Anthropogenic factors affecting European river lamprey Lampetra fluviatilis in the Humber River Basin, north-east England

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Anthropogenic factors affecting European river lamprey *Lampetra fluviatilis* in the Humber River Basin, north-east England

By

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ABSTRACT

Anadromous lampreys have declined throughout the world due to damaging anthropogenic activities. This is particularly evident for the European river lamprey *Lampetra fluviatilis*, and studies in the Humber River Basin have shown that poor longitudinal connectivity (between their feeding and suitable spawning habitats) due to man-made barriers and their commercial exploitation for recreational angling bait, are potentially impacting upon this population.

The objectives of this thesis were two-fold. Firstly, to evaluate the efficacy of technical, conventional fishways for upstream migrating river lamprey, as the effectiveness of these fishways to provide free passage for lamprey at man-made barriers in the Humber and elsewhere in Britain is unclear. Secondly, to reassess the level of exploitation in the tidal Ouse, Humber River Basin, and investigate both the scale and structure of the lamprey bait market in Britain and the knowledge and attitudes of key stakeholders within the market, which so far remain unknown.

Passive Integrated Transponder telemetry revealed that two fishways of different technical designs, plain Denil and pool and weir, were extremely inefficient for river lamprey, with passage efficiencies of 0.0 and 5.0% and attraction efficiencies of 91.8 and 42.6%, respectively. Lamprey were significantly delayed, up to 150 days, at the Denil fishway and lamprey failed to pass despite re-entering fishways on up to 12 separate days.

Analysis of catch data suggests that there has not been a decline in the river lamprey stock in the Ouse, although up until 2009 (inclusive) the exploitation level may have been at least twice (~20%) the level reported previously. Telephone interviews of angling wholesale supplier and tackle shop managers in Britain revealed that *c.*9 tonnes of river lamprey were supplied to tackle shops and anglers in Britain between 2011-2012. It also revealed that the majority of lamprey were sourced from The Netherlands and Estonia. The vast majority of tackle shop managers were unaware of which species of lamprey they sold, where they originated from and whether they were threatened, although most (77%) said there should be a ban on the capture and selling of lamprey in Britain if they were considered to be threatened. Conversely, supplier managers were generally more knowledgeable about the lamprey they sold but were more indecisive over a ban.

CONTENTS

DECLARATION

I, William Luke Foulds, hereby declare that this thesis entitled:

"Anthropogenic factors affecting European river lamprey *Lampetra fluviatilis* in the Humber river basin, north-east England"

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

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Chapter 1: General Introduction

1.1. DECLINE OF FRESHWATER FISHES

Freshwater fishes represent the world's most endangered vertebrates, although little attention is given to them in comparison to other vertebrate groups (Dudgeon *et al.,* 2006; Duncan and Lockwood, 2001; Maitland, 1995; Richter *et al.,* 1997; Saunders *et al.,* 2002). The most significant threats towards freshwater ecosystems and their associated fauna are anthropogenic and mostly relate to human population expansion and socio-economic development. Most often the decline of freshwater species can be attributed to extensive river regulation for hydropower and water abstraction (Baras and Lucas, 2001; Pringle *et al.,* 2000), industrial and domestic pollution (Maitland, 1995), over-exploitation (Allan *et al.,* 2005; Cooke and Cowx, 2004) and the introduction of invasive species (Richter *et al.,* 1997). Threats towards freshwater fish are predicted to continue, with over 20% of extant freshwater fishes being at risk of extinction in the near future (Leidy and Moyle, 1998). In North America, for instance, the future extinction rate of freshwater fishes is forecast at 4% per decade, a figure five times larger than that for terrestrial vertebrates (Ricciardi and Rasmussen, 1999).

The problems associated with anthropogenic pressures on freshwater ecosystems can be particularly severe for diadromous fishes i.e. those that migrate between freshwater and the sea (McDowall, 1992). Although diadromous fishes only represent 1.5% of all freshwater fishes, they represent 3% of those regarded as 'endangered'. Diadromous fishes are often more susceptible to human activities than non-migratory fishes as they require multiple habitats during their lifetime in order to complete different stages of their life cycle. The construction of dams or weirs can impede their upstream and downstream migration, causing habitat fragmentation and loss of longitudinal connectivity, which may ultimately restrict access to critical habitats (Calles and Greenberg, 2007; Lucas *et al.* 2009). Moreover, physical 'bottlenecks' may form downstream of a barrier, as diadromous fishes tend to migrate in dense concentrations; this has the potential to increase predation and encourage commercial exploitation (McDowall, 1992).

This chapter reviews the anthropogenic factors which threaten lampreys around the world, and discusses in the depth the impacts these factors have had on the anadromous European river lamprey *Lampetra fluviatilis* in the Humber River Basin, UK, and elsewhere in Europe.

