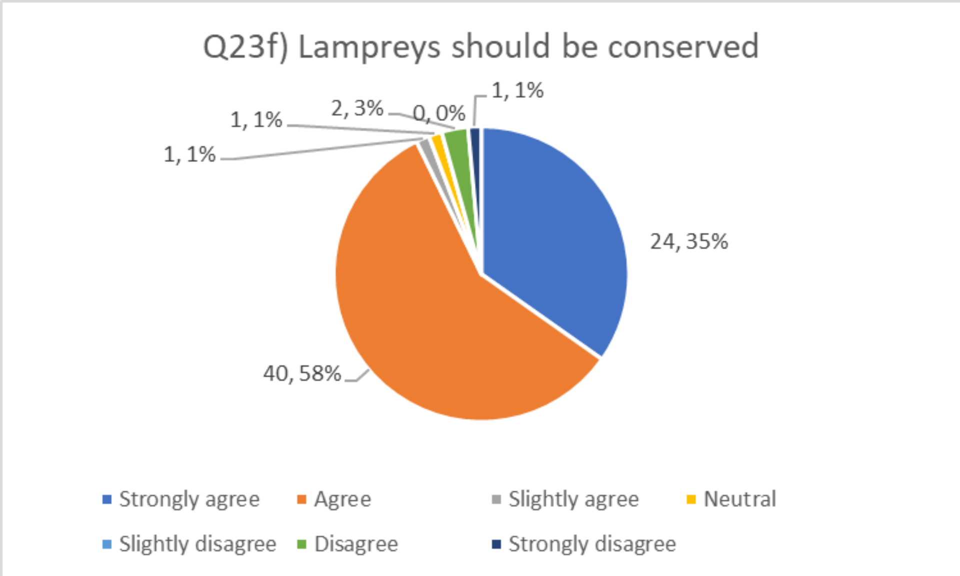
Q23c) Lamprey are responsibly sourced for bait
2, 3%
1, 1%
9, 13%
19, 28%
16, 23%
7, 10%
15, 22%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree

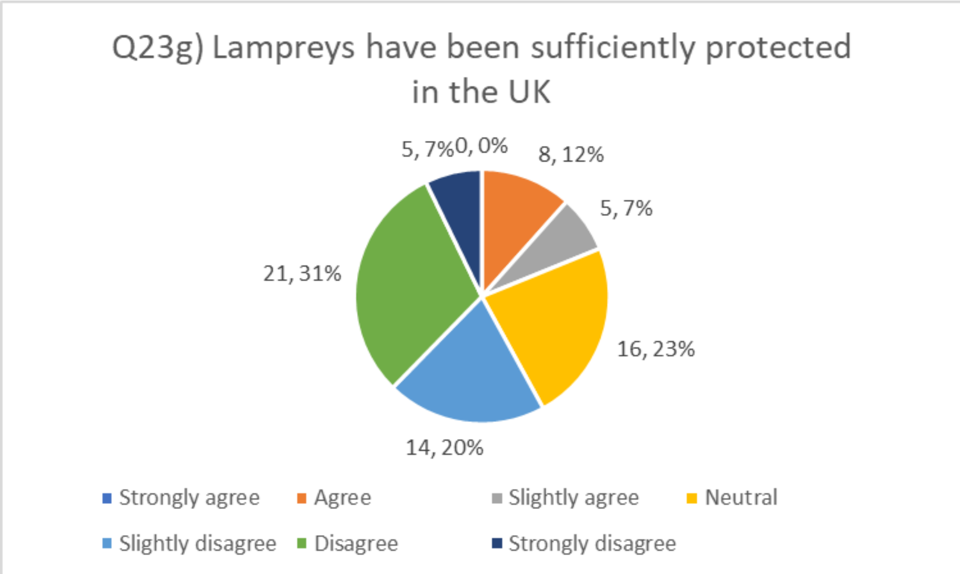



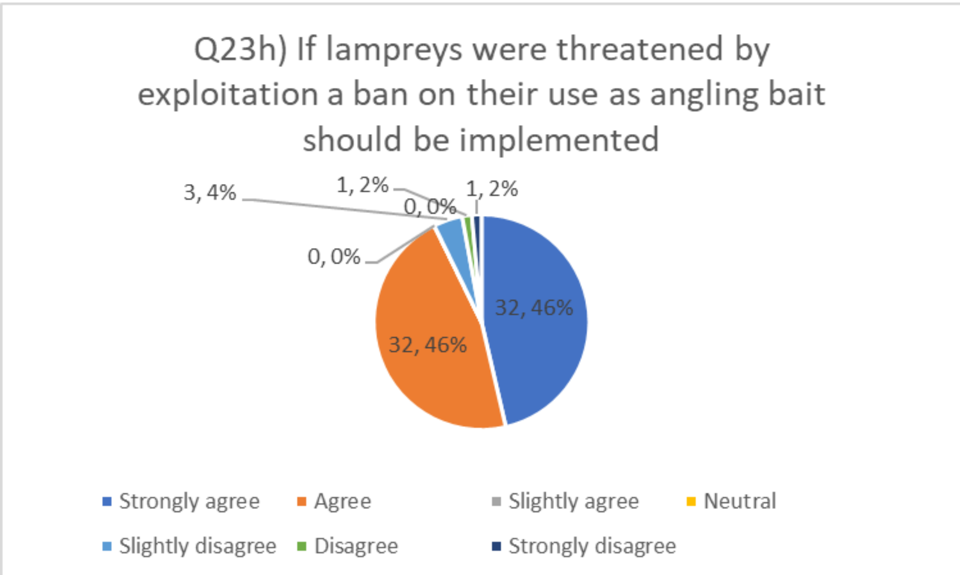
Q23d) You could not replace lamprey with other natural baits and still catch as effectively
0, 0%
5, 7%
4, 6%
21, 30%
4, 6%
0, 0%
35, 51%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree

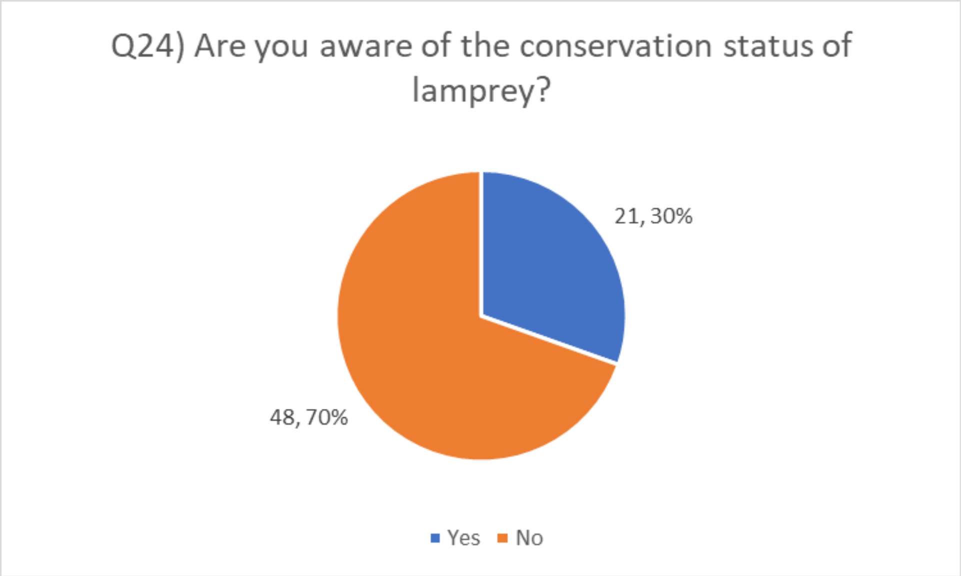



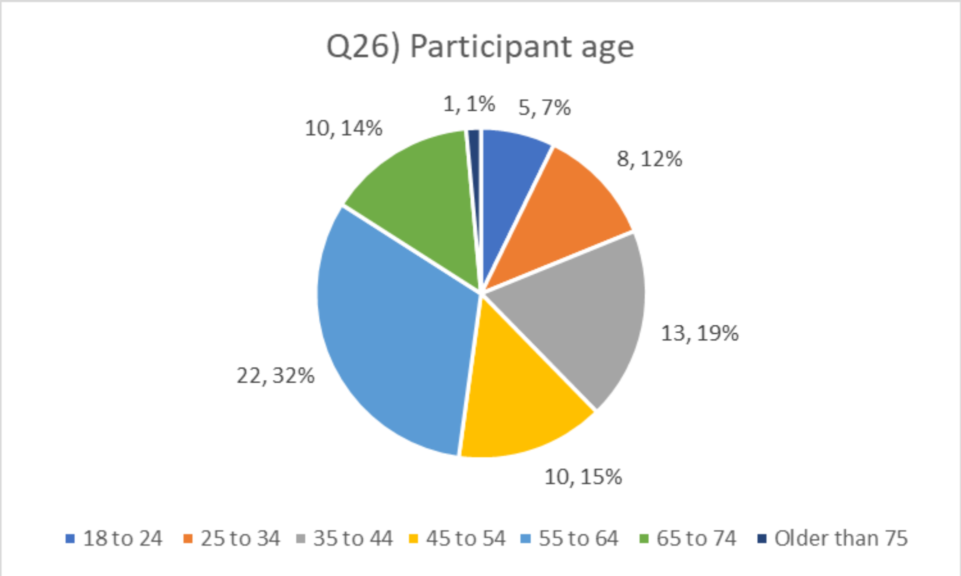
Q23e) You could not replace lampreys with artificial baits for predator fishing and still catch as effectively
2, 3%
15, 22%
19, 27%
2, 3%
2, 3%
25, 36%
4, 6%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree

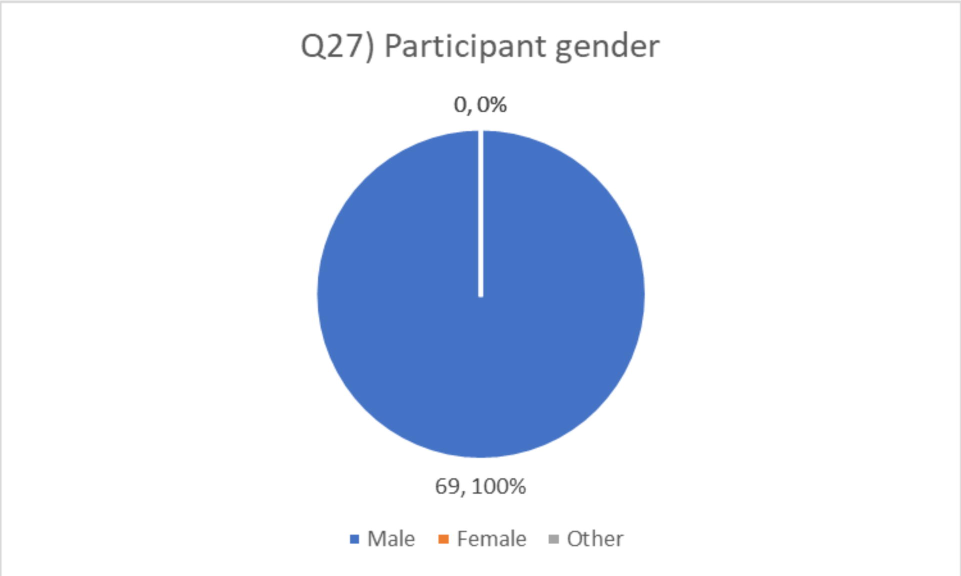

Q23f) Lampreys should be conserved
1, 1%
2, 3%
0, 0%
1, 1%
1, 1%
24, 35%
40, 58%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree

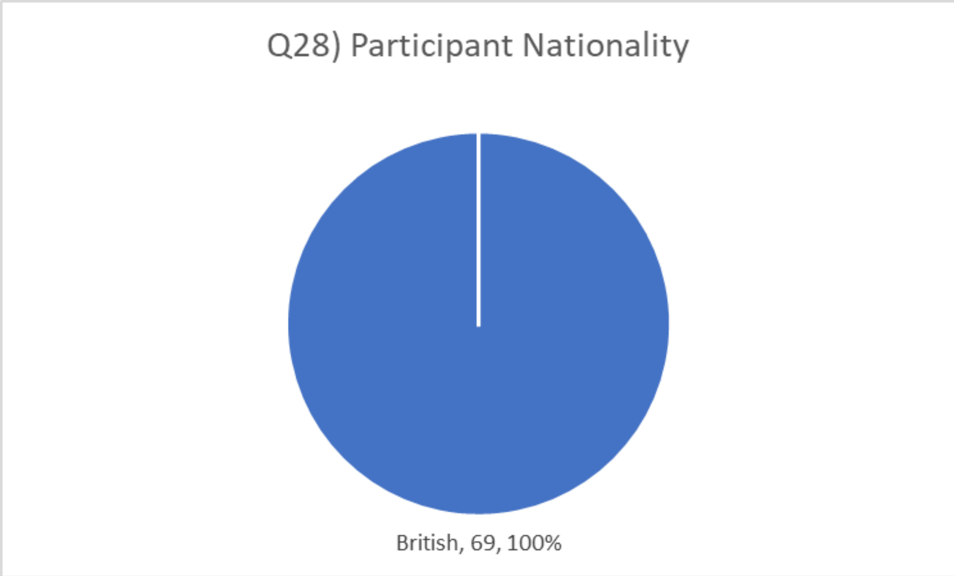

Q23g) Lampreys have been sufficiently protected in the UK
5, 7%
0, 0%
8, 12%
5, 7%
21, 31%
16, 23%
14, 20%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree

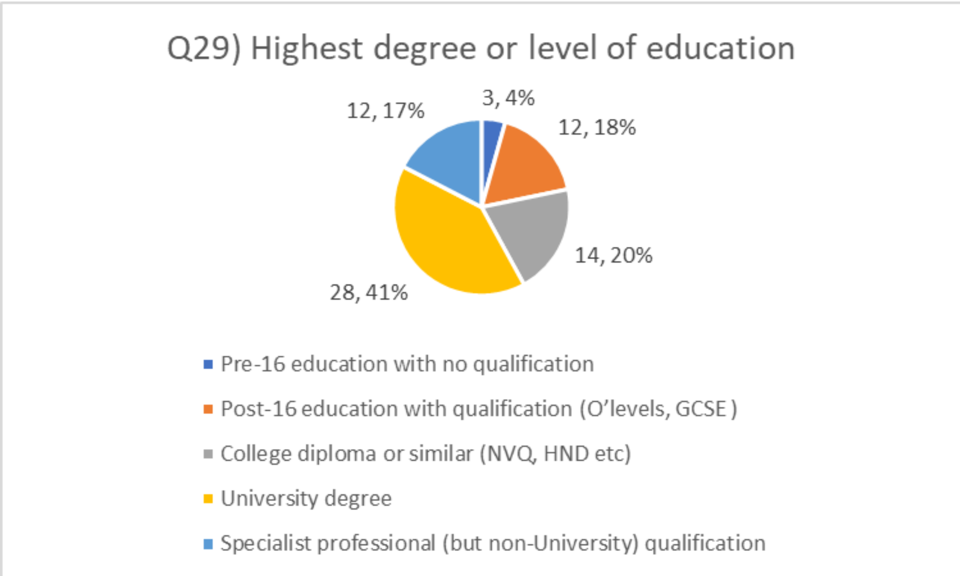

Q23h) If lampreys were threatened by exploitation a ban on their use as angling bait should be implemented
3, 4%
1, 2%
1, 2%
0, 0%
0, 0%
32, 46%
32, 46%
Strongly agree
Agree
Slightly agree
Neutral
Slightly disagree
Disagree
Strongly disagree


Q24) Are you aware of the conservation status of lamprey?
21, 30%
48, 70%
Yes
No


Q26) Participant age
1, 1%
5, 7%
10, 14%
8, 12%
13, 19%
22, 32%
10, 15%
18 to 24
25 to 34
35 to 44
45 to 54
55 to 64
65 to 74
Older than 75


Q27) Participant gender
0, 0%
69, 100%
Male
Female
Other


Q28) Participant Nationality
British, 69, 100%


Q29) Highest degree or level of education
3, 4%
12, 18%
14, 20%
28, 41%
12, 17%
Pre-16 education with no qualification
Post-16 education with qualification (O'levels, GCSE )
College diploma or similar (NVQ, HND etc)
University degree
Specialist professional (but non-University) qualification

# References

Aarestrup, K., Lucas, M. C., & Hansen, J. A. (2003). Efficiency of a nature-like bypass channel for sea trout (*Salmo trutta*) ascending a small Danish stream studied by PIT telemetry. *Ecology of Freshwater Fish*, **12**, 160-168. https://doi.org/10.1034/j.1600-0633.2003.00028.x

Aas, Ø. (2002). The next chapter: multicultural and cross-disciplinary progress in evaluating recreational fisheries. In *Recreational Fisheries: Ecological, Economic and Social Evaluation* (eds Pitcher, T. J., & Hollingworth, C. E.). 252–263. Oxford: Blackwell Science.