1.2. LAMPREY ECOLOGY

Lampreys (order Petromyzontiformes) are a group of serpentine, jawless sucker-mouthed fish which have existed since the late Devonian period (*c.* 360 MYA) and, together with the marine hagfish (Myxinidae), represent the oldest extant vertebrates (Gill *et al.,* 2006). Lampreys are eel-like in shape and have distinctive phenotypic characteristics: an oral-disc, with variable numbers and forms of teeth of different arrangements (Hardisty and Potter, 1971), seven gill pores and lack paired fins and scales (Maitland, 2003). Lampreys have an antitropical distribution, as their larvae are dependent upon cool river temperatures to survive (Potter, 1980a; Renaud, 2011), and the majority of species (36 belonging to the family Petromyzontidae). are found across the temperate Northern Hemisphere between 20^{o} and 72^{o} latitude However, 4 species also exist in the Southern Hemisphere and are contained within two families: Geotridae and Mordaciidae (Potter and Gill, 2003; Renaud, 2011). As a general rule, the greater the size attained by a species, the greater its distributional range (Potter, 1980b). The European river lamprey, brook lamprey *Lampetra planeri* and sea lamprey *Petromyzon marinus* are the only species found in the UK and exhibit a wide distribution in Europe (see Fig. 1.1 for river lamprey distribution). Populations of sea lamprey, the largest of the three species, also extend across North America, Greenland and Iceland (Freyhof and Kottelat, 2008).

Most species of lamprey have a similar life cycle, characterised by a protracted larval development in freshwater followed by a radical metamorphosis to become adults (Hardisty and Potter, 1971; Kelly and King, 2001). The adults ultimately migrate upstream to reach spawning grounds and spawn in pairs or in groups from spring to early summer, during which they disperse their eggs in shallow depressions in gravel/cobble substrates (Jang and Lucas, 2005; Maitland, 2003). All lamprey species are semelparous and die shortly after spawning, following deterioration in body condition and the onset of fungal infection (Hagelin and Steffner, 1958; Larsen, 1980);

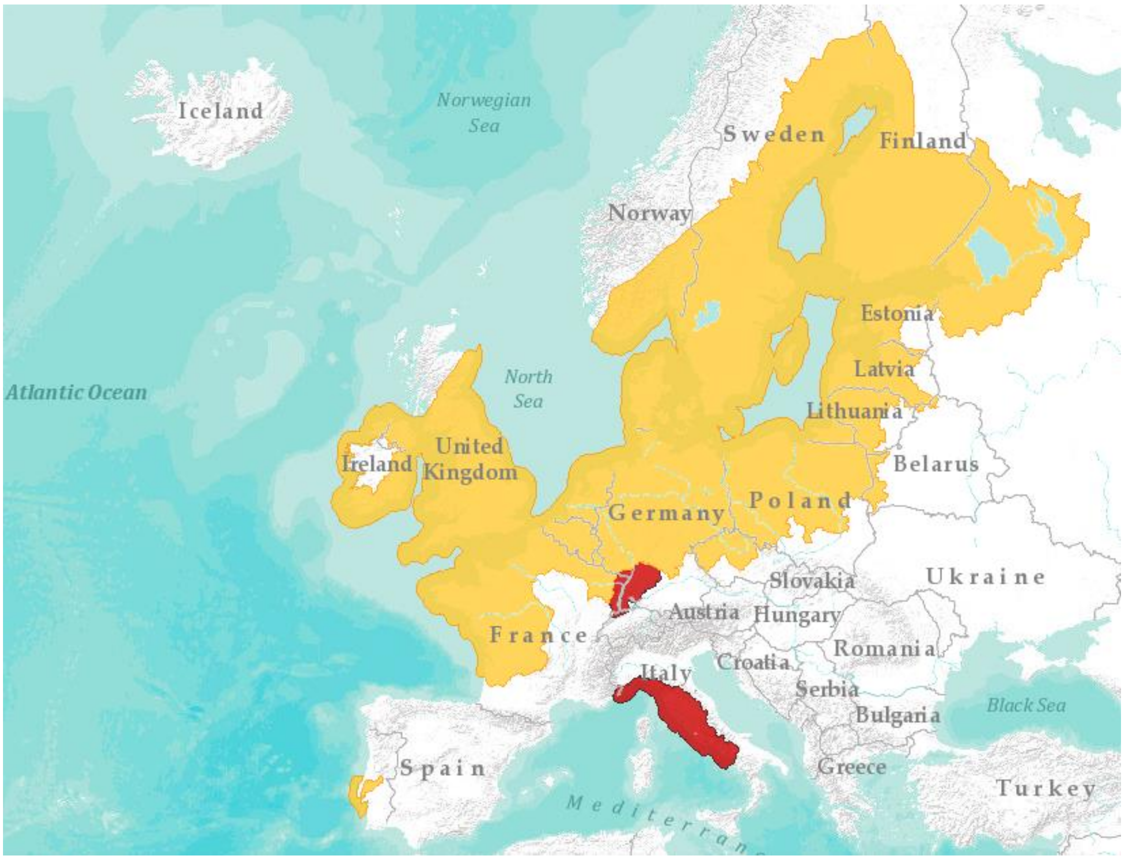


Figure 1.1. Current distribution of the European river lamprey *Lampetra fluviatilis* in Europe (yellow shading). Red shading indicates extinct populations. After Kottelat and Freyhof (2011).

however, repeat spawning has been documented in the past (Michael, 1980), yet this is considered to be an exceptional case. After hatching, the blind larvae (ammocoetes) are passively displaced downstream by the current, although they may also actively migrate downstream *or* upstream to colonise suitable burrowing and feeding habitat (Hardisty and Potter, 1971; Quintella *et al.,* 2005). Ammocoetes remain burrowed in the "ammocoete beds" for three to eight years where they filter feed on organic particles, and are often redistributed during flood events (Hardisty and Potter, 1971; Kelly and King, 2001). In general, ammocoetes undergo a highly programmed and synchronous metamorphosis during the summer months, and the main external transformations begin from July – September (Kelly and King, 2001; Youson, 1980).