Aas, Ø., & Kaltenborn, B. P. (1995). Consumptive orientation of anglers in Engerdal, Norway. *Environmental Management*, **19**, 751–761.

Aberdeen Bestiary (1200) University of Aberdeen MS 24

Abersons, K. (2019). Efficiency of stocking of river lamprey ammocoetes – first results. *Environmental and Experimental Biology,* **17**, 43–44. https://doi.org/10.22364/eeb.17.06

Adam, B. (2012). Fish ladders on the River Elbe near Geesthacht. From sea to source; international guidance for the restoration of fish migration highways. 214-217.

Agostinho, A. A., Gomes, L. C., Veríssimo, S., & Okada, E. K. (2004). Flood regime, dam regulation and fish in the upper Paraná river: effects on assemblage attributes, reproduction and recruitment. *Reviews in Fish Biology and Fisheries*, **14**, 11–19.

Ahne, W. (1985), Viral infection cycles in pike (*Esox lucius* L.). *Journal of Applied Ichthyology*, **1**, 90-91. https://doi.org/10.1111/j.1439-0426.1985.tb00417.x

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, **19**, 716-723. https://doi.org/10.1109/TAC.1974.1100705.

Almodóvar, A., & Nicola, G. G. (2004). Angling impact on conservation of Spanish stream-dwelling brown trout *Salmo trutta*. *Fisheries Management and Ecology*, **11**, 173-182. https://doi.org/10.1111/j.1365-2400.2004.00402.x

Andersen, H. B., Caldwell, R. S., Toll, J., Doi, J., & Saban, L. (2010). Sensitivity of lamprey ammocoetes to six chemicals. *Archives of Environmental Contamination and Toxicology,* **59,** 622-631. https://doi.org/10.1007/s00244-010-9514-5

Andrade, N. O., Quintella, B. R., Ferreira, J., PinelaI. S., Póvoa, S., Pedro, P., & Almeida, R. (2007). Sea lamprey (*Petromyzon marinus* L.) spawning migration in the Vouga river basin (Portugal): poaching impact, preferential resting sites and spawning grounds. *Developments in Fish Telemetry*, 121-132. https://doi.org/10.1007/978-1-4020-6237-7_13

APEM. (2009). Prevention of lamprey entrainment at Elvington WTW – feasibility study. Draft report, APEM, Stockport, draft report no.YW 410652

Arlinghaus, R. & Cooke, S. J. (2009). Recreational fisheries: socioeconomic importance, conservation issues and management challenges. In: *Recreational hunting, conservation and rural livelihoods: science and practice* (eds Dickson, B., Hutton, J., & Adams, W. A.), 39–58. Oxford: Blackwell Publishing.

Arlinghaus, R. & Mehner, T. (2003). Management preferences of urban anglers. *Fisheries*, **28**, 10-17. https://doi.org/10.1577/1548-8446(2003)28[10:MPOUA]2.0.CO;2

Arlinghaus, R. (2007). Voluntary catch-and-release can generate conflict within the recreational angling community: a qualitative case study of specialised carp, *Cyprinus carpio*, angling in Germany. *Fisheries Management and Ecology*, **14**, 161-171. https://doi.org/10.1111/j.1365-2400.2007.00537.x

Arlinghaus, R., & Cooke, S. J. (2009). Recreational fisheries: socioeconomic importance, conservation issues and management challenges. In Recreational Hunting, Conservation and Rural Livelihoods: Science and Practice (eds Dickson, B., Hutton, J., & Adams, W. A.), 39–58. Oxford: Blackwell Publishing.

Arlinghaus, R., & Mehner, T. (2004). A management-orientated comparative analysis of urban and rural anglers living in a metropolis (Berlin, Germany). *Environmental Management*, **33**, 331–344. https://doi.org/10.1007/s00267-004-0025-x

Arlinghaus, R., & Mehner, T. (2005). Determinants of management preferences of recreational anglers in Germany: habitat management versus fish stocking. *Limnologica,* **35**, 2-17. https://doi.org/10.1016/j.limno.2004.10.001.

Arlinghaus, R., Alós, J., Pieterek, T., & Klefoth, T. (2017). Determinants of angling catch of northern pike (*Esox lucius*) as revealed by a controlled whole-lake catch-and-release angling experiment—the role of abiotic and biotic factors, spatial encounters and lure type. *Fisheries Research*, **186**, 648-657. https://doi.org/10.1016/j.fishres.2016.09.009.

Arlinghaus, R., Cooke, S. J., Schwab, A., & Cowx, I. G. (2009). Contrasting pragmatic and suffering-centred approaches to fish welfare in recreational angling. *Journal of Fish Biology*, **75**, 2448–2463. https://doi.org/10.1111/j.1095-8649.2009.02466.x

Arlinghaus, R., Klefoth, T., Kobler, A., & Cooke, S. J. (2008). Size selectivity, injury, handling time, and determinants of initial hooking mortality in recreational angling for northern pike: the influence of type and size of bait. *North American Journal of Fisheries Management*, **28**, 123-134. https://doi.org/10.1577/M06-263.1

Arlinghaus, R., Mehner, T., & Cowx, I. G. (2002). Reconciling traditional inland fisheries management and sustainability in industrialized countries, with emphasis on Europe. *Fish and Fisheries,* **3**, 261–316. https://doi.org/10.1046/j.1467-2979.2002.00102.x

Aronsuu, K., & Tertsunen, J. (2015). Selection of spawning substratum by European river lampreys (*Lampetra fluviatilis*) in experimental tanks. *Marine and Freshwater Behaviour and Physiology,* **48**, 41-50. https://doi.org/10.1080/10236244.2014.987453

Aronsuu, K., & Virkkala, P. (2014). Substrate selection by subyearling European river lampreys (*Lampetra fluviatilis*) and older larvae (*Lampetra* spp.). *Ecology of Freshwater Fish,* **23**, 644–655. https://doi.org/10.1111/eff.12119

Aronsuu, K., Marjomäki, T., Tuohino, J., Wennman, K., Vikström, R., & Ojutkangas, E. (2015). Migratory behaviour and holding habitats of adult river lampreys (*Lampetra fluviatilis*) in two Finnish rivers. *Boreal Environment Research*, **20**, 120-144.

Aronsuu, K., Vikström, R., Marjomäki, T. J., Wennman, K., Pakkala, J., Mäenpää, E., Tuohino, J., Sarell, J., & Ojutkangas, E. (2019). Rehabilitation of two northern river lamprey (*Lampetra fluviatilis*) populations impacted by various anthropogenic pressures – lessons learnt in the past three decades, *Proceedings of the department of biological and environmental science, University of Jyväskylä.* https://doi.org/10.17011/jyx/18282/64592

Baker, C. F. (2014). Effect of ramp length and slope on the efficacy of a baffled fish pass. *Journal of Fish Biology,* **84**, 491-502. https://doi.org/10.1111/jfb.12298

Balabanis, G., & Diamantopoulos, A. (2004). Domestic country bias, country-of-origin effects, and consumer ethnocentrism: a multidimensional unfolding approach. *Journal of the Academy of Marketing Science*, **32**, 80-95. https://doi.org/10.1177/0092070303257644

Barron, J. M, Hanson, K. C., Headley, R. R., Hawke, K. A., Twibell, R. G., & Gannam, A. L. (2020). Evaluation of effluent waste water from salmonid culture as a potential food and water supply for culturing larval Pacific lamprey *Entosphenus tridentatus*. *Aquaculture*, **517**. https://doi.org/10.1016/j.aquaculture.2019.734791.

Bartholomew, A., & Bohnsack, J. A. (2005). A review of catch-and-release angling mortality with implications for no-take reserves. *Reviews in Fish Biology and Fisheries*, **15**, 129–154. https://doi.org/10.1007/s11160-005-2175-1

Barton, K. (2009) Mu-MIn: multi-model inference. R Package Version 0.12.2/r18. http://R-Forge.R-project.org/projects/mumin/

Bate, R. (2001). Saving our streams: the role of the anglers' conservation association in protecting English and Welsh rivers. London: The Institute of Economic Affairs and Profile Books.

Baumgartner, L. J. (2007). Diet and feeding habits of predatory fishes upstream and downstream of a low-level weir. *Journal of Fish Biology*, **70**: 879-894. https://doi.org/10.1111/j.1095-8649.2007.01352.x

Baumgartner, L., Zampatti, B., Jones, M., Stuart, I., & Mallen-Cooper, M. (2014). Fish passage in the Murray-Darling basin, Australia: not just an upstream battle. *Ecological Management and Restoration*, **15**, 28-39. https://doi.org/10.1111/emr.12093

Beamish, R. J. (1980). Adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentate*) from the Pacific coast of Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 1906-1923. https://doi.org/10.1139/f80-232

Beamish, R. J., & Northcote, T. G. (1986). Extinction of a population of anadromous parasitic lamprey, *Lampetra tridentata*, upstream of an impassable dam. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 420-425. https://doi.org/10.1139/f89-056

Bear, C. & Eden, S. (2011). Thinking like a fish? Engaging non-human difference through recreational angling. *Environment and Planning D: Society and Space*, **29**, 336–352. https://doi.org/10.1068/d1810

Beaulaton, L., Taverny, C., Castelnaud, G. (2008). Fishing, abundance and life history traits of the anadromous sea lamprey (*Petromyzon marinus*) in Europe. *Fisheries Research*, **92**, 90-101. https://doi.org/10.1016/j.fishres.2008.01.001.

Behnke, R. J. (1972). The systematics of salmonid fishes of recently glaciated lakes. *Journal of the Fisheries Research Board of Canada*, **29**, 639-71.

Belletti, B., Garcia de Leaniz, C., Jones, J., Bizzi, S., Börger, L., Segura, G., Castelletti, A., Van de Bund, W., Aarestrup, K., Barry, J., Belka, K., Berkhuysen, A., Birnie-Gauvin, K., Bussettini, M., Carolli, M., Consuegra, S., Dopico, E., Feierfeil, T., Fernández, S., Fernandez Garrido, P., Garcia-Vazquez, E., Garrido, S., Giannico, G., Gough, P., Jepsen, N., Jones, P. E., Kemp, P., Kerr, J., King, J., Łapińska, M., Lázaro, G., Lucas, M. C., Marcello, L., Martin, P., McGinnity, P., O'Hanley, J., Olivo del Amo, R., Parasiewicz, P., Pusch, M., Rincon, G., Rodriguez, C., Royte, J., Schneider, C. T., Tummers, J. S., Vallesi, S., Vowles, A., Verspoor, E., Wanningen, H., Wantzen, K. M., Wildman, L., & Zalewski, M. (2020). More than one million barriers fragment Europe's rivers. *Nature,* **588**, 436–441. https://doi.org/10.1038/s41586-020-3005-2

Berg, L. S. (1948). Ryby presnykh vod i sopredel'nykh stran (Fishes of Freshwaters and Adjacent Countries), Moscow: Akad. Nauk SSSR

Bettaso, J. B., & Goodman, D. H. (2010). A comparison of mercury contamination in mussel and ammocoete filter feeders. *Journal of Fish and Wildlife Management,* **1**, 142-145. https://doi.org/10.3996/112009-JFWM-019

Beukemaj, J. J. (1970). Acquired hook-avoidance in the pike *Esox lucius* L. fished with artificial and natural baits. *Journal of Fish Biology*, **2**, 155-160. https://doi.org/10.1111/j.1095-8649.1970.tb03268.x

Biernacki, P., & Waldorf, D. (1981). Snowball sampling: problems and techniques of chain referral sampling. *Sociological Methods & Research*. **10**, 141–163. https://doi.org/10.1177/004912418101000205

Binder, T. R., & McDonald, D. G. (2008). The role of temperature in controlling diel activity in upstream migrant sea lampreys (*Petromyzon marinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, **65**, 1113-1121. https://doi.org/10.1139/F08-070

Birnie-Gauvin, K., Franklin, P., Wilkes, M., & Aarestrup, K. (2019). Moving beyond fitting fish into equations: progressing the fish passage debate in the Anthropocene. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **29**, 1095– 1105. https://doi.org/10.1002/aqc.2946

Birnie-Gauvin, K., Larsen, M. H., Nielsen, J., & Aarestrup, K. (2017). 30 years of data reveal dramatic increase in abundance of brown trout following the removal of a small hydrodam. *Journal of Environmental Management*, **204**, 467-471. https://doi.org/10.1016/j.jenvman.2017.09.022.

Birzaks, J., & Abersons, K. (2011). Anthropogenic influence on the dynamics of the river lamprey *Lampetra fluviatilis* landings in the river Daugava basin. *Scientific journal of Riga Technical University, Environmental and Climate Technologies,* **7,** 32–38. https://doi.org/10.2478/v10145-011-0025-z

Bjerselius, R., Li, W., Teeter, J. H., Seelye, J. G., Johnsen, P. B., Maniak, P. J., Grant, G. C., Polkinghorne, C. N., & Sorensen, P. W. (2000). Direct behavioral evidence that unique bile acids released by larval sea lamprey (*Petromyzon marinus*) function as a migratory pheromone. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 557-569. https://doi.org/10.1139/f99-290

Bourque, L. B., & Fielder, E. P. (2003). How to conduct telephone surveys. Second Ed. SAGE publications, Thousand Oaks, California.