Depending on the species, lampreys may either actively migrate downstream towards lacustrine, estuarine or marine environments, or remain as freshwater residents in fluvial environments after metamorphosis. Migration and locomotory activity, at least up until the spawning period, is predominantly nocturnal (Hardisty and

Potter, 1971; Sjöberg, 1977). Although all lamprey species exhibit migratory habits (Renaud, 1997), there are currently nine anadromous lamprey, eight of which are parasitic and the remaining species, the Caspian lamprey *Caspiomyzon wagneri*, is considered to be a scavenger (Renaud, 2011). However, most anadromous species have also established permanent freshwater resident populations (Renaud, 1997). The adult phase of parasitic lampreys is longer than the non-parasitic species, which typically lasts up to two or more years in comparison to less than one year, respectively (Renaud, 2011). Whilst parasitic lampreys feed on a wide range of fish species (Hardisty and Potter, 1971; Kelly and King, 2001), non-parasitic lampreys do not feed after metamorphosis. Both the European river lamprey and sea lamprey are anadromous and parasitic, whilst the brook lamprey is a freshwater resident and non-parasitic.

The European river lamprey and brook lamprey are considered to be ‘paired species’, as they are morphologically similar and closely related yet exhibit different life-history strategies as adults (Zanandrea, 1959). It is often difficult to conduct accurate conditional assessments of both species where their range overlaps, as their larvae cannot be differentiated in the field (Gardiner, 2003; Nunn *et al.,* 2008). More recently, it has been demonstrated that river and brook lamprey can successfully hybridise after *in vitro* fertilisation, and that offspring are viable at least through till completion of their larval development (Hume *et al.,* 2013). Hume *et al.,* (2013) suggest hybridisation may occur in the wild between European brook and river lamprey, and indeed Lasne *et al.,* (2010) have reported a high frequency of communal spawning in the River Oir, France.

1.3. LAMPREY CONSERVATION

According to Renaud (1997) over half of all lamprey species in the Northern Hemisphere are vulnerable, endangered or extinct at least in parts of their range, for which anthropogenic activities are chiefly responsible (Close *et al.,* 2002; Mateus *et al.,* 2012; Thiel *et al.,* 2009). The principal drivers of lamprey declines are river regulation and pollution, which either restrict access to, or lead to the degradation of, critical habitats (Renaud, 1997). As a result, anadromous lampreys are the most susceptible of all lamprey species to these threats, as they rely on multiple habitats and the free passage between them in order to complete their life cycle (Beamish and

Northcote, 1989; Kelly and King, 2001). Numerous lamprey species are also exploited, or have been exploited, for a wide variety of purposes (Renaud, 2011), and it has been suggested that the exploitation of their prey has also been a limiting factor for some lamprey populations (Birzaks and Aberson, 2011; Murauskas *et al.,* 2013). These threats are rarely isolated, and they often have a synergistic effect on their populations. Furthermore, given that all lamprey species are completely semelparous, restricting access to, or destroying, spawning habitat and capturing adult migrants before they have had the opportunity to spawn can render their populations more vulnerable to extirpation (Masters *et al.,* 2006).

The impacts of river regulation and obstruction on lamprey populations are amongst the most commonly cited reasons for their declines. To illustrate with a severe case, a population of anadromous Pacific lamprey *Lampetra tridentata* in British Columbia, Canada, became extinct approximately seven years after the construction of five dams at the outlet of Elsie Lake in 1957 – 1959, which obstructed both the young adults' downstream movement to sea and the spawning adults' migration above the dams (Beamish and Northcote, 1989). Other Pacific lamprey populations have declined at a remarkable rate as a result of dam constructions; Pacific lamprey counts at Winchester Dam on the Umpqua River, Oregon, decreased by 99% from 1996 to 2001, and decreased by 96% from 1963 and 2001 at Ice Harbour Dam on the Snake River, Washington (Close *et al.,* 2002). The abundance of Caspian lamprey in the Volga and Kura rivers dropped so low, due to river engineering projects, that the harvesting of this species, which once supported a commercially important industry, has now ceased (Renaud, 2011).

In most cases, river regulation has delayed or prevented spawning adult lampreys from reaching their spawning areas, often located above barriers in the upper reaches of tributaries. Mateus *et al.,* (2012) indicates that, on average, 80% of spawning habitat in the major river basins in the Iberian Peninsula used by anadromous sea lamprey and river lamprey is now unavailable due to the extensive construction of dams in the lower stretches of the rivers. Similarly, on the River Derwent, north-east England, Lucas *et al.,* (2009) revealed that although 98% of spawning habitat was present above five low-head weirs (2-3 m high), on average just 1.8% of river lamprey spawners were recorded there. Furthermore, the stark attrition of migrating lamprey populations past multiple barriers along river stretches has been well described for both the Pacific lamprey and European river lamprey (Keefer *et al.,* 2009; Lucas *et al.,* 2009; Moser *et al.,* 2002). For instance, the annual cumulative passage rate of 3 598 Pacific lamprey past five consecutive dams on the Columbia and Snake Rivers, Columbia River Basin, was approximately 50%, 30%, 20%, 5% and <1% (Keefer *et al.,* 2009). The requirement of lampreys to negotiate multiple barriers along a river channel to reach spawning habitat can also lead to fatigue and depletion of energy reserves which may impact upon reproductive success (Jackson and Moser, 2012; Quintella *et al.,* 2004, Russon *et al.,* 2011). Ultimately, reductions in the fitness of spawning lampreys and/or the number of migrants able to reach spawning grounds can lead to poor recruitment. For instance, Moser and Close (2003) found an absence of ammocoetes in the upper reaches of most tributaries sampled in the Columbia River Basin, and suggested that complete recruitment failure in some areas was due to large hydropower dams and low-head diversion dams restricting adult migrants' access to spawning grounds. Poor recruitment of lamprey populations has often been linked to prolonged low flows during the adult spawning migration which has reduced their ability to negotiate in-stream barriers (Jackson and Moser, 2012; Lucas *et al.,* 2009; Nunn *et al.,* 2008). Therefore, it is clear that there is an urgent need to restore connectivity between habitats and allow the free passage of migrant adults, through the installation of more efficient fishways or barrier removal (see sections 1.6.1 and 1.6.1.1), in order to safeguard and promote lamprey populations worldwide.