Bracken, F. S. A., & Lucas, M. C. (2013). Potential impacts of small-scale hydroelectric power generation on downstream moving lampreys. *River research and applications*, **29**, 1073-1081. https://doi.org/10.1002/rra.2596

Bracken, F. S. A., Hoelzel, A. R., Hume, J. B., & Lucas, M. C. (2015). Contrasting population genetic structure among freshwater-resident and anadromous lampreys: the role of demographic history, differential dispersal and anthropogenic barriers to movement. *Molecular Ecology*, **24**, 1188–1204. https://doi.org/10.1111/mec.13112

Brönmark, C., Brodersen, J., Chapman, B. B., Nicolle, A., Nilsson, P. A., Skov, C., & Hansson, L. A. (2010). Regime shifts in shallow lakes: the importance of seasonal fish migration. *Hydrobiologia,* **646,** 91-100. https://doi.org/10.1007/s10750-010-0165-3

Bunt, C. M., Katopodis, C., & McKinley, R. S. (1999). Attraction and passage efficiency of white suckers and smallmouth bass by two denil fishways. *North American Journal of Fisheries Management*, **19**, 793-803. https://doi.org/10.1577/1548-8675(1999)019<0793:AAPEOW>2.0.CO;2

Burger, J. (2000). Consumption advisories and compliance: the fishing public and the deamplification of risk. *Journal of Environmental Planning and Management*, **43**, 471-488. https://doi.org/10.1080/713676577

Burns, A. C., Sorensen, P. W., & Hoye, T. R. (2011). Synthesis and olfactory activity of unnatural, sulfated 5β-bile acid derivatives in the sea lamprey (*Petromyzon marinus*). *Steroids*, **76**, 291-300. https://doi.org/10.1016/j.steroids.2010.11.010.

Byrum, K. (2019). “Hey friend, buy green”: social media use to influence eco-purchasing involvement. *Environmental Communication*, **13**, 209-221. https://doi.org/10.1080/17524032.2017.1308404

Cabon, J., Almeras, F., Baud, M., Pallandre, L., Morin, T., & Louboutin, L. (2020). Susceptibility of pike *Esox lucius* to VHSV and IHNV and potential transmission to rainbow trout *Oncorhynchus mykiss*. *Disease of Aquatic Organisms,* **139**, 175-187. https://doi.org/10.3354/dao03474

Calles, E. O., & Greenberg, L. A. (2007). The use of two nature-like fishways by some fish species in the Swedish River Emån. *Ecology of Freshwater Fish*, **16**, 183-190. https://doi.org/10.1111/j.1600-0633.2006.00210.x

Campbell, M. D., Patino, R., Tolan, J., Strauss, R., & Diamond, S. L. (2010). Sublethal effects of catch-and-release fishing: measuring capture stress, fish impairment, and predation risk using a condition index. *ICES Journal of Marine Science*, **67**, 513–521. https://doi.org/10.1093/icesjms/fsp255

Cao, P., Meister, S., & Klante, O. (2014). How social media influence apparel purchasing behavior. *Marketing Review St. Gallen*, **31**, 77–86. https://doi.org/10.1365/s11621-014-0427-y

Castro-Santos, T., Cotel, A., & Webb, P. W. (2009). Fishway evaluations for better bioengineering: an integrative approach. In: *Challenges for diadromous fishes in a dynamic global environment* (eds Haro, A. J., Smith, K. L., Rulifson, R. A., Moffitt, C. M., Klauda, R. J., Dadswell, M. J., Cunjak, R. A., Cooper, J. E., Beal, K. L., & Avery, T. S.). 557–575, American Fisheries Society.

Castro-Santos, T., Haro, A., & Walk, S. (1996). A passive integrated transponder (PIT) tag system for monitoring fishways. *Fisheries Research,* **28,** 253–261. https://doi.org/10.1016/0165-7836(96)00514-0

Castro-Santos, T., & Perry, R. W. (2012). Time-to-event analysis as a framework for quantifying fish passage performance. In: *Telemetry techniques* (Eds, Adams, N. S., Beeman, J. W., & Eiler, J.), Bethesda, MD: American Fisheries Society

Castro-Santos, T., Shi, X., & Haro, A. (2017). Migratory behavior of adult sea lamprey and cumulative passage performance through four fishways. *Canadian Journal of Fisheries and Aquatic Sciences*, **74**, 790–800. https://doi.org/10.1139/cjfas-2016-0089

Chaudhuri, C., Wade, J., & Robertson, C. (2020). Fluctuating water levels influence access to critical habitats for threatened Cowichan Lake lamprey. *Facets*. https://doi.org/10.1139/facets-2019-0054

Clay, C. H. (1995). Design of fishways and other fish facilities, Second Ed. Lewis, Boca Raton.

Clemens, B. J., Beamish, R. J., Coates, K. C., Docker, M. F., Dunham, J. B., Gray, A. E., Hess, J. E., Jolley, J. C., Lampman, R. T., McIlraith, B. J., Moser, M. L., Murauskas, J. G., Noakes, D. L. G., Schaller, H. A., Schreck, C. B., Starcevich, S. J., Streif, B., van de Wetering, S. J., Wade, J., Weitkamp, L. A., & Wyss, L. A. (2017). Conservation challenges and research needs for Pacific lamprey in the Columbia river basin, *Fisheries*, **42**, 268-280. https://doi.org/10.1080/03632415.2017.1305857

Close, D. A., Fitzpatrick, M. S., & Li, H. W. (2002). The ecological and cultural importance of a species at risk of extinction, Pacific lamprey. *Fisheries*, **27**, 19-25. https://doi.org/10.1577/1548-8446(2002)027<0019:TEACIO>2.0.CO;2

Close, D. A., Fitzpatrick, M. S., Lorion, C. M., Li, H. W., & Schreck, C. B. (2003). Effects of intraperitoneally implanted radio transmitters on the swimming performance and physiology of Pacific lamprey, *North American Journal of Fisheries Management*, **23**, 1184-1192, DOI: 10.1577/MO2-057

Cochran, P. A., & Lyons, J. (2004). Field and laboratory observations on the ecology and behavior of the silver lamprey (*Ichthyomyzon unicuspis*) in Wisconsin. *Journal of Freshwater Ecology*, **19**, 245-253. https://doi.org/10.1080/02705060.2004.9664538.

Cohen, A. H., Mackler, S. A., & Selzer, M. E. (1988). Behavioral recovery following spinal transection: functional regeneration in the lamprey CNS. *Trends in Neurosciences*, **11**, 227-231. https://doi.org/10.1016/0166-2236(88)90131-2.

Collin S, P. (2010). Evolution and ecology of retinal photoreception in early vertebrates. *Brain, behavior and evolution*, **75**, 174-185. https://doi.org/10.1159/000314904

Convention on the conservation of European wildlife and natural habitats. (1979). accessible at https://www.coe.int/en/web/conventions/full-list/-/conventions/treaty/104. Last accessed 10/12/2020

Cooper, M. D., & Alder, M. N. (2006). The evolution of adaptive immune systems. *Cell*, **124**, 815-822. https://doi.org/10.1016/j.cell.2006.02.001.

Cornide-Petronio, M. E., Ruiz, M. S., Barreiro-Iglesias, A., & Rodicio, M. C. (2011). Spontaneous regeneration of the serotonergic descending innervation in the sea lamprey after spinal cord injury. *Journal of Neurotrauma*, **28**, 2535-2540. https://doi.org/10.1089/neu.2011.1766

Cowx, I.G., Arlinghaus, R., & Cooke, S. J. (2010). Harmonizing recreational fisheries and conservation objectives for aquatic biodiversity in inland waters. *Journal of Fish Biology*, **76**, 2194-2215. https://doi.org/10.1111/j.1095-8649.2010.02686.x

Danylchuk, A. J., & Cooke, S. J., (2010). Engaging the recreational angling community to implement and manage aquatic protected areas. *Conservation Biology*, **25**, 458-464. https://doi.org/10.1111/j.1523-1739.2010.01631.x

Darwall, W. R. T., & Freyhof, J. (2016). Lost fishes, who is counting? The extent of the threat to freshwater fish biodiversity. In: *Conservation of* *freshwater fishes* (eds Closs, G. P., Krkosek, M., & Olden, J. D.). Cambridge University Press: Cambridge.

Dawson H., Quintella B., Almeida P., Treble A., & Jolley J. (2015). The ecology of larval and metamorphosing lampreys. In: *Lampreys: Biology, Conservation and Control* (eds Docker, M.), 75-137, Springer, Dordrecht. https://doi.org/10.1007/978-94-017-9306-3_3.

Dawson, H. A., Jones, M. L., Irwin, B. J., Johnson, N. S., Wagner, M. C., & Szymanski, M. D. (2016). Management strategy evaluation of pheromone-baited trapping techniques to improve management of invasive sea lamprey. *Natural Resource Modelling*, **29**, 448-469. https://doi.org/10.1111/nrm.12096

Deinet, S., Scott-Gatty, K., Rotton, H., Twardek, W. M., Marconi, V., McRae, L., Baumgartner, L. J., Brink, K., Claussen, J. E., Cooke, S. J., Darwall, W., Eriksson, B. K., Garcia de Leaniz, C., Hogan, Z., Royte, J., Silva, L. G. M., Thieme, M. L., Tickner, D., Waldman, J., Wanningen, H., Weyl, O. L. F., & Berkhuysen, A. (2020). The living planet index (LPI) for migratory freshwater fish - technical report. World Fish Migration Foundation, The Netherlands.

Dekker, W. (2003). Status of the European eel stock and fisheries. In: *Eel Biology* (eds Aida, K., Tsukamoto, K., Yamauchi, K.), Springer, Tokyo. https://doi.org/10.1007/978-4-431-65907-5_17

Delle-Palme, C. A., Nguyen, V. M., Gutowsky, L. F. G., & Cooke, S. J. (2016). Do fishing education programs effectively transfer catch-and-release best practices to youth yielding improvements in fish condition and survival? *Knowledge and Management of Aquatic Ecosystems*, **417**, 42. https://doi.org/10.1051/kmae/2016029

Dias, E., Miranda, M. L., Sousa, R., & Antunes, C. (2019). Riparian vegetation subsidizes sea lamprey ammocoetes in a nursery area. *Aquatic Sciences*, **81**. https://doi.org/10.1007/s00027-019-0641-4.

DiFranceisco, W., McAuliffe, T. L., & Sikkema, K. J. (1998). Influences of survey instrument format and social desirability on the reliability of self-reported high-risk sexual behavior. *AIDS and Behavior*. **2**, 329-337.

Dillman, D. A., Sangster, R. L., Tarnai, J., & Rockwood, T. H. (1996). Understanding differences in people's answers to telephone and mail surveys. *New Directions for Evaluation*. 45-61. doi:10.1002/ev.1034

Dingle, H., & Drake, V. A. (2007). What Is migration? *BioScience*, **57**, 113–121. https://doi.org/10.1641/B570206.

Doadrio, I. (2001). Atlas y libro rojo de los peces continentales de España. Dirección General de Conservación de la Naturaleza, Museo Nacional de Ciencias Naturales, Madrid

Docker M., Hume J., & Clemens B. (2015). Introduction: A surfeit of lampreys. In: *Lampreys: Biology, Conservation and Control* (eds Docker, M.), 1-34, Springer, Dordrecht. https://doi.org/10.1007/978-94-017-9306-3_1.

Docker, M. F. (2009). A review of the evolution of non-parasitism in lampreys and an update of the paired species concept. *Biology, management and conservation of lampreys in North America*, **1**, 71–114.

Docker, M. F., Beamish, F. W. H., Yasmin, T., Bryan, M. B., & Khan, A. (2019). The lamprey gonad. In: *Lampreys: Biology, Conservation and Control* (eds Docker, M.). 75-137, Springer, Dordrecht. https://doi.org/10.1007/978-94-024-1684-8_1

Dodd, J. R., Cowx, I. G., & Bolland, J. D. (2018). Win, win, win: low cost baffle fish pass provides improved passage efficiency, reduced passage time and broadened passage flows over a low-head weir. *Ecological engineering,* **120**, 68-75. https://doi.org/10.1016/j.ecoleng.2018.05.028

Dorow, M., & Arlinghaus, R. (2012). The relationship between personal commitment to angling and the opinions and attitudes of German anglers towards the conservation and management of the European eel *Anguilla anguilla*. *North American Journal of Fisheries Management*, **32**, 466-479. https://doi.org/10.1080/02755947.2012.680006

Dorow, M., Beardmore, B., Haider, W., & Arlinghaus, R. (2010). Winners and losers of conservation policies for European eel*, Anguilla anguilla*: an economic welfare analysis for differently specialised eel anglers. *Fisheries Management and Ecology*, **17**, 106-125. https://doi.org/10.1111/j.1365-2400.2009.00674.x

Dudgeon, D., Arthington, A., Gessner, M., Kawabata, Z., Knowler, D., Lévêque, C., Naiman, R., Prieur-Richard, A., Soto, D., Melanie L., Stiassny, J., & Sullivan, C. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, **81**, 163-182. https://doi.org/10.1017/S1464793105006950

Duffus, D. A., & Dearden, P. (1990). Non-consumptive wildlife-oriented recreation: a conceptual framework. *Biological Conservation*. **53**, 213-231. https://doi.org/10.1016/0006-3207(90)90087-6

Easman, E. S., Abernethy, K. E., & Godley, B. J. (2018). Assessing public awareness of marine environmental threats and conservation efforts. *Marine Policy*, **87**, 234-240. https://doi.org/10.1016/j.marpol.2017.10.030.

Entec. (2010). Opportunity and environmental mapping sensitivity for hydropower in England and Wales. Environment Agency, Bristol.

Environment Agency. (2016). Humber river basin management plan. Part 1. Available at https://www.gov.uk/government/publications/humber-river-basin-district-river-basin-management-plan#history (last accessed 10/12/2020)

Environment Agency. (2020). Annual summary of rod licence sales. Available at: https://data.gov.uk/dataset/2b303513-bc81-4bef-880f-8a587db9b3a1/annual-summary-of-rod-licence-sales. Last accessed 10/12/2020

Etheridge, E. C., Adams, C. E., Bean, C. W., Durie, N. C., Gowans, A. R. D., Harrod, C., Lyle, A. A., Maitland, P. S., & Winfield, I. J. (2012). Are phenotypic traits useful for differentiating among a priori Coregonus taxa? *Journal of Fish Biology*, **80**, 387-407. https://doi.org/10.1111/j.1095-8649.2011.03189.x

Evans, T. M., & Bauer, J. E. (2016). Identification of the nutritional resources of larval sea lamprey in two Great Lakes tributaries using stable isotopes. *Journal of Great Lakes Research*, **42**, 99-107.

Fedler, A. J., & Ditton, R. B. (1994). Understanding angler motivations in fisheries management, *Fisheries*, **19**, 6-13. https://doi.org/10.1577/1548-8446(1994)019<0006:UAMIFM>2.0.CO;2

Feng, B., Zhang, T., Wu, F., Chen, S., & Xu, A. (2018). Artificial propagation and embryonic development of Yalu river lamprey, *Lampetra morii*. *Acta Biochimica et Biophysica Sinica*, **50**, 828–830. https://doi.org/10.1093/abbs/gmy067

Ferguson, A. (1974). The genetic relationships of the coregonid fishes of Britain and Ireland indicated by electrophoretic analysis of tissue proteins. *Journal of Fish Biology*, **6**, 311-315. https://doi.org/10.1111/j.1095-8649.1974.tb04548.x

Ferguson, A., Himberg, K.-J. M., & Svardson, G. (1978). Systematics of the Irish pollan (Coregonus pollan Thompson): an electrophoretic comparison with other holarctic Coregoninae. *Journal of Fish Biology*, **12**, 221-33.