Whilst river regulation has delayed and obstructed the migration of anadromous lampreys, this activity has also led to the destruction of lamprey spawning and larval habitat through dredging, drastic river level fluctuations and declines in water quality. In Finland, the construction of hydroelectric power stations has reduced European river lamprey spawning areas in most rivers, and circadial and seasonal regulations of water levels have led to lamprey ammocoete mortalities (Tuunainen *et al.,* 1980). In 1978, there was also a marked decrease in the number of river lampreys in the Pyhäjoki River due to construction works and dredging in the upper reaches of the river (Valtonen, 1980), and high iron and low oxygen concentrations in both the Siikajoki and Kalajoki Rivers caused by engineering works in the 1970s resulted in poor year-classes of lamprey (Kainua and Valtonen, 1980). It is also suggested that channelization has destroyed 40% of the most productive area in the River Perhonjoki through the destruction of suitable lamprey habitats, such as silt beds (Ojutkangas *et al.,* 1995). Dam construction, dredging and channelization have also impacted upon threatened sea lamprey populations in Portuguese river basins (Quintella *et al.,* 2007). Dredging and dramatic changes in river levels due to dam regulation can often leave ammocoetes stranded, and a single dewatering event can have a major effect on multiple year-classes (Streif, 2009). For instance, in the

Klamath River, northern California, Yaruk tribe members have recalled how they found hundreds, even thousands, of stranded Pacific lamprey ammocoetes in little side pools when there were drastic increases and decreases in water releases from dams (Peterson Lewis, 2009). Pacific lamprey are an integral part of the cultural heritage of indigenous peoples in the Pacific Northwest, and river engineering activities such as these are contributing to the ecological and cultural extinction risk of this species (Close *et al.,* 2002).

Lampreys are also demonstrably susceptible to pollution, and it is likely that entire populations were extirpated from rivers that became heavily polluted (Mateus *et al.,* 2012; Renaud, 1979). Populations of anadromous sea lamprey and river lamprey in Britain suffered major declines up until the late 20th century because of industrial pollution. For instance, in the rivers Clyde in Scotland and Thames in south-east England, whole populations of river lamprey were suggested to have been eliminated due to severe pollution, although the water quality of both rivers has improved in recent years (Maitland, 2003). Pollution has also had a decisive effect on river lamprey abundance in Polish rivers (Witkowski, 1992), and unpurified wasterwater and domestic sewage led to significant reductions in river lamprey catches in the Lestijoki River, Finland, in 1978 (Valtonen, 1980). However, by 2015 all EU member states must achieve at least ‘Good Status’ in all bodies of surface and ground water under the Water Framework Directive (WFD) (EC, 1992), therefore industrial pollution is unlikely to act as a significant limiting factor on lamprey populations in Europe, at least, in the future.

Lamprey populations also face the additional pressures of exploitation, as several species have been harvested around the world for a wide variety of purposes (Renaud, 2011). In Europe, anadromous lampreys have first and foremost been harvested for human consumption (Kelly and King, 2001). Today, river lamprey fishing for human consumption is concentrated in the Baltic Sea area, where the tradition has existed since at least the 15th century, and is particularly important in Finland and Latvia (Sjöberg, 2011). Sea lamprey commercial fisheries do not currently operate in the Baltic region (Thiel *et al.,* 2009) and are, at the moment, restricted to the Iberian Peninsula and France (Beaulaton *et al.,* 2008; Mateus *et al.,* 2012). Furthermore, whilst Caspian lamprey were once harvested in the rivers Volga and Kura as food for humans (up to 33.4 million individuals in the early 1900s) their abundance in these rivers have dropped so low that they are no longer a commercially important species (Renaud, 2012). An interesting phenomenon exists in Britain, where, despite being a European protected species, adult river lamprey are captured during their spawning migration and sold to fishing tackle shops to be used as recreational sport-bait for northern pike *Esox lucius* (Master *et al.,* 2006; section 1.6.2). However, there are several accounts of lamprey ammocoetes being used for sport-bait around the world, including European river lamprey, Pacific lamprey, sea lamprey and Carpathian lamprey *Eudontomyzon danfordi* ammocoetes (Buller and Falkus, 1994; Close *et al.,* 2002; Renaud, 2012; Vladykov, 1952).

The harvesting of lamprey is not restricted to Europe. In Japan, Arctic lamprey *Lethenteron camtschaticum* have been highly valued as a medicinal cure for night blindness and are also served in restaurants (Honma, 1960). In the mid-Columbia River plateau, Native Americans have harvested Pacific lamprey for food, medicinal and cosmetic purposes and this species continues to be a key part of their tribal heritage (Close *et al.,* 2002). Similarly, in several of New Zealand's rivers, the Maori capture pouched lamprey *Geotria australis* during their spawning migration and this species represents a historically important food source, although they are also used for ceremonial purposes (James, 2008).