Fickling, N. (2012). Ever thought of provenance..by Neville Fickling. Accessible at: http://thepikepool.blogspot.co.uk/2012/12/ever-thought-of-provenancebyneville.html. Last accessed 10/12/2020

Fine, J. M., & Sorensen, P. W. (2010). Production and fate of the sea lamprey migratory Pheromone. *Fish Physiology and Biochemistry*, **36**, 1013–1020. https://doi.org/10.1007/s10695-010-9379-6

Fisheries Regulations (Northern Ireland) 2014, available at https://www.legislation.gov.uk/nisr/2014/17/contents/made. Last accessed 10/12/2020

Font, T., Gil, J., & Lloret, J. (2018). The commercialization and use of exotic baits in recreational fisheries in the north-western Mediterranean: environmental and management implications. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **28**, 651– 661. https://doi.org/10.1002/aqc.2873

Forbes, S. L., Cohen, D. A., Cullen, R., Wratten, S. D., & Fountain, J. (2009). Consumer attitudes regarding environmentally sustainable wine: an exploratory study of the New Zealand marketplace, *Journal of Cleaner Production*, **17**, 1195-1199. https://doi.org/10.1016/j.jclepro.2009.04.008.

Foulds, W. J. (2013). Anthropogenic factors affecting European river lamprey *Lampetra fluviatilis* in the Humber River Basin, north-east England, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/7750/

Foulds, W. L., & Lucas, M. C. (2013). Extreme inefficiency of two conventional, technical fishways used by European river lamprey (*Lampetra fluviatilis*). *Ecological Engineering*, **58**, 423–433. https://doi.org/10.1016/j. ecoleng.2013.06.038.

Foulds, W. L., & Lucas, M. C. (2014). Paradoxical exploitation of protected fishes as bait for anglers: evaluating the lamprey bait market in Europe and developing sustainable and ethical solutions. *PLoS ONE*, **9.** https://doi.org/10.1371/journal.pone.0099617.

Franklin, P., Gee, E., Baker, C., & Bowie, S. (2018). New Zealand fish passage guidelines: for structures up to 4 metres.

Frary, R. B. (1996). Hints for designing effective questionnaires. *Practical Assessment, Research, and Evaluation*. **5**, 3. https://doi.org/10.7275/h53m-b438

Frear, P. (2004). Lampreys. In: *Freshwater Fishes in Britain: The Species and their Distribution* (eds Davies, C. E., Shelley, J., Harding, P. T., McLean, I. F. G., Gardiner, R., & Peirson, G.). Harley Books, Essex, England. 44-49.

Freyhof, J. & Kottelat, M. (2008). *Coregonus pollan*. *The IUCN red list of threatened species 2008*: e.T135704A4186887. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T135704A4186887.en.

Freyhof, J. (2011). *Lampetra fluviatilis* (errata version published in 2016). The IUCN Red List of Threatened Species 2011: e.T11206A97805807. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T11206A3263535.en.

Gadd, T., Jakava-Viljanen, M., Einer-Jensen, K., Ariel, E., Koski, P., & Sihvonen, L. (2010). Viral haemorrhagic septicaemia virus (VHSV) genotype II isolated from European river lamprey *Lampetra fluviatilis* in Finland during surveillance from 1999 to 2008. *Disease of Aquatic Organisms*, **88**, 189-198. https://doi.org/10.3354/dao02169

Gallagher, A. J., Cooke, S. J., & Hammerschlag, N. (2015). Risk perceptions and conservation ethics among recreational anglers targeting threatened sharks in the subtropical Atlantic. *Endangered Species Research*, **29**, 81-93. https://doi.org/10.3354/esr00704

Garavelli, L, Linley, T. J., Bellgraph, B. J., Rhode, B. M., Janak, J. M., & Colotelo, A. H. (2019). Evaluation of passage and sorting of adult Pacific salmonids through a novel fish passage technology. *Fisheries Research*, **212**, 40-47. https://doi.org/10.1016/j.fishres.2018.12.010.

Garcia de Leaniz, C. (2008). Weir removal in salmonid streams: implications, challenges and practicalities. *Hydrobiologia*, **609**, 83–96. https://doi.org/10.1007/s10750-008-9397-x

Garlock, T. M., & Lorenzen, K. (2017). Marine angler characteristics and attitudes toward stock enhancement in Florida. *Fisheries Research*, **186**, 439-445. https://doi.org/10.1016/j.fishres.2016.08.017.

Gaudron, S. M., & Lucas, M. C. (2006). First evidence of attraction of adult river lamprey in the migratory phase to larval odour. *Journal of Fish Biology*, **68**, 640-644. https://doi.org/10.1111/j.0022-1112.2006.00937.x

Genner, M. J., Hillman, R., McHugh, M., Hawkins, S. J., Lucas, M. C. (2012). Contrasting demographic histories of European and North American sea lamprey (Petromyzon marinus) populations inferred from mitochondrial DNA sequence variation. Marine and Freshwater Research, 63, 827-833. https://doi.org/10.1071/MF12062

Gess, R., Coates, M. & Rubidge, B. (2006). A lamprey from the Devonian period of South Africa. *Nature*, **443**, 981–984. https://doi.org/10.1038/nature05150.

Gibson, C. C., & Marks, S. A. (1995). Transforming rural hunters into conservationists: an assessment of community-based wildlife management programs in Africa. *World Development*, **23**, 941-957. https://doi.org/10.1016/0305-750X(95)00025-8.

Goodman, D. H., & Reid, S. B. (2017). Climbing above the competition: innovative approaches and recommendations for improving Pacific lamprey passage at fishways. *Ecological Engineering*, **107**, 224-232. https://doi.org/10.1016/j.ecoleng.2017.07.041.

Gozlan, R. E. (2008). Introduction of non-native freshwater fish: is it all bad? *Fish and Fisheries*, **9**, 106-115. https://doi.org/10.1111/j.1467-2979.2007.00267.x

Gozlan, R. E., Burnard, D., Andreou, D., & Britton, J. R. (2013). Understanding the threats posed by non-native species: public vs. conservation managers. *PLoS ONE*, **8**. https://doi.org/10.1371/journal.pone.0053200

Gray, S. A., & Jordan, R. (2010). Ecosystem-based angling: incorporating recreational anglers into ecosystem-based management. *Human Dimensions of Wildlife*, **15**, 233-246. https://doi.org/10.1080/10871209.2010.490972

Greaves, R. K., Bubb, D. H., & Lucas, M. C. (2007). Adult river lamprey occurrence and migration in the River Trent in relation to barriers and environmental conditions. Report to University of Durham.

Gresh, T., Lichatowich, J., & Schoonmaker. P. (2000). An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem. *Fisheries,* **25,** 15–21. https://doi.org/10.1577/1548-8446(2000)025<0015:AEOHAC>2.0.CO;2

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S., Borrelli, P., Cheng, L., Crochetiere, H., Ehalt Macedo, H., Filgueiras, R., Goichot, M., Higgins, J., Hogan, Z., Lip, B., McClain, M. E., Meng, J., Mulligan, M., Nilsson, C., Olden, J. D., Opperman, J. J., Petry, P., Reidy Liermann, C., Saenz, L., SalinasRodriguez, S., Schelle, P., Schmitt, R. J. P., Snider, J., Tan, F., Tockner, K., Valdujo, P. H., van Soesbergen, A., & Zarfl, C. (2019). Mapping the world’s free-flowing rivers. *Nature*, **569**, 215-221.

Grillner, S., & Jessell, T. M. (2009). Measured motion: searching for simplicity in spinal locomotor networks. *Current Opinion in Neurobiology*, **19**, 572-586. https://doi.org/10.1016/j.conb.2009.10.011.

Guckian, M. L., Danylchuk, A. J., Cooke, S. J., & Markowitz, E. M. (2019). Peer pressure on the riverbank: assessing catch-and-release anglers' willingness to sanction others' (bad) behavior. *Journal of Environmental Management*, **219**, 252-259. https://doi.org/10.1016/j.jenvman.2018.04.117.

Guo, Z., Andreou, D., & Britton, J. (2017). Sea lamprey *Petromyzon marinus* biology and management across their native and invasive ranges: promoting conservation by knowledge transfer. *Reviews in Fisheries Science & Aquaculture*, **25**, 84–99.

Haas, B., Fleming, A., Haward, M., & McGee, J. (2019). Big fishing: the role of the large-scale commercial fishing industry in achieving sustainable development goal 14. *Reviews in Fish Biology and Fisheries*, **29**, 161–175. https://doi.org/10.1007/s11160-018-09546-8

Hagelin, L. O., & Steffner, N. (1958). Notes on the spawning habits of the river lamprey (*Petromyzon fluviatilis*). *Oikos*, **9**, 221–238. https://doi.org/10.2307/3564766

Hall, R. J., Milner-Gulland, E. J., & Courchamp, F. (2008). Endangering the endangered: The effects of perceived rarity on species exploitation. *Conservation Letters*, **1**, 75-81. https://doi.org/10.1111/j.1755-263X.2008.00013.x

Hard, A., & Kynard, B. (1997). Video evaluation of passage efficiency of American shad and sea lamprey in a modified ice harbor fishway. *North American Journal of Fisheries Management*, **17**, 981-987. https://doi.org/10.1577/1548-8675(1997)017<0981:VEOPEO>2.3.CO;2

Hardisty, M. W., & Huggins, R. J. (1970). Larval growth in the river lamprey, *Lampetra fluviatilis*. *Journal of Zoology*, **161**, 549-559. https://doi.org/10.1111/j.1469-7998.1970.tb02055.x

Hardisty, M. W., & Potter, I. C. (1971). The biology of lampreys. Volume 1. Academic Press, London.

Harrison, A., Connor, L., Morrissey, E., & Kelly, F. (2012). Current status of pollan *Coregonus autumnalis* pollan in Lough Ree, Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy*, **112**, 225-233.

Harrod, C., Griffiths, D., McCarthy, T. K., & Rosell, R. (2001). The Irish pollan, *Coregonus autumnalis*: options for its conservation. *Journal of Fish Biology*, **59**, 339-355. https://doi.org/10.1111/j.1095-8649.2001.tb01395.x

Heermann, L., Emmrich, M., Heynen, M., Dorow, M., König, U., Borcherding, J., & Arlinghaus, R. (2013). Explaining recreational angling catch rates of Eurasian perch, *Perca fluviatilis*: the role of natural and fishing-related environmental factors. *Fisheries Management and Ecology*, **20**, 187-200. https://doi.org/10.1111/fme.12000

Heimberg, A. M., Cowper-Sal·lari, R., Sémon, M., Donoghue, P. C. J., & Peterson, K. J. (2010). MicroRNAs reveal the interrelationships of hagfish, lampreys, and gnathostomes and the nature of the ancestral vertebrate. *Proceedings of the National Academy of Sciences*, **107**, 19379-19383. https://doi.org/10.1073/pnas.1010350107.

Hervé-Claude, P. L., Carpenter, T.E., & Hedrick, R. P. (2008). Risk of introducing viral hemorrhagic septicemia virus (VHSV) to the Chilean south Pacific via sardine imports from Europe. *Disease of Aquatic Organisms,* **78**, 199-207. https://doi.org/10.3354/dao01862

Hess, J. E., Campbell, N. R., Docker, M. F., Baker, C., Jackson, A., Lampman, R., McIlraith, B., Moser, M. L., Statler, D. P., Young, W. P., Wildbill, A. J., & Narum, S. R. (2015). Use of genotyping by sequencing data to develop a high-throughput and multifunctional SNP panel for conservation applications in Pacific lamprey. *Molecular Ecology Resources*, **15**, 187-202. https://doi.org/10.1111/1755-0998.12283

Hilderbrand, G. V., Farley, S. D., Schwartz, C. C., & Robbins, C. T. (2004). Importance of salmon to wildlife: implications for integrated management. *Ursus*, **15**, 1–9. https://doi.org/10.2192/1537-6176(2004)015<0001:IOSTWI>2.0.CO;2

Hoffmann, S., Balderjahn, I., Seegebarth, B., Mai, R., & Peyer, M. (2018). Under which conditions are consumers ready to boycott or buycott? The roles of hedonism and simplicity. *Ecological Economics*, **147**, 167-178. https://doi.org/10.1016/j.ecolecon.2018.01.004.

Hogg, R. S., Coghlan, S. M., Zydlewski, J., & Simon, K. S. (2014). Anadromous sea lampreys (*Petromyzon marinus*) are ecosystem engineers in a spawning tributary. *Freshwater Biology*, **59**, 1294-1307. https://doi.org/10.1111/fwb.12349

Hogg, R. S., Coghlan-Jr, S. M., Zydlewski, J., & Gardner, C. (2015). Fish community response to a small-stream dam removal in a Maine coastal river tributary. *Transactions of the American Fisheries Society*, **144**, 467-479. https://doi.org/10.1080/00028487.2015.1007164

Hogg, R., Coghlan Jr, S. M., & Zydlewski, J. (2013). Anadromous sea lampreys recolonize a Maine coastal river tributary after dam removal. *Transactions of the American Fisheries Society*, **142**, 1381-1394. https://doi.org/10.1080/00028487.2013.811103.