Although lamprey population declines around the world have most often been attributed to river regulation and pollution, commercial exploitation has, in some instances, represented a significant threat to their sustainability. For instance, the high economic value of the sea lamprey in Portugal, and some regions in Spain, has encouraged poaching, which currently represents a serious threat to their populations; Andrade *et al.* (2007) found that 76% of sea lamprey released in the Vouga River Basin in 2005 during tagging experiments were caught by poachers.

In summary, the majority of lamprey species are of conservation concern due to damaging anthropogenic activities, such as river regulation, habitat degradation, pollution and exploitation, and the manifestation of these threats is most apparent when reviewing literature concerning European river lamprey populations. The remaining sections of this chapter consider the decline of river lamprey in Europe in more detail and, in particular, emphasise the main anthropogenic factors which are currently affecting the river lamprey population in the Humber River Basin.

1.4. EUROPEAN RIVER LAMPREY ECOLOGY

The distribution of the European river lamprey (Figure 1.2.) extends through much of western and northern Europe, ranging from the western Mediterranean to southern Norway and countries in the Baltic Sea area, where it is found in the sea and adjacent estuaries and rivers (Maitland, 1980; Mateus *et al.,* 2012; Sjöberg, 2011; Thiel *et al.,* 2009). In Britain, the river lamprey occurs in many rivers south of the Great Glen, northern Scotland (Maitland *et al.,* 1994). They are typically anadromous, spawning in freshwater and migrating to estuarine and marine environments as adults to parasitically feed on a range of teleost fish, including sprat *Sprattus sprattus*, flounder *Platichthys flesus*, herring *Clupea spp.* and smelt *Osmerus eperlanus* (Kelly and King, 2001). As with other lamprey species, the river lamprey has also developed permanent freshwater resident populations. Stable isotope analysis of C and N in muscle tissue of two forms of adult river lamprey in the Endrick Water, Loch Lomond, Scotland, revealed that the 'small body form' feeds in freshwater, whilst the 'large body form' either migrates to sea to forage or feeds on an anadromous fish with a strong marine C signature (Adams *et al.,* 2008). Similarly, it is suggested there is a freshwater-feeding river lamprey population in Lough Neigh, Northern Ireland, which feeds on pollan *Coregonus autumnalis* (Goodwin *et al.,* 2006). Other freshwater-feeding river lamprey populations can be found in lakes in Finland and Russia (Maitland, 2003; Renaud, 1997).

Figure 1.2. Adult European river lamprey *Lampetra fluviatilis* caught during its spawning migration in the Yorkshire tidal Ouse, Humber River Basin, north-east England. Photograph taken on 03/02/12.

For those river lamprey that are anadromous, the adult parasitic phase typically lasts between one to two years (Kelly and King, 2001). The length and weight attained by adult river lamprey varies significantly, both geographically and seasonally. Bartel *et al.,* (2010) found that the size of river lamprey was negatively correlated with both latitude and longitude; the smallest lampreys (12 – 90g) were observed in Finland, whilst the largest lampreys (45 – 230g) were observed in Poland. A similar relationship between adult body size and latitude has also been revealed for sea lamprey (Beaulaton *et al.,* 2008). According to Maitland (2003), the average weight of adult river lamprey in Britain is about 60g, although the average weight of lamprey taken from the Yorkshire tidal Ouse, Humber River system, north-east England, during their spawning migration was 101.2g. It is also well established that river lamprey caught nearer to the spawning season in spring are smaller than those caught during their spawning migration in autumn and winter (Bartel *et al.,* 2010; Jang and Lucas, 2005; Maitland *et al.,* 1994).

The commencement of the upstream (spawning) migration usually occurs in late summer and autumn, although the timing can vary significantly between rivers (Hardisty and Potter, 1971; Pickering, 1993). In Britain, the spawning migration is usually initiated between August and October (Maitland, 1980), although in the Severn Estuary, south-west England, adult migrants have been detected as early as July (Abou-Seedo and Potter, 1979). Similarly, in the rivers Meuse (Holland), Neva (Russia) and Daugava (Latvia) river lamprey typically begin their spawning migration in July and August (Birzaks and Abersons, 2011; Hardisty and Potter, 1971; Lanzig, 1959). The adult migration occurs predominantly at night; however, they exhibit additional diurnal activity during spawning through the loss of their negative phototaxic behaviour, resulting in a 24 hour locomotory activity (Jang and Lucas, 2005; Sjöberg, 1977). Although adult Pacific lamprey and pouched lamprey are capable of climbing high gradient structures during their upstream migration (Kemp *et al.,* 2009; McDowall, 1988), European river lamprey do not exhibit this climbing behaviour (Kemp *et al.,* 2011; Russon *et al.,* 2011). The river lamprey overwinters in rivers in Britain before spawning in early spring, unlike the sea lamprey whose migration is consolidated into one or two months before spawning in late spring – early summer (Hardisty and Potter, 1971). There is evidence that river lamprey adults are attracted to ammocoete pheromones during their spawning migration in order to locate suitable spawning habitat (Gaudron and Lucas, 2006). However, similar to sea lamprey and Pacific lamprey, they do not exhibit natal homing (Bergstedt and Seelye, 1995; Hatch and Whiteaker, 2009; Tunnainen *et al.,* 1980).