Holland, S. M., & Ditton, R. B. (1992). Fishing trip satisfaction: a typology of anglers. *North American Journal of Fisheries Management*, **12**, 28-33. https://doi.org/10.1577/1548-8675(1992)012<0028:FTSATO>2.3.CO;2

Holmes, T. Q. (2020). Impact of UK sport fishing on fish welfare and conservation. *Animal Sentience*, **3**

Honma, Y. (1960). Sado awashima kinkai no okeru kuromekura unagi to kawayatsume. *Saishu Shiiku*, **22**, 34–36

Hoover, J. J., & Murphy, C. E. (2018). Maximum swim speed of migrating sea lamprey (*Petromyzon marinus*): reanalysis of data from a prior study. U.S. Army Engineer Research and Development Center, Vicksburg, MS, 9p

Horreo, J, L. (2017). Revisiting the mitogenomic phylogeny of Salmoninae: new insights thanks to recent sequencing advances. *PeerJ*, **5**. https://doi.org/10.7717/peerj.3828

Hsu, L. -J., Zelenin, P. V., Grillner, S., Orlovsky, G. N., & Deliagina, T. G. (2013). Intraspinal stretch receptor neurons mediate different motor responses along the body in lamprey. *Journal of Comparative Neurology*, **521**, 3847-3862. https://doi.org/10.1002/cne.23382.

https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/789024/Decision_Statement.pdf (Last accessed: 10/12/2020)

https://britishseafishing.co.uk (Last accessed 10/12/2020)

https://nrfa.ceh.ac.uk/data/station/meanflow/27009 (Last accessed 10/12/2020)

https://www.anglingtimes.co.uk/advice/bait/articles/the-best-deadbaits-to-use-when-pike-fishing (Last accessed 10/12/2020)

https://www.bbc.co.uk/news/av/uk-england-somerset-18496330 (Last accessed 10/12/2020)

https://www.bbc.co.uk/news/uk-northern-ireland-43811208 (Last accessed 10/12/2020)

https://www.fishbase.in/summary/Coregonus-pollan.html (Last accessed 10/12/2020)

https://fishbuddy.directory/ (Last accessed 10/12/2020)

https://www.gov.uk/government/news/latest-rod-licence-figures-show-increase-as-restrictions-lifted (Last accessed 10/12/2020)

https://www.gov.uk/guidance/regional-rod-fishing-byelaws-north-west-region#legal-fishing-tackle-lures-and-bait (Last accessed 10/12/2020)

https://www.heraldry-wiki.com/ (Last accessed 10/12/2021)

https://lampreysurveys.com/ (Last accessed 19/06/2021)

https://www.legislation.gov.uk/ukpga/1975/51. (Last accessed 10/12/2020)

https://www.mcsuk.org/goodfishguide/search. (Last accessed 10/12/2020)

https://www.timeanddate.com (Last accessed 10/12/2020)

https://www2.gov.scot/Topics/marine/Salmon-Trout-Coarse/game/rights. (Last accessed 10/12/2020) https://www.youtube.com/watch?v=OKVXKuavJtQ (Last accessed 19/06/2021)

Hume, J. B., & Wagner, M. (2018). A death in the family: Sea lamprey (*Petromyzon marinus*) avoidance of confamilial alarm cues diminishes with phylogenetic distance. *Ecology and Evolution*, **8**, 3751– 3762. https://doi.org/10.1002/ece3.3930

Hume, J. B., Adams, C. E., Mable, B., & Bean, C. (2013). Post-zygotic hybrid viability in sympatric species pairs: a case study from European lampreys. *Biological Journal of the Linnean Society*, **108**, 378–383, https://doi.org/10.1111/j.1095-8312.2012.02007.x

Hume, J. B., Luhring, T. M., & Wagner, C. M. (2020). Push, pull, or push–pull? An alarm cue better guides sea lamprey towards capture devices than a mating pheromone during the reproductive migration. *Biological Invasions*, **22**, 2129–2142. https://doi.org/10.1007/s10530-020-02242-4

Hume, J. B., Meckley, T. D., Johnson, N. S., Luhring, T. M., Siefkes, M. J., Wagner, C. M., & Ramcharan, C. (2014). Application of a putative alarm cue hastens the arrival of invasive sea lamprey (*Petromyzon marinus*) at a trapping location. *Canadian Journal of Fisheries and Aquatic Sciences*, **72**, 1799-1806. https://doi.org/10.1139/cjfas-2014-0535

Hunt, K. M., & Ditton. R. B. (1998). Characteristics of anglers and guides at Lake Texoma, their fishing participation patterns and attitudes towards management of the recreational fishery. Texas A&M University. College Station

Igoe, F., Quigley, D., Marnell, F., Meskell, E., O'Connor, W., & Byrne, C. (2004). The sea lamprey *Petromyzon marinus* (L.), river lamprey *Lampetra fluviatilis* (L.) and brook lamprey *Lampetra planeri* (Bloch) in Ireland: general biology, ecology, distribution and status with recommendations for conservation. *Biology and Environment: Proceedings of the Royal Irish Academy*, **104B**, 43-56.

Jacklin, T. E. (2006). The status of lamprey species in the River Trent with particular regard to the Humber Estuary SAC. Environment Agency internal report.

Jackson, A. D., Moser, M. L., Onjukka, S. T., LaPatra, S., Lujan, K. M., Samson, C., White, M. G., Blair, M., Rhodes, L., Lampman, R., Maine, A. N., & Jolley, J. C. (2019). Occurrence of pathogens in Pacific lamprey (*Entosphenus tridentatus*). *Reviews in Fish Biology and Fisheries*, **29**, 653–668. https://doi.org/10.1007/s11160-019-09572-0

Jaffry, S., Pickering, H., Ghulam, Y., Whitmarsh, D., & Wattage, P. (2004). Consumer choices for quality and sustainability labelled seafood products in the UK. *Food Policy*, **29**, 215-228. https://doi.org/10.1016/j.foodpol.2004.04.001.

Jain, R. Rivera, M. C., Moore, J. E., & Lake, J. A. (2003). Horizontal gene transfer accelerates genome innovation and evolution. *Molecular Biology and Evolution*, **20**, 1598–1602. https://doi.org/10.1093/molbev/msg154

Jang, M. H., & Lucas, M. C. (2005). Reproductive ecology of the river lamprey. *Journal of Fish Biology*, **66**, 499–512. https://doi.org/10.1111/j.0022-1112.2005.00618.x

Janvier, P. (2007). Living primitive fishes and fishes from deep time. *Fish Physiology*, **26**, 1-51. https://doi.org/10.1016/S1546-5098(07)26001-7.

Jardine, T. I., Roussel, M., Mitchell, S. C., & Cunjak., R. A. (2009). Detecting marine nutrients and organic matter inputs into multiple trophic levels in streams of Atlantic Canada and France. *American Fisheries Society Symposium,* **69,** 427–445

Jarvie, H. P., Neal, C., & Robson, A. J. (1997). The geography of the Humber catchment. *Science of the Total Environment*, **194**, 87-99. https://doi.org/10.1016/S0048-9697(96)05355-7

Jepsen, N., Schreck, C., Clements, S., & Thorstad, E. B. (2005). A brief discussion on the 2% tag/bodymass rule of thumb. In: *Aquatic Telemetry: Advances and Applications: Proceedings of the Fifth Conference on Fish Telemetry held in Europe* (eds M.T. Spedicato, G. Lembo and G. Marmulla). FAO/COISPA, Rome

JNCC. (2019). Fourth report by the United Kingdom under article 17 on the implementation of the habitats directive from January 2013 to December 2018. Peterborough.

Johnson, N. S., Thompson, H. T., Holbrook, C. & Tix, J. A. (2014). Blocking and guiding adult sea lamprey with pulsed direct current from vertical electrodes. *Fisheries Research*, **150**, 38-48. https://doi.org/10.1016/j.fishres.2013.10.006.

Johnson, N. S., Yun, S. -S., Thompson, H. T., Brant, C. O., & Li, W. (2009). A synthesized pheromone induces upstream movement in female sea lamprey and summons them into traps. *Proceedings of the National Academy of Sciences*, **106**, 1021-1026. https://doi.org/10.1073/pnas.0808530106

Johnson, N., Buchinger, T., & Li, W. (2015). Reproductive ecology of lampreys. In: *Lampreys: Biology, Conservation and Control*, (eds Docker, M.). 265-303, Springer, Dordrecht.  https://doi.org/10.1007/978-94-017-9306-3_6

Jones, J., Börger, L., Tummers, J., Jones, P., Martyn, L., Kerr, J., Kemp, P., Bizzi, S., Consuegra, S., Marcello, L., Vowles, A., Belletti, B., Verspoor, E., Van de Bund, W., Gough, P., & Garcia de Leaniz, C. (2019). A comprehensive assessment of stream fragmentation in Great Britain. *Science of the Total Environment,* **673**, 756–762. https://doi.org/10.1016/j.scitotenv.2019.04.125

Jonsson, B., Waples, R. S., & Friedland, K. D. (1999). Extinction considerations for diadromous fishes. *ICES Journal of Marine Science*, **56**, 405–409. https://doi.org/10.1006/jmsc.1999.0483

Jorge, G., & Sónia, S. (2014). How illegal capture of Glass Eel (*Anguilla anguilla*) affect biodiversity in Tagus river. *International Conference on Hands-on Science*, **11**, 324-330

Jungwirth, M. (1996). Bypass channels at weirs as appropriate aids for fish migration in Rhithral rivers. *River Research and Applications*, **12**, 483-492. https://doi.org/10.1002/(SICI)1099-1646(199607)12:4/5<483::AID-RRR402>3.0.CO;2-B

Jungwirth, M., Schmutz, S., & Weiss, S. (1998). Fish migration and fish bypasses. Fishing News Books, University Press, Cambridge.

Kainzinger, S., Burns, R. C., & Arnberger. A. (2015). Whitewater boater and angler conflict, crowding and satisfaction on the North Umpqua river, Oregon. *Human Dimensions of Wildlife*, **20**, 542-552. https://doi.org/10.1080/10871209.2015.1072757

Kalous, L., Musil, J., Petrtýl, M., Vajglová, T., Romočuský, S., & Bušta, L. (2013). The danger in the anglers' bucket: qualitative and quantitative insight into bait fish market in Prague (Czech Republic). *Acta Societatis Zoologicae Bohemicae*, **77**, 27–35.

Katopodis, C., & Eng, P. (1992). Introduction to fishway design. Unpublished data.

Katopodis, C., Kells, J. A., & Acharya, M. (2001). Nature-like and conventional fishways: alternative concepts? *Canadian Water Resources Journal*, **26**, 211-232, https://doi.org/10.4296/cwrj2602211

Kearney, R. E. (2002). Co-management: the resolution of conflict between commercial and recreational fishers in Victoria, Australia. *Ocean & Coastal Management*, **45**, 201-214. https://doi.org/10.1016/S0964-5691(02)00055-8.

Keefer, M. L., Caudill, C. C., Clabough, T. S., Jepson, M. A., Johnson, E. J., Peery, C. A., Higgs, M. D., & Moserd, M. L. (2013). Fishway passage bottleneck identification and prioritization: a case study of Pacific lamprey at Bonneville dam. *Canadian Journal of Fisheries and Aquatic Sciences,* **70**, 1551–1565. https://doi.org/10.1139/cjfas-2013-0164

Keller, P. R., Cox, A. N., Loon, C. V., Lodge, D. M., Herborg, L. M., & Rothlisberger, J. (2007). From bait shops to the forest floor: earthworm use and disposal by anglers. *The American Midland Naturalist*, **158**, 321-328. https://doi.org/10.1674/0003-0031(2007)158[321:FBSTTF]2.0.CO;2

Kelly, F., & King, J. (2001). A review of the ecology and distribution of three lamprey species, *Lampetra fluviatilis* (L.), *Lampetra planeri* (Bloch) and *Petromyzon marinus* (L.): a context for conservation and biodiversity considerations in Ireland. *Biology and Environment*, **3**, 165-185.

Kemp, P. S., Russon, I. J., Vowles, A., & Lucas, M. C. (2010). The influence of discharge and temperature on the ability of upstream migrant adult river lamprey (*Lampetra fluviatilis*) to pass experimental overshot and undershot weirs. *River Research and Applications,* **27**,488-498. https://doi.org/10.1002/rra.1364

Kerr, J. R., Karageorgopoulos, P., & Kemp, P. S. (2015). Efficacy of a side-mounted vertically oriented bristle pass for improving upstream passage of European eel (*Anguilla anguilla*) and river lamprey (*Lampetra fluviatilis*) at an experimental Crump weir. *Ecological Engineering,* **85**, 121-131. https://doi.org/10.1016/j.ecoleng.2015.09.013

Kilian, J. V., Klauda, R. J., Widman, S., Kashiwagi, M., Borquin, R., Weglein, S., & Schuster, J. (2012). An assessment of a bait industry and angler behavior as a vector of invasive species. *Biological Invasions*, **14**, 1469–1481. https://doi.org/10.1007/s10530-012-0173-5

Kim, J.-H., Yoon, J.-D., Baek, S.-H., Park, S.-H., Lee, J.-W., Lee, J.-A., & Jang, M.-H. (2016). An efficiency analysis of a nature-like fishway for freshwater fish ascending a large Korean river. *Water*, **8**. https://doi.org/10.3390/w8010003

King J. J., Hanna G., & Wightman G. D. (2008). Ecological impact assessment (EcIA) of the effects of statutory arterial drainage maintenance activities on three lamprey species (*Lampetra planeri* Bloch, *Lampetra fluviatilis* L., and *Petromyzon marinus* L.). Series of Ecological Assessments on Arterial Drainage Maintenance No 9 Environment Section, Office of Public Works, Headford, Co. Galway.

King, S., & O'Hanley, J. R. (2016). Optimal fish passage barrier removal—revisited. *River Research and Application*, **32**, 418– 428. https://doi.org/10.1002/rra.2859.

Kirillova, E. A., Kirillov, P. I., Kucheryavyy, A. V. & Pavlov, D. S. (2011). Downstream migration in ammocoetes of the Arctic lamprey *Lethenteron* *camtschaticum* in some Kamchatka rivers. *Journal of Ichthyology*, **51**, 1117–1125. https://doi.org/10.1134/S0032945211110051

Knight, G. A. (1999). Consumer preferences for foreign and domestic products. *Journal of Consumer Marketing*, **16**, 1-11.

Kreuter, F., Presser, S., & Tourangeau, R. (2008). Social desirability bias in CATI, IVR, and web surveys: the effects of mode and question sensitivity. *Public Opinion Quarterly*. **72**, 847–865. https://doi.org/10.1093/poq/nfn063

Kujawa, R., Cejkob, B., I., Fopp-Bayatc, D., Judyckab, S., Glińska-Lewczukd, K., Timofted, C. M., Nowosada, J., & Kucharczyk, D. (2019). Reproduction of endangered river lamprey (*Lampetra fluviatilis*) in controlled conditions. *Animal Reproduction Science*, **203**, 75-83. https://doi.org/10.1016/j.anireprosci.2019.02.010

Kuparinen, A., Klefoth, T., & Arlinghaus, R. (2010). Abiotic and fishing-related correlates of angling catch rates in pike (*Esox lucius*). *Fisheries Research*, **105**, 111-117. https://doi.org/10.1016/j.fishres.2010.03.011.

Kuraku, S., Qiu, H., & Meyer, A. (2012). Horizontal transfers of Tc1 elements between teleost fishes and their vertebrate parasites. *Lampreys, Genome Biology and Evolution*, **4**, 929–936. https://doi.org/10.1093/gbe/evs069.

Lanzing, W. J. R. (1959). Studies on the river lamprey, *Lampetra fluviatilis*, during its anadromous migration. Uitgeversmaatschappij Neerlandia, Utrecht.

Lavis, D. S., Hallett, A., Koon, E. M., & McAuley, T. C. (2003). History of and advances in barriers as an alternative method to suppress sea lampreys in the Great Lakes. *Journal of Great Lakes Research*, **29**, 362-372. https://doi.org/10.1016/S0380-1330(03)70500-0.

Lennon, R. E. (1954). Feeding mechanism of the sea lamprey and its effect on host fishes. *Fishery Bulletin of the Fish and Wildlife Service*, 56, 247–293.

Li, W., Scott, A.P., Siefkes, M.J., Yun, S. -S., & Zielinski, B. (2003). A male pheromone in the sea lamprey (*Petromyzon marinus*): an overview. *Fish Physiology and Biochemistry*, **28**, 259–262. https://doi.org/10.1023/B:FISH.0000030546.09761.64

Liermann, C. R., Nilsson, C., Robertson, J., & Ng, R. Y. (2012). Implications of dam obstruction for global freshwater fish diversity. *Bioscience,* **62**, 539–548. https://doi.org/10.1525/bio.2012.62.6.5

Limburg, K. E., & Waldman, J. R. (2009). Dramatic declines in north Atlantic diadromous fishes. *Bioscience,* **59**, 955–965. https://doi.org/10.1525/bio.2009.59.11.7

Lothian, A. J., Tummers, J. S., Albright, A. J., O'Brien, P., & Lucas, M. C. (2020). River connectivity restoration for upstream-migrating European river lamprey: The efficacy of two horizontally-mounted studded tile designs. *River Research and Applications*, 1– 11. https://doi.org/10.1002/rra.3734

Lucas, M. C., & Baras, E. (2001). Migration of freshwater fishes. Blackwell Science, Oxford.

Lucas, M. C., Bubb, D. H., Jang, M. H., Ha, K., & Masters, J. E. G. (2009). Availability of and access to critical habitat in regulated rivers: effects of low-head barriers on threatened lampreys. *Freshwater Biology,* **54**, 621–634. https://doi.org/10.1111/j.1365-2427.2008.02136.x

Lucas, M. C., Hume, J. B., Almeida, P. R., Aronsuu, K., Habit, E., Silva, S., Wang, C. J., & Zampatti, B. (2020). Emerging conservation initiatives for lampreys: research challenges and opportunities. *Journal of Great Lakes Research*. https://doi.org/10.1016/j.jglr.2020.06.004.

Lucas, M. C., Mercer, T., Batley, E., Frear, P. A., Peirson, G., Duncan, A., & Kubecka, J. (1998). Spatio–temporal variations in the distribution and abundance of fish in the Yorkshire Ouse system. *Science of The Total Environment*, **210**, 437-455. https://doi.org/10.1016/S0048-9697(98)00030-8.

Luehring, M. A., Wagner, C. M., & Li, W. (2011). The efficacy of two synthesized sea lamprey sex pheromone components as a trap lure when placed in direct competition with natural male odors. *Biological Invasions*, **13**, 1589–1597. https://doi.org/10.1007/s10530-010-9916-3

Lundblad, L., & Davies, I. A. (2016). The values and motivations behind sustainable fashion consumption. *Journal of Consumer Behaviour*, **15**, 149–162. https://doi.org/10.1002/cb.1559.

Lungenhausen, M., Lange, S., Maier, C., Schaub, C., Trampisch H. J., Endres, H. G. (2007). Randomised controlled comparison of the health survey short form (SF-12) and the graded chronic pain scale (GCPS) in telephone interviews versus self-administered questionnaires. Are the results equivalent? *BMC Medical Research Methodology*. **7**, 50. https://doi.org/10.1186/1471-2288-7-50

Luzier, C. W., Schaller, H. A., Bostrom, J. K., Cook-Tabor, C., Goodman, D. H., Nelle, R. D., Ostrand, K., & Strief, B. (2011). Pacific lamprey (*Entosphenus tridentata*) assessment and template for conservation measures. U.S. Fish and Wildlife Service, Portland, Oregon.

Lynch, T. P., Wilkinson, E., Melling, L., Hamilton, R., Macready, A., & Feary, S. (2004). Conflict and impacts of divers and anglers in a marine park. *Environmental Management*, **33**, 196-211. https://doi.org/10.1007/s00267-003-3014-6

MacAvoy, S. E., Garman, G. C., & Macko. S. A. (2009). Anadromous fish as marine nutrient vectors. *Fishery Bulletin,* **107**, 165–174

MacEachen, D. C., Russell, R. W., & Whittle, D. M. (2000). Spatial distribution of mercury and organochlorine contaminants in Great Lakes sea lamprey (*Petromyzon marinus*). *Journal of Great Lakes Research*, **26**, 112-119. https://doi.org/10.1016/S0380-1330(00)70678-2.

Maitland, P. S. (2003). Ecology of the river, brook and sea lamprey. Conserving Natura 2000 Rivers Ecology Series No.5. English Nature, Peterborough.

Maitland, P. S., Morris, K. H., & East, K. (1994). The ecology of lampreys (Petromyzonidae) in the Loch Lomond area. *Hydrobiologia*, **290**, 105–120. https://doi.org/10.1007/BF00008958

Maitland, P. S., Renaud, C. B., Quintella, B. R., Close D. A., & Docker M. F. (2015). Conservation of native lampreys. In: L*ampreys: Biology, Conservation and Control* (eds Docker, M.). 375-428 Springer, Dordrecht. https://doi.org/10.1007/978-94-017-9306-3_8

Mallen-Cooper, M., & Brand, D. A. (2007). Non-salmonids in a salmonid fishway: what do 50 years of data tell us about past and future fish passage? *Fisheries Management and Ecology,* **14**, 319–332. https://doi.org/10.1111/j.1365-2400.2007.00557.x

Mallen-Cooper, M., Zampatti, B., Stuart, I. G., & Baumgartner, L. J. (2008). Innovative fishways – manipulating turbulence in the vertical slot design to improve performance and reduce cost. Murray Darling Basin Authority, NSW Australia.

Manzon R., Youson J., Holmes J. (2015). Lamprey metamorphosis. In: *Lampreys: Biology, Conservation and Control*, (eds Docker, M.). 139-214, Springer, Dordrecht. https://doi.org/10.1007/978-94-017-9306-3_4

Marsden, J. E., & Siefkes, M. J. (2019). Control of invasive sea lamprey in the Great Lakes, Lake Champlain, and Finger Lakes of New York. In: *Lampreys: Biology, Conservation and Control* (eds Docker, M.). Springer, Dordrecht. https://doi.org/10.1007/978-94-024-1684-8_5

Marshall, G. (2005). The purpose, design and administration of a questionnaire for data collection. *Radiography*. **11**, 131-136. https://doi.org/10.1016/j.radi.2004.09.002.

Marzano, M., Carss, D. N., & Cheyne, I. (2013). Managing European cormorant-fisheries conflicts: problems, practicalities and policy. *Fish Management Ecology*, **20**, 401-413. https://doi.org/10.1111/fme.12025

Masters, J. E. G., Jang, M. -H., Ha, K., Bird, P. D., Frear, P. A., & Lucas, M. C. (2006). The commercial exploitation of a protected anadromous species, the river lamprey (*Lampetra fluviatilis* (L.)), in the tidal River Ouse, north-east England. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **16,** 77-92. https://doi.org/10.1002/aqc.686

Mateus, C. S., Rodríguez-Muñoz, R., Quintella, B. R., Alves, M. J., & Almeida, P. R. (2012). Lampreys of the Iberian Peninsula: distribution, population status and conservation. *Endangered Species Research*, **16**, 183-198. https://doi.org/10.3354/esr00405

McBride, R. S., & Matheson, R. E. (2011). Florida's diadromous fishes: biology, ecology, conservation, and management. *Florida Scientist*, **74**, 187-213.

McClenachan, L. (2013). Recreation and the “right to fish” movement: anglers and ecological degradation in the Florida Keys. *Environmental History*, **18**, 76–87. https://doi.org/10.1093/envhis/ems110

McClenachan, L., Dissanayake, S. T. M., & Chen, X. (2016). Fair trade fish: consumer support for broader seafood sustainability. *Fish and Fisheries*, **17**, 825-838. https://doi.org/10.1111/faf.12148

McDowall, R. M. (1988). Diadromy in fishes: migrations between freshwater and marine environments. London: Croom Helm.

McDowall, R. M. (1997). The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. *Reviews in Fish Biology and Fisheries*, **7**, 443-462. https://doi.org/10.1023/A:1018404331601

McDowall, R. M. (1999) Different kinds of diadromy: different kinds of conservation problems, *ICES Journal of Marine Science*, **56**, 410–413. https://doi.org/10.1006/jmsc.1999.0450

McDowall, R. M. (2011). Ikawai: freshwater fishes in Māori culture and economy. Canterbury University Press: Christchurch, New Zealand.

Meffe, G. K. (2002). Connecting science to management and policy in freshwater fish conservation. In: *Conservation of freshwater fish: options for the future* (eds Collares-Pereira, M. J., Cowx, I. G., & Coelho, M. M.). Fishing News Books, Blackwell Science, Oxford, 363-372.

Merivirta, L. O., Nordlund, J., & Korkeala, H. J. (2001). Cadmium, mercury and lead content of river lamprey caught in Finnish rivers. *Arch Lebensmittelhyg,* **52,** 69–71.

Merivirta, L., Kivisaari, M., Berg, S., Peltonen, K., Björkroth, J., & Korkeala, H. (2006). Accumulation of PCBs and organochlorine pesticides in river-caught European river lamprey (*Lampetra fluviatillis*) in Finland. *Bulletin of Environmental Contamination & Toxicology,* **76**, 97-504

Merz, J. E., & Moyle, P. B. (2006). Salmon, wildlife, and wine: marine-derived nutrients in human-dominated ecosystems of central California. *Ecological Applications*, **16**, 999-1009. https://doi.org/10.1890/1051-0761(2006)016[0999:SWAWMN]2.0.CO;2

Mesa, M. G., Bayer, J. M. & Seelye, J. G. (2003). Swimming performance and physiological responses to exhaustive exercise in radio-tagged and untagged pacific lampreys. *Transactions of the American Fisheries Society*, **132**, 483-492. https://doi.org/10.1577/1548-8659(2003)132<0483:SPAPRT>2.0.CO;2

Michael, J. H. (1980). Repeat spawning of Pacific lamprey. *California Fish and Game*, **66**, 186–187

Miehls, S. M., Johnson, N. S., & Hrodey, P. J. (2017). Test of a nonphysical barrier consisting of light, sound, and bubble screen to block upstream movement of sea lampreys in an experimental raceway. *North American Journal of Fisheries Management*, **37**, 660-666. https://doi.org/10.1080/02755947.2017.1308892

Minson, J. A., VanEpps, E. M., Yip, J. A., & Schweitzer, M. E. (2018). Eliciting the truth, the whole truth, and nothing but the truth: The effect of question phrasing on deception. *Organizational Behavior and Human Decision Processes*. **147**, 76-93. https://doi.org/10.1016/j.obhdp.2018.05.006.

Moore, J. W., & Mallatt, J. M. (1980). Feeding of larval lamprey. *Canadian Journal of Fisheries and Aquatic Sciences,* **37**, 1658-1664, https://doi.org/10.1139/f80-213

Morris, K. H., & Maitland, P. S. (1987). A trap for catching adult lampreys (Petromyzonidae) in running water. *Journal of Fish Biology*, **31**, 513–516.

Moser M., Almeida P., Kemp P. & Sorensen P. (2015). Lamprey spawning migration. In: *Lampreys: biology, conservation and control* (eds Docker M.). 215-263. Springer, Dordrecht. https://doi.org/10.1007/978-94-017-9306-3_5

Moser, M. L., Hume, J. B., Aronsuu, K. K., Lampman, R. T., & Jackson A. D. (2019). Lamprey reproduction and early life history: insights from artificial propagation. In: *Lampreys: Biology, Conservation and Control* (eds Docker, M.). 187-245, Springer, Dordrecht. https://doi.org/10.1007/978-94-024-1684-8_2

Moser, M. L., Jackson, A. D., Lucas, M. C., & Mueller, R. P. (2015). Behavior and potential threats to survival of migrating lamprey ammocoetes and macrophthalmia. *Reviews in Fish Biology and Fisheries,* **25**, 103-116. https://doi.org/10.1007/s11160-014-9372-8

Moser, M. L., Keefer, M. L., Pennington, H. T., Ogden, D. A., & Simonson, J. E. (2010). Development of Pacific lamprey fishways at a hydropower dam. *Fisheries Management and Ecology*, **18**, 190–200. https://doi.org/10.1111/j.1365-2400.2010.00773.x

Moursund, R. A., Dauble, D. D., & Langeslay, M. J. (2003). Turbine intake diversion screens: investigating effects on Pacific lamprey. *Hydro Review*, **22**, 40–46.

Musseau, C., Boulenger, C., Crivelli, A. J., Lebel, I., Pascal, M., Boulétreau, S., & Santoul, F. (2014). Native European eels as a potential biological control for invasive crayfish. *Freshwater Biology*, **60**, 636-645.

Myers, G. (1949). Usage of anadromous, catadromous and allied terms for migratory fishes. *Copeia*, **2**, 89-97. https://doi.org/10.2307/1438482

Myllynen, K. E., Ojutkangas, E. & Nikinmaa, M. (1997). River water with high iron concentration and low pH causes mortality of lamprey roe and newly hatched larvae. *Ecotoxicology and Environmental Safety,* **36**, 43–48. https://doi.org/10.1006/eesa.1996.1484

Näslund, I., Eriksson, T., Hannersjö, D., Bergwall, L., Jacobsson, G., & Leonardsson, K. (2010). Time trends in angler compliance with harvest regulations in stream fisheries. *Fisheries Management and Ecology*, **17**, 52-62. https://doi.org/10.1111/j.1365-2400.2009.00707.x

NatureServe. 2013. Petromyzon marinus. The IUCN Red List of Threatened Species 2013: e.T16781A18229984. https://dx.doi.org/10.2305/IUCN.UK.2013-1.RLTS.T16781A18229984.en.

Nguyen, V. M., Rudd, M. A., Hinch, S. G., & Cooke, S. J. (2013). Recreational anglers' attitudes, beliefs, and behaviors related to catch-and-release practices of Pacific salmon in British Columbia. *Journal of Environmental Management*, **128**, 852-865. https://doi.org/10.1016/j.jenvman.2013.06.010

Nielsen, J. R., & Mathiesen, C. (2006). Stakeholder preferences for Danish fisheries management of sand eel and Norway pout. *Fisheries Research*, **77**, 92-101. https://doi.org/10.1016/j.fishres.2005.08.002.

Nigel W Arnell, N. W. (2003). Relative effects of multi-decadal climatic variability and changes in the mean and variability of climate due to global warming: future streamflows in Britain. *Journal of Hydrology*, **270**, 195-213. https://doi.org/10.1016/S0022-1694(02)00288-3.

Nijman, V. (2017). North Africa as a source for European eel following the 2010 EU CITES eel trade ban. *Marine Policy*, **85**, 133-137. https://doi.org/10.1016/j.marpol.2017.06.036.

Nilsen, E. B., Hapke, W. B., McIlraith, B., & Markovchick, D. (2015). Reconnaissance of contaminants in larval Pacific lamprey (*Entosphenus tridentatus*) tissues and habitats in the Columbia River Basin, Oregon and Washington, USA. *Environmental Pollution*, **201**, 121-130, https://doi.org/10.1016/j.envpol.2015.03.003.

Noble, M., Duncan, P., Perry, D., Prosper, K., Rose, D., Schnierer, S., Tipa, G., Williams, E., Woods, R., & Pittock, J. (2016). Culturally significant fisheries: keystones for management of freshwater social-ecological systems. *Ecology and Society*, **21**. http://dx.doi.org/10.5751/ES-08353-210222

Nolan, E. T., Britton. J. R., & Curtin, S. (2019). Angler behaviours and motivations for exploiting invasive and native predatory fishes by catch-and-release: a case study on the River Severn catchment, Western England. *Human Dimensions of Wildlife*, **24**, 463-479. https://doi.org/10.1080/10871209.2019.1628324

Noonan, M. J., Grant, J. W. A., & Jackson, C. D. (2011). A quantitative assessment of fish passage efficiency. *Fish and Fisheries,* **13**, 450-464. https://doi.org/10.111/j.1467-2979.2011.00445.x.

Novacek, M. J. (2008). Engaging the public in biodiversity issues. *Proceedings of the National Academy of Sciences*, **105**, 11571-11578. https://doi.org/10.1073/pnas.0802599105

Nunn, A. D., & Cowx, I. G. (2012). Restoring river connectivity: prioritizing passage improvements for diadromous fishes and lampreys. *Ambio*, **41**, 402–409. https://doi.org/10.1007/s13280-012-0281-6

Nunn, A., Harvey, J., Noble, R., & Cowx, I. (2008). Condition assessment of lamprey populations in the Yorkshire Ouse catchment, north-east England, and the potential influence of physical migration barriers. *Aquatic Conservation Marine and Freshwater Ecosystems*, **18**, 175-189. https://doi.org/10.1002/aqc.863

O'Connor, W. (2007). A survey of juvenile lamprey populations in the Corrib and Suir catchments. Irish Wildlife Manuals No. 26. National Parks and Wildlife Service, Department of Environment, Heritage and Local Government, Dublin, Ireland.