In Britain, river lamprey begin to spawn when water temperatures reach 10 - 11°C, which is usually between March and April (Kelly and King, 2001). They have also been observed to spawn at much lower temperatures (Maitland *et al.,* 1994). Whilst many studies have shown that male river lamprey initiate nest building (Applegate, 1950; Hagelin and Steffner, 1958), observations of spawning activity in rivers in the Yorkshire Ouse catchment reveal that females construct nests before signs of courtship or spawning behaviour (Jang and Lucas, 2005). However, it is clear that river lamprey have a communal, promiscuous mating system, and that spawning usually occurs at gravel sites where water depths are between 0.2 and 1.5m (Jang and Lucas, 2005). Once spent, most lampreys die after a few days (Pickering, 1993). River lamprey have a relatively low fecundity rate in comparison to sea lamprey; an average of 16,000 eggs per female compared with an average of 172,000 eggs per female, respectively (Maitland, 1980). Once the larvae hatch after an incubation period of 15 – 30 days, the ammocoetes either actively migrate or drift downstream, and burrow into silt deposits where they feed for three to five years (Maitland, 2003; Pickering, 1993). In Britain, river lamprey metamorphose between July and September during which they develop functional eyes, an oral disc, and a silvery appearance (Fig. 1.3; Pickering, 1993). Fully metamorphosed river lamprey are referred to as either 'transformers' or macrophthalmia. 'Transformers' emigrate downstream to estuarine and marine environments between winter and early summer to begin the parasitic phase of their lifecycle (Bracken and Lucas, 2012; Hardisty and Potter, 1971).

Figure 1.3. European river lamprey 'transformer' caught in the River Eden, north-west England. Photograph taken on 10/11/11.

1.5. STATUS OF RIVER LAMPREY IN THE HUMBER, BRITAIN AND EUROPE

Despite river lamprey having an IUCN status of 'least concern' (Freyhof, 2011), they are widely considered to be endangered in Europe (Lusk *et al.,* 2004; Renaud, 1997). Although there are indications that river lamprey populations are recovering in some European watersheds, mostly due to reductions in pollution levels (Freyhof, 2011), catch data from lamprey fisheries across Europe suggest that current populations are only a fraction of the size of those that existed historically (Birzaks and Abersons, 2011; Kesminas and Švagždys, 2010; Masters *et al.,* 2006; Sjöberg, 2011; Thiel *et al.,* 2009; Witkowski, 1992). Moreover, river lamprey have become regionally extinct in Spain, Italy, Switzerland and Czech Republic, and Wallonia, Belgium (Freyhof, 2011; Mateus *et al.,* 2012; Renaud, 1997). Although there is no *Red Data Book* for fish in Britain (Maitland, 2003), river lamprey have been classified in several *Red Data Book*s by individual nations in Europe, as described by numerous authors (Kelly and King, 2001; Mateus *et al.,* 2012; Sjöberg, 2011; Thiel *et al.,* 2009) As with other anadromous lampreys (section 1.3), the decline of river lamprey has most commonly been associated with river regulation, over-exploitation, habitat degradation, pollution and reductions in their prey populations (see sections 1.3. and 1.6.).

As a result of their extensive decline, river lamprey are listed in European conservation agreements. Firstly, they are listed in Appendix III of the Bern Convention, whereby all contracting parties declare to protect listed species through "appropriate and necessary legislative and administrative measures" (COE, 1979). Furthermore, they are listed under Annex II of the EC Habitats and Species Directive, which necessitates the assignment of Special Areas of Conservation (SACs) that must be preserved in good condition for featured species, and Annex V, which states that taking in the wild and exploitation may be subject to management measures (EC, 1992). Collectively, SACs designated for featured species, such as the river lamprey, form part of a European-wide ecological network called Natura 2000. SACs for lampreys must be characterised by good water quality, clean substrate at spawning grounds and offer fine sand/silt beds downstream of spawning areas. In addition, access to spawning areas from the sea must be ensured for sea lamprey and river lamprey (Kelly and King, 2001; Mateus *et al.,* 2012). In England and Wales there are currently 17 SACs were river lamprey as a designated feature. The sea lamprey and brook lamprey, both of which are also afforded protection under Annex II of the EC

Habitats and Species Directive, are featured species in 18 and 10 designated SACs, respectively (APEM, 2008; JNCC, 2007).

River lamprey are generally rare in Britain but exhibit a wide distribution (Fig 1.4), and populations in the rivers Severn, Thames, and the Derwent, Trent and Ouse of the Humber River Basin have supported commercial lamprey fisheries in the past (Frear, 2004; Maitland, 2003; Masters *et al.,* 2006; Spicer, 1937). However, the JNCC (2007), in an audit of the data and judgements on the conservation status of river lamprey in the UK, concluded that their overall status was “unfavourable – inadequate but improving”; the assessment was deemed to be moderately reliable, as survey data were often lacking. It is believed that improvements in the water quality of tidal rivers in Britain have assisted the recovery of river lamprey populations (Frear, 2004), although there is a paucity of reliable historic data to interpret the degree to which individual populations have recovered (Bubb and Lucas, 2006). Although there have been concerted efforts to monitor and assess the status of river lamprey populations around Britain in recent years, significant knowledge gaps still remain.