O'Cathain, A., & Thomas, K. J. (2004). "Any other comments?" open questions on questionnaires – a bane or a bonus to research? *BMC Medical Research Methodology*. **4**, 25. https://doi.org/10.1186/1471-2288-4-25

Ojutkangas, E., Aronen, K., & Laukkanen, E. (1995). Distribution and abundance of river lamprey (*Lampetra fluviatilis*) ammocoetes in the regulated river Perhonkoki. *Regulated Rivers: Research and Management*, **10**, 239–245. https://doi.org/10.1002/rrr.3450100218

Osório, J., & Rétaux, S. (2008). The lamprey in evolutionary studies. *Development genes and evolution*, **218**, 221–235. https://doi.org/10.1007/s00427-008-0208-1

Pendergrass, A. G., Knutti, R., Lehner, F., Deser, C., & Sanderson, B. M. (2017). Precipitation variability increases in a warmer climate. *Scientific Reports*, **7**, 17966. https://doi.org/10.1038/s41598-017-17966-y

Pereira, E., Cardoso, G. R., Quintella, B. R., Mateus, C. S., Alexandre, C. M., Oliveira, R. L., Belo, A. F., Telhado, A., Quadrado, M. F., Batista, C. M., & Almeida, P. R. (2019). Proposals for optimizing sea lamprey passage through a vertical-slot fishway. *Ecohydrology*, **12**. https://doi.org/10.1002/eco.2087

Pereira, E., Quintella, B. R., Mateus, C. S., Alexandre, C. M., Belo, A. F., Telhado, A., Quadrado, M. F., & Almeida, P. R. (2017). Performance of a vertical-slot fish pass for the sea lamprey Petromyzon marinus L. and habitat recolonization. *River Research and Application*, **33**, 16– 26. https://doi.org/10.1002/rra.3054.

Petersen Lewis, R. S. (2009). Yurok and Karuk traditional ecological knowledge: insights into Pacific lamprey populations of the lower Klamath basin. *Biology, management, and conservation of lampreys in North America*, 1, 1–39.

Petrinovich, L., & O'Neill, P. (1996). Influence of wording and framing effects on moral intuitions. *Ethology and Sociobiology*. **17**, 145-171. https://doi.org/10.1016/0162-3095(96)00041-6.

Phelps, N. B. D., Goodwin, A. E., Marecaux, E., & Goyal, S. M. (2013). Comparison of treatments to inactivate viral hemorrhagic septicemia virus (VHSV-IVb) in frozen baitfish. *Disease of Aquatic Organisms,* **102**, 211-216. https://doi.org/10.3354/dao02549

Pickering, A. D. (1978). Physiological aspects of the life cycle of the river lamprey, *Lampetra fluviatilis* L. In: *Forty-sixth annual report for the year ended 31st March 1978*. Ambleside, UK, Freshwater Biological Association, 40-46.

Pike, C., Crook, V., & Gollock, M. (2020). *Anguilla anguilla*. *The IUCN red list of threatened species 2020*: e.T60344A152845178. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T60344A152845178.en.

Poff, N, L., Olden, J. D., Merritt, D. M., & Pepin, D. M. (2007). Homogenization of regional river dynamics by dams and global biodiversity implications. *Proceedings of the National Academy of Sciences*, **104**, 5732-5737. https://doi.org/10.1073/pnas.0609812104

Potter I., Gill H., Renaud C., & Haoucher D. (2015). The taxonomy, phylogeny, and distribution of lampreys. *Lampreys: Biology, Conservation and Control* (eds Docker, M.). 35-73, Springer, Dordrecht. https://doi.org/10.1007/978-94-017-9306-3_2

Potter, I. C. (1970). The life cycles and ecology of Australian lampreys of the genus *Mordacia*. *Journal of Zoology*, **161**, 487-511. https://doi.org/10.1111/j.1469-7998.1970.tb02051.x

Potter, I. C. (1980). The Petromyzoniformes with particular reference to paired species. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 1595-1615. https://doi.org/10.1139/f80-207

Potter, I. C., Hilliard, R. W., & Bird, D. J. (1982). Stages in metamorphosis. In: *Biology of lampreys* (eds Hardisty, M. W., & Potter, I. C.), **4b**, 137–164. Academic Press, London.

Privolnyev, T. I. (1964). Ecological and physiological features of the larval river lamprey, *Lampetra fluviatilis* (L.). *Izv Vses Nauchno-Issledovatelskogo Instituta Ozernogo i Rechnogo Rÿbnogo,* **58**, 180–185

Proctor, N., & Musk, W. (2001). Fish impingement assessment: Final report. Humber Power Ltd. Institute of Estuarine and Coastal Studies, University of Hull, report no. ZO109-F2001.

Quintella, B. R., Andrade, N. O., Dias, N. M., & Almeida, P. R. (2007). Laboratory assessment of sea lamprey larvae burrowing performance. *Ecology of Freshwater Fish*, **16**, 177-182. https://doi.org/10.1111/j.1600-0633.2006.00209.x

Quintella, B. R., Andrade, N. O., Espanhol, R., & Almeida, P. R. (2005). The use of PIT telemetry to study movements of ammocoetes and metamorphosing sea lampreys in river beds. *Journal of Fish Biology*, **66**, 97-106. https://doi.org/10.1111/j.0022-1112.2005.00584.x

Radomski, P., Heinrich, T., Jones, T. S., Rivers, P., & Talmage, P. (2006). Estimates of tackle loss for five Minnesota walleye fisheries. *North American Journal of Fisheries Management*, **26**, 206-212. https://doi.org/10.1577/M05-121.1

Reed, J. R., & Parsons, B. G. (1999). Angler opinions of bluegill management and related hypothetical effects on bluegill fisheries in four Minnesota lakes. *North American Journal of Fisheries Management*, **19**, 515-519. https://doi.org/10.1577/1548-8675(1999)019<0515:AOOBMA>2.0.CO;2

Rees, E. M. A., Edmonds-Brown, V. R., Alam, M. F., Wright, R. M., Britton, J. R., Davies, G. D., & Cowx, I. G. (2017). Socio-economic drivers of specialist anglers targeting the non-native European catfish (*Silurus glanis*) in the UK. *PLOS ONE*, **12**. https://doi.org/10.1371/journal.pone.0178805

Reinhardt, U. G., Eidietis, l., Friedl, S. E., &  Moser, M. L. (2008). Pacific lamprey climbing behavior. *Canadian Journal of Zoology,* **86**, 1264–1272. https://doi.org/10.1139/Z08-112

Renaud C. B., & Cochran P. A. (2019). Post-metamorphic feeding in lampreys*. Lampreys: Biology, Conservation and Control* (eds Docker, M.). 247-285, Springer, Dordrecht. https://doi.org/10.1007/978-94-024-1684-8_3

Renaud, C. B. (1997). Conservation status of northern hemisphere lampreys. *Journal of Applied Ichthyology,* **13**, 143–148. https://doi.org/10.1111/j.1439-0426.1997.tb00114.x

Renaud, C. B. (2011). Lampreys of the world. An annotated and illustrated catalogue of lamprey species known to date. FAO Species Catalogue for Fishery Purposes. No. 5. Rome, FAO.

Renyard, T. S., & Hilborn, R. (1986). Sports anglers preferences for alternative regulatory methods. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 240–242. https://doi.org/10.1139/f86-029

Reynolds, J. D., Dulvy, N. K., & Roberts, C. M. (2002). Exploitation and other threats to fish conservation. In: *Handbook of fish and fisheries, 2: fisheries* (eds Hart, P. J. B., & Reynolds, J. D.). Oxford: Blackwell Science. 319–341.

Richards, S. A. (2008). Dealing with overdispersed count data in applied ecology. *Journal of Applied Ecology*, **45**, 218-227. https://doi.org/10.1111/j.1365-2664.2007.01377.x

Richards, J. L., Sheng, V., Yi, C. W., Ying, C. L., Ting, N. S., Sadovy, Y., & Baker, D. (2020). Prevalence of critically endangered European eel (*Anguilla anguilla*) in Hong Kong supermarkets. *Science Advances*, **6**. https://doi.org/10.1126/sciadv.aay0317

Rodgers, C. J., Mohan, C. V., & Peeler, E. J. (2011). The spread of pathogens through trade in aquatic animals and their products. *Revue scientifique et technique*, **30**, 241–56

Rose, B. P, & Mesa, M. G. (2012). Effectiveness of common fish screen materials to protect lamprey ammocoetes. *North American Journal of Fisheries Management*, **32**, 597-603. https://doi.org/10.1080/02755947.2012.678965

Rosell, R., Harrod, C., Griffiths, D., & McCarthy, T. (2004). Conservation of the Irish populations of the pollan *Coregonus autumnalis*. *Biology and Environment: Proceedings of the Royal Irish Academy*, **104**, 67-72.

Rouder, J. N., Engelhardt, C. R., McCabe, S., & Morey, R. D. (2016). Model comparison in ANOVA. *Psychonomic Bulletin and Review*, **23**, 1779–1786. https://doi.org/10.3758/s13423-016-1026-5

Rowley, J. (2014). Designing and using research questionnaires. *Management Research Review*. **37**, 308-330. https://doi.org/10.1108/MRR-02-2013-0027

Russon, I. J., & Kemp, P. S. (2011). Experimental quantification of the swimming performance and behaviour of spawning run river lamprey *Lampetra fluviatilis* and European eel *Anguilla anguilla*. *Journal of Fish Biology,* **78**, 1965–1975. https://doi.org/10.1111/j.1095-8649.2011.02965.x

Russon, I. J., Kemp, P. S., & Lucas, M. C. (2011). Gauging weirs impede the upstream migration of adult river lamprey *Lampetra fluviatilis*. *Fisheries Management and Ecology,* **18**, 201–210. https://doi.org/10.1111/j.1365-2400.2010.00778.x

Salado R., & Vencovska, J. (2018). A survey of freshwater angling in England, Phase 1. Environment Agency. Available at https://www.gov.uk/government/publications/a-survey-of-freshwater-angling-in-england (Last accessed 10/12/2020)

Salmelin, J., Karjalainen, A. K., Hämäläinen, H., Leppänen, M. T., Kiviranta, H., Kukkonen, J. V. K., & Vuori, K. M. (2016). Biological responses of midge (*Chironomus riparius*) and lamprey (*Lampetra fluviatilis*) larvae in ecotoxicity assessment of PCDD/F-, PCB- and Hg-contaminated river sediments. *Environmental Science and Pollution Research,* **23**, 18379–18393. https://doi.org/10.1007/s11356-016-7014-5

Salmon and Freshwater Fisheries Act. (1975). Available at https://www.legislation.gov.uk/ukpga/1975/51. (Last accessed 10/12/2020)

Sandlund, O. T., Museth, J., & Øistad, S. (2016). Migration, growth patterns, and diet of pike (*Esox lucius*) in a river reservoir and its inflowing river. *Fisheries Research*, **173**, 53-60. https://doi.org/10.1016/j.fishres.2015.08.010.

Santos, J. M., Ferreira, M. T., Godinho, F. N., & Bochechas, J. (2005). Efficacy of a nature-like bypass channel in a Portuguese lowland river. *Journal of Applied Ichthyology*, **21**, 381-388. https://doi.org/10.1111/j.1439-0426.2005.00616.x

Santucci Jr., V, J., Gephard, S. R., & Pescitelli, S. M. (2005). Effects of multiple low-head dams on fish, macroinvertebrates, habitat, and water quality in the Fox River, Illinois. *North American Journal of Fisheries Management*, **25**, 975-992. https://doi.org/10.1577/M03-216.1

Saunders, C., Guenther, M., Tait, P. R., Kaye-Blake, W., Saunders, J., Miller, S., & Abell, W. (2011). Consumer attitudes towards sustainability attributes on food labels in the UK and Japan. 85th Annual conference of the agricultural economics society. Warwick University, Coventry, UK.

Schakner, Z., Purdy, C., & Blumstein, D. T. (2019). Contrasting attitudes and perceptions of California sea lions by recreational anglers and the media. *Marine Policy*, **109**, 103710. https://doi.org/10.1016/j.marpol.2019.103710.

Schmetterling, D. A. (2001). Seasonal movements of fluvial westslope cutthroat trout in the Blackfoot river drainage, Montana. *North American Journal of Fisheries Management*, **21**, 507-520. https://doi.org/10.1577/1548-8675(2001)021<0507:SMOFWC>2.0.CO;2

Schroeder, S. A., & Fulton, D. C. (2013). Comparing catch orientation among Minnesota walleye, northern pike, and bass anglers. *Human Dimensions of Wildlife*, **18**, 355-372. https://doi.org/10.1080/10871209.2013.789938

Schuett, M. A., Kyle, G. T., Leitz, J., Kurzawski, K., & Lee, K. (2014). Anglers' motivations for volunteering with fishing or conservation organizations. *Fisheries*, **39**, 7, 305-311. https://doi.org/10.1080/03632415.2014.924407

Shao, J., & Ünal, E. (2019). What do consumers value more in green purchasing? Assessing the sustainability practices from demand side of business. *Journal of Cleaner Production*, **209**, 1473-1483. https://doi.org/10.1016/j.jclepro.2018.11.022.

Sherburne, S., & Reinhardt, U. G. (2016). First test of a species-selective adult sea lamprey migration barrier. *Journal of Great Lakes Research*, **42**, 893-898. https://doi.org/10.1016/j.jglr.2016.04.009.

Shirakawa, H., Yanai, S., & Goto, A. (2013). Lamprey larvae as ecosystem engineers: physical and geochemical impact on the streambed by their burrowing behavior. *Hydrobiologia*, **701**, 313-322. https://doi.org/10.1007/s10750-012-1293-8

Siewert, H. F., & Cave, J. B. (1990). Survival of released bluegill, *Lepomis macrochirus*, caught on artificial flies, worms, and spinner lures. *Journal of Freshwater Ecology*, **5**, 407-411. https://doi.org/10.1080/02705060.1990.9665256

Silva, A. T., Lucas, M. C., Castro-Santos, T., Christos Katopodis, C., Baumgartner, L. J., Thiem, J. D., Aarestrup, K., Pompeu, P. S., O'Brien, G. C., Douglas C. Braun, D. C., Burnett, N. J., Zhu, D. Z., Fjeldstad, H. P., Forseth, T., Rajaratnam, N., Williams, J. G., & Cooke, S. J. (2018). The future of fish passage science, engineering, and practice. *Fish and Fisheries*, **19**, 340–362. https://doi.org/10.1111/faf.12258

Silva, S., Barca, S. & Cobo, F. (2016). Advances in the study of sea lamprey *Petromyzon marinus* Linnaeus, 1758, in the NW of the Iberian Peninsula. In: *Jawless Fishes of the World* (Volume 1 (eds. A. Orlov & R. Beamish)), 346–385. Cambridge Scholars Publishing, Newcastle upon Tyne, UK.