Figure 1.4. Distribution of European river lamprey in Britain (after APEM, 2008)

According to historical records, the River Humber, north-east England, has been a major site for migrating river lamprey in Britain since at least the late 19th century (Masters *et al.* 2006). The River Humber is formed through the confluence of the River Ouse (whose main tributaries include the rivers Derwent, Wharfe, Nidd, Ure, Swale, Aire, Calder and Don) and the River Trent, and the Humber River Basin refers to the catchment containing those constituent rivers (Fig. 1.5). The Humber Estuary is the largest coastal plain estuary on the east coast of Britain (Jarvie *et al.,* 1997) and, along with the lower River Derwent, is a designated SAC in which river lamprey are a listed feature. The Humber River Basin offers suitable lamprey habitats for lifecycle completion through the provision of productive, estuarine feeding grounds for their parasitic stage and widespread larval and spawning habitat in its tributaries (Lucas *et al.,* 2009).

The Ouse catchment is suggested to maintain one of the most important river lamprey populations in the UK (Jang and Lucas, 2005). A cautious population estimate of 300 000 migrating adults was calculated for the River Ouse, upstream of the River Wharfe, in 2003-2004 (Masters *et al.,* 2006). Moreover, the spawning population in 2003 at Stamford Bridge, River Derwent, was considered to be in the order of *c.* 5 800 individuals, although this was deemed to be an exceptional year and a typical spawning population in the River Derwent is likely to be *c.* 750 (Jang and Lucas, 2005; Lucas pers.comm.). Within the Ouse catchment, 11 out of 16 sites sampled in 2004 held favourable *Lampetra* ammocoete populations (>10 individuals m^{-2}; Harvey and Cowx, 2003), with sites at Langton (River Swale) and Bellflask (River Ure) holding the greatest densities (Nunn *et al.,* 2008). However, these ammocoetes could not be distinguished to species level (see section 1.2), thus it is not entirely clear whether the results signify favourable river lamprey ammocoete populations. Towards the beginning of the 20th century, chronic pollution in the Trent (Spicer, 1937) and Ouse catchments, particularly in the rivers Aire, Don and Calder (Axford, 1991), threatened river lamprey populations and other migratory fish, although water quality has dramatically improved over recent years (Bradley, 2005; Edwards *et al.,* 1997; Frear, 2004). Currently, the main factors affecting the viability of river lamprey populations in the Ouse are chronic longitudinal fragmentation of habitat through river regulation (Lucas *et al.,* 2009) (see section 1.6.1) and commercial exploitation (Masters *et al.,* 2006) (see 1.6.2).

There is evidence to suggest that river lamprey were relatively abundant in the River Trent during the late 19th century to mid-20th century (Jacklin, 2006). According