Silva, S., Gooderham, A., Forty, M., Morland, B., & Lucas, M. C. (2014). Egg drift and hatching success in European river lamprey *Lampetra fluviatilis*: is egg deposition in gravel vital to spawning success? *Aquatic Conservation: Marine and Freshwater ecosystems,* **25**, 534-543. https://doi.org/10.1002/aqc.2486.

Silva, S., Lowry, M., Macaya-Solis, C., Byatt, B., & Lucas, M. C. (2017). Can navigation locks be used to help migratory fishes with poor swimming performance pass tidal barrages? A test with lampreys. *Ecological Engineering*, **102**, 291-302. https://doi.org/10.1016/j.ecoleng.2017.02.027.

Sjöberg, K. (1989). Time-related predator/prey interactions between birds and fish in a northern Swedish river. *Oecologia,* **80**, 1-10. https://doi.org/10.1007/BF00789924

Sjöberg, K. (2011). River lamprey *Lampetra fluviatilis* (L.) fishing in the area around the Baltic sea. *Journal of Northern Studies*, **5**, 51–86.

Smith, C. L., Gilden, J. D., Cone, J. S., & Steel, B. S. (1997). Contrasting views of coastal residents and coastal Coho restoration planners. *Fisheries*, **22**, 8-15. https://doi.org/10.1577/1548-8446(1997)022<0008:CVOCRA>2.0.CO;2

Smith, J. S., & Marsden, J. E. (2009). Factors affecting sea lamprey egg survival. *North American Journal of Fisheries Management,* **29**, 859-868. https://doi.org/10.1577/M07-196.1

Smith, P. A. (2002). The relationship between stock and catch and the effect of bait on catch as determined for a UK recreational catch and release fishery. *Fisheries Management and Ecology*, **9**, 261-266. https://doi.org/10.1046/j.1365-2400.2002.00311.x

Smith-Vaniz, W. F., Sidibe, A., Nunoo, F., Lindeman, K., Williams, A. B., Quartey, R., Camara, K., Carpenter, K. E., Montiero, V., de Morais, L., Djiman, R., Sylla, M., & Sagna, A. (2015). *Trachurus trachurus*. *The IUCN red list of threatened species 2015*: e.T198647A43157137. https://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T198647A43157137.en.

Soga, M., & Baston, K. L. (2018). Shifting baseline syndrome: causes, consequences, and implications. *Frontiers in Ecology and the Environment*, **16**, 222– 230. https://doi.org/10.1002/fee.1794

Sorensen, P. W., & Hoye, T. R. (2007). A critical review of the discovery and application of a migratory pheromone in an invasive fish, the sea lamprey *Petromyzon marinus* L. *Journal of Fish Biology*, **71**, 100-114. https://doi.org/10.1111/j.1095-8649.2007.01681.x

Sorensen, P., Fine, J., Dvornikovs, V., Jeffrey, C. S., Shao, F., Wang, J., Vrieze, L. A., Anderson, K. A., & Hoye, T. R. (2005). Mixture of new sulfated steroids functions as a migratory pheromone in the sea lamprey. *Natural Chemical Biology*, **1**, 324–328. https://doi.org/10.1038/nchembio739

Starkie, A. (2003). Management issues relating to the European eel, *Anguilla anguilla*. *Fisheries Management and Ecology*, **10**, 361-364. https://doi.org/10.1111/j.1365-2400.2003.00351.x

Stewart-Russon, I. J. (2011). The response of eel, lamprey and brown trout to conditions associated with barriers to up- and downstream movement under experimental conditions in a flume, University of Southampton, School of Civil Engineering and the Environment, PhD Thesis, 177 pages.

Stoll, J. R., Ditton, R. B., & Stokes, M. E. (2009). Sturgeon viewing as nature tourism: to what extent do participants value their viewing experiences and the resources upon which they depend? *Journal of Ecotourism*, **8**, 254-268. https://doi.org/10.1080/14724040902730573

Strayer, D. L., & Dudgeon, D. (2020). Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society*, **29**, 344-358. https://doi.org/10.1899/08-171.1

Streif, B. (2009). Considering Pacific lampreys when implementing instream activities. *Biology, management, and conservation of lampreys in North America*, **1**, 255–268.

Sun, J., Yu, S., Xue, Z., Liu, C., Wu, Y., Liu, X., & Li, Q. (2010). Lamprey buccal gland secretory protein-2 (BGSP-2) inhibits human T lymphocyte proliferation. *Current Zoology*, **56**, 252–258. https://doi.org/10.1093/czoolo/56.2.252

Sutton, S. (2003). Personal and situational determinants of catch-and-release choice of freshwater anglers. *Human Dimensions of Wildlife*, **8**, 109-126. https://doi.org/10.1080/10871200304300

Syväranta, J., Cucherousset, J., Kopp, D., Martino, A., Céréghino, R., & Santoul, F. (2009). Contribution of anadromous fish to the diet of European catfish in a large river system. *Naturwissenschafte,* **96,** 631-635. https://doi.org/10.1007/s00114-009-0511-3

Tamario, C., Degerman, E., Donadi, S., Spjut, D., & Sandin, L. (2018). Nature-like fishways as compensatory lotic habitats. *River Research and Applications*, **34**, 253– 261. https://doi.org/10.1002/rra.3246

Teague N, & Clough, S. J. (2014). The survival of lamprey on travelling screens at potable water intakes. *International fish screening techniques*. WIT Press, Southampton

The Habitats Directive, 1992. Available at https://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm. (Last accessed 10/12/2020)

Thøgersen, J. (2004). A cognitive dissonance interpretation of consistencies and inconsistencies in environmentally responsible behavior. *Journal of Environmental Psychology*, **24**, 93-103. https://doi.org/10.1016/S0272-4944(03)00039-2.

Thorstad, E. B., Rikardsen, A. H., Alp, A., & Økland, F. (2013). The use of electronic tags in fish research – an overview of fish telemetry methods. *Turkish Journal of Fisheries and Aquatic Sciences,* **13**, 881–896. https://doi.org/10.4194/1303-2712-v13_5_13

Tourangeau, R., & Yan, T. 2007. Sensitive questions in surveys. *Psychological Bulletin*, **133**, 859–883. https://doi.org/10.1037/0033-2909.133.5.859

Tulenko, F. J., McCauley, D. W., MacKenzie, E. L., Mazan, S., Kuratani, S., Sugahara, F., Kusakabe, R., & Burke, A. C. (2013). Somatopleure evolution and origin of paired fins. *Proceedings of the National Academy of Sciences*, **110**, 11899-11904. https://doi.org/10.1073/pnas.1304210110

Tummers, J. S., Hudson, S., & Lucas, M. C. (2016b). Evaluating the effectiveness of restoring longitudinal connectivity for stream fish communities: towards a more holistic approach. *Science of the Total Environment,* **569,** 850-860. https://doi.org/10.1016/j.scitotenv.2016.06.207

Tummers, J. S., Kerr, J. R., O'Brien, P., Kemp, P., & Lucas, M. C. (2018). Enhancing the upstream passage of river lamprey at a microhydropower installation using horizontally-mounted studded tiles. *Ecological Engineering,* **125**, 87–97. https://doi.org/10.1016/j.ecoleng.2018.10.015

Tummers, J. S., Winter, E., Silva, S., O'Brien, P., Jang, M. H., & Lucas, M. C. (2016a). Evaluating the effectiveness of a larinier super active baffle fish pass for European river lamprey *Lampetra fluviatilis* before and after modification with wall-mounted studded tiles. *Ecological Engineering,* **91,** 183-194. https://doi.org/10.1016/j.ecoleng.2016.02.046

Turgeon, K., Turpin, C., & Gregory-Eaves, I. (2019), Dams have varying impacts on fish communities across latitudes: a quantitative synthesis. *Ecology Letters*, **22**, 1501-1516. https://doi.org/10.1111/ele.13283

Turner, L. M. (1886). Contributions to the natural history of Alaska, part IV, fishes. The Miscellaneous Documents of the Senate of the United States for the first session of the 49th Congress, Washington, DC, **8**, 87–113.

Tuunainen, P., Ikonen, E., & Auvinen, H. (1980). Lamprey and lamprey fisheries in Finland. *Canadian Journal of Fisheries and Aquatic Sciences,* **37**, 1953–1959. https://doi.org/10.1139/f80-235

Valtonen, T. (1980). European river lamprey (*Lampetra fluviatilis*) fishing and lamprey populations in some rivers running into Bothnian bay, Finland. *Canadian Journal of Fisheries and Aquatic Sciences,* **37**, 1967–1973. https://doi.org/10.1139/f80-237

Vogler, D., Macey, S., & Sigouin, A. (2017). Stakeholder analysis in environmental and conservation planning. *Lessons in Conservation*, **7**, 5–16.

Vollmar, L., McIntosh, G, R., & Bossenbroek, J. (2015). Anglers' responses to bait certification regulations: the case of virus-free bait demand. *Journal of Environmental Economics and Policy*, **4**, 223-237. https://doi.org/10.1080/21606544.2014.974677

Voulvoulis, N., Arpon, K. D., & Giakoumis. T. (2017). The EU water framework directive: from great expectations to problems with implementation. *Science of The Total Environment,* **575**, 358-366. https://doi.org/10.1016/j.scitotenv.2016.09.228

Vowles, A. S., Don, A. M., Karageorgopoulos, P., & Kemp, P. S. (2017). Passage of European eel and river lamprey at a model weir provisioned with studded tiles. *Journal of Ecohydraulics,* **2**, 88–98. https://doi.org/10.1080/24705357.2017.1310001

Wagner, C. M., Jones, M. L., Twohey, M. B., & Sorensen, P. W. (2006). A field test verifies that pheromones can be useful for sea lamprey (*Petromyzon marinus*) control in the Great Lakes. *Canadian Journal of*

*Fisheries and Aquatic Sciences*, **63**, 475-479. https://doi.org/10.1139/f06-008

Walton, I. (1653). The complete angler. Macmillan and Co. Limited, London.

Ward, D. L., Clemens, B. J., Clugston, D., Jackson, A. D., Moser, M. L., Peery, C., & Statler, D. P. (2012). Translocating adult Pacific lamprey within the Columbia river basin. *State of the Science, Fisheries*, **37**, 351-361. https://doi.org/10.1080/03632415.2012.704818

Watkinson, S. (2000). Life after death: the importance of salmon carcasses to British Columbia's watersheds. *Arctic*, **53**, 92–99. https://doi.org/10.14430/arctic839

Watson, G. J., Murray, J. M., Schaefer, M., & Bonner, A. (2015). Successful local marine conservation requires appropriate educational methods and adequate enforcement. *Marine Policy*. **52**, 59-67. https://doi.org/10.1016/j.marpol.2014.10.016.

Weaver, D. M., Coghlan, S. M., Zydlewski, J., Hogg, R. S., & Canton, M. (2015). Decomposition of sea lamprey *Petromyzon marinus* carcasses: temperature effects, nutrient dynamics, and implications for stream food webs. *Hydrobiologia,* **760**, 57-67. https://doi.org/10.1007/s10750-015-2302-5

Weltersbach, M. S., Lewin, W. C., Gröger, J. P., & Strehlow, H. V. (2019). Effect of lure and bait type on catch, size, hooking location, injury and bycatch in the western Baltic Sea recreational cod fishery. *Fisheries Research*, **210**, 121-130. https://doi.org/10.1016/j.fishres.2018.10.002.

White, P. C. L., Vaughan Jennings, N., Renwick, A. R., & Barker, N. H. L. (2005). Questionnaires in ecology: a review of past use and recommendations for best practise. *Journal of Applied Ecology*. **42**, 421-430.

Whitton, B. A., & Lucas, M. C. (1997). Biology of the Humber rivers. *Science of The Total Environment*, **194,** 247-262. https://doi.org/10.1016/S0048-9697(97)88162-4

Wilde, G. R., & Ditton, R. B. (1991). Diversity among anglers in support for fishery management tools. *U.S. Forest Service General Technical Report RM-*, **207**, 329–335.

Williams, A. E., & Moss, B. (2001). Angling and conservation at sites of special scientific interest in England: economics, attitudes and impacts. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **11**, 357-372. https://doi.org/10.1002/aqc.466

Williams, J. E., Rummel, S., Lemon, J., Barney, M., Smith, K., Fesenmyer, K., & Schoen, J. (2016). Engaging a community of interest in water quality protection: anglers monitoring wadeable streams. *Journal of Soil and Water Conservation*. **71**, 114A-119A. https://doi.org/10.2489/jswc.71.5.114A

Williams, J. G., Armstrong, G., Katopodis, C., Larinier, M., & Travade, F. (2012). Thinking like a fish: a key ingredient for development of effective fish passage facilities at river obstructions. *River Research and Applications*, **28**, 407-417. https://doi.org/10.1002/rra.1551

Winfield, I. J., Fletcher, J. M., & James, J. B. (2011). Invasive fish species in the largest lakes of Scotland, Northern Ireland, Wales and England: the collective UK experience. *Hydrobiologia*, **660**, 93–103. https://doi.org/10.1007/s10750-010-0397-2

Woodby, D., Carlile, D., Siddeek, S., Funk, F., Clark, J. H., & Hulbert. L. (2005). Commercial fisheries of Alaska. Alaska Department of Fish and Game, Special Publication No. 05-09, Anchorage.

WWF. (2020). Living Planet Report 2020 -Bending the curve of biodiversity loss. Almond, R.E.A., Grooten M. and Petersen, T. (Eds). WWF, Gland, Switzerland.

Xiao, R., Pang, Y., & Li, Q. W. (2012). The buccal gland of *Lampetra japonica* is a source of diverse bioactive proteins. *Biochimie*, **94**, 1075-1079. https://doi.org/10.1016/j.biochi.2011.12.025.

Youson, J. H., Holmes, J. A., Guchardi, J. A., Seelye, J. G., Beaver, R. E., Gersmehl, J. E., Sower, S. A., & Beamish, F. W. H. (1993). Importance of condition factor and the influence of water temperature and photoperiod on metamorphosis of sea lamprey *Petromyzon marinus. Canadian Journal of Fisheries and Aquatic Sciences*, **50**, 2448-2456. https://doi.org/10.1139/f93-269

Yun, S. -S. (2012). Comparative studies of bile acid release in the mature male lampreys. *Fisheries and Aquatic Sciences*, **15**, 63-67

Zander, K., & Feucht, Y. (2018). Consumers' willingness to pay for sustainable seafood made in Europe. *Journal of International Food & Agribusiness Marketing*, **30**, 251-275. https://doi.org/10.1080/08974438.2017.1413611

Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L., & Tockner, K. (2015). A global boom in hydropower dam construction. *Aquatic Sciences*, **77**, 161-170. https://doi.org/10.1007/s00027-014-0377-0

Zeng, L., Zhou, L., Guo, D-L., Fu, D-H., Xu, P., Zen, S., Tang, Q-D., Chen, A-L., Chen, F-Q., Luo, Y., & Li, G-F. (2017). Ecological effects of dams, alien fish, and physiochemical environmental factors on homogeneity/heterogeneity of fish community in four tributaries of the Pearl River in China. *Ecology and Evolution*, **7**, 3904– 3915. https://doi.org/10.1002/ece3.2920

Zhu, Q., Moser, M. L., & Kemp, P. S. (2011). Numerical analysis of a unique mode of locomotion: vertical climbing by Pacific lamprey. *Bioinspiration & Biomimetics*, **6**. https://doi.org/10.1088/1748-3182/6/1/016005