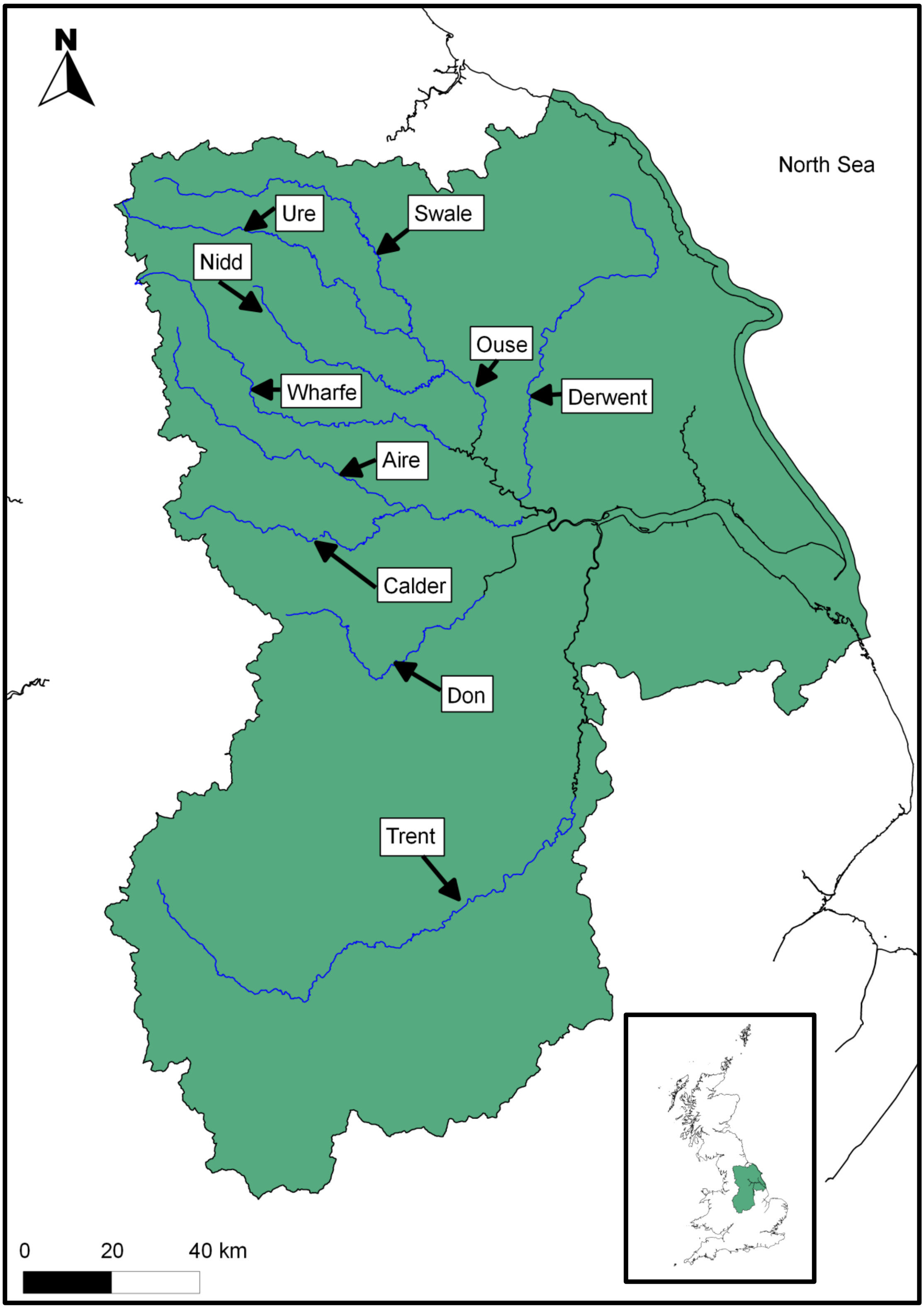


Figure 1.5. Map of the Humber River Basin, including the catchment area (green) and the main rivers.

to a Salmon Fishery report in 1878, 3 000 river lamprey were caught in a single night at Averham weir, lower Trent (Jacklin, 2006), and catches of up to 400 river lamprey per night were still being recorded at the same site in 1954 (Morris, 1954). However, after the construction of Cromwell weir in the lower Trent in 1956 there have been significantly fewer river lamprey being documented in the Trent, and of the few recent studies carried out, all suggest that the Trent supports a relatively small proportion of river lamprey in the Humber River Basin in comparison to the Ouse; catch per unit effort (CPUE) in the Trent was 20% of that of the Ouse (Greaves *et al.,* 2007), no juvenile river lamprey were found during brief electro-fishing surveys (Jacklin, 2006) and just two adult river lamprey were found impinged on trash screens of Keadby Power Station on the Trent between the period of November 2005 and May 2006 (Jacklin, 2006). Thermal outflows from power stations may also be limiting the river lamprey population in the Trent. However, the annual run of river lamprey in the Trent remains significant (Greaves *et al.,* 2007; P. Bird, pers. comm.) and it is possible that spawning occurs in the upper tidal reaches. Furthermore, one can speculate that ammocoetes are present at sites along the Trent (given that there are large silt areas in the tidal Trent (Greaves *et al.,* 2007)), as it is known that adults are attracted to ammocoete pheromones during their adult migration in order to locate suitable spawning habitat (Gaudron and Lucas, 2006). However, it is possible that river lamprey are being attracted by pheromones produced by brook lamprey ammocoetes upstream of Cromwell weir. In summary, all evidence suggests that Cromwell weir is the main significant factor limiting the river lamprey population in the Trent.

1.6. ANTHROPOGENIC FACTORS AFFECTING RIVER LAMPREY POPULATIONS IN THE HUMBER, BRITAIN AND EUROPE

1.6.1. RIVER REGULATION

River regulation through the construction of barriers represents one of the largest and most prevalent threats to global freshwater fish populations (Baras and Lucas, 2001; Duncan and Lockwood, 2001; Pringle *et al.,* 2000). Over half of the world's largest river systems are affected by dams, and Europe contains the smallest number of completely unfragmented large river systems than any other continent (Nilsson *et al.,* 2005). Extensive river modification on this scale has caused severe alterations to ecological processes within lotic systems, either by preventing or delaying seasonal migrations (Moser *et al.,* 2002), altering fish assemblages (Gillette *et al.,* 2005; Quinn and Kwak, 2003), impacting spawning and nursery grounds (Thiel *et al.,* 2009), or, in some instances, facilitating the invasion of exotic species (Beamish and Northcote, 1989; Johnson *et al.,* 2008). The impacts of dams and weirs on diadromous fishes are particularly severe, as the required movement between different habitats, in order to complete different stages of their life-cycle, can be severely inhibited (McDowall, 1992).

Numerous studies have documented the negative impact that man-made barriers have had on river lamprey populations, principally through the destruction of key habitats and the delay and restriction of their upstream migration. In the Perhonjoki River, Finand, the total number of 1+ and older ammocoetes reduced from an estimated 1.4 million in 1982, before completion of the Kaitfors hydroelectric power station, to just 155 000 in 1993, several years after completion, due to reductions in larval and spawning habitats (Ojutkangas *et al.,* 1995). To increase the number of river lamprey reaching spawning habitat above dams in several rivers in Finland, thousands of river lamprey are transported above dams each year, although as of yet there has been no discernible increase in the number of spawning migrants in response to these measures (Sjöberg, 1980). The construction of the hydroelectric power station cascade in the River Daugava, Latvia, has also blocked river lamprey spawning migration routes and is considered to be the most important factor that has negatively influenced river lamprey abundance in this river (Birzaks and Abersons, 2011).

In England and Wales, river regulation is mostly characterised by low-head weirs, many of which were constructed before the 20th century to provide navigation connections and water supplies to mills (Rickard *et al.,* 2003). Although many of these weirs no longer serve their original function, they may be necessary for water level management and water abstraction schemes and they provide opportunities for renewable, small-scale hydropower generation (Entec, 2010). The negative impacts that these low-head weirs have had on fish communities has been underappreciated in the past, and given they are far more numerous than large-scale dams, the cumulative effect of multiple low-head weirs in a catchment can be significant (Baras and Lucas, 2001; McLaughlin *et al.,* 2006). It is widely acknowledged that these structures have contributed to the decline of river lamprey populations in Britain (Maitland, 2003), and it is field studies conducted in the Humber River Basin that have provided the most compelling evidence for this.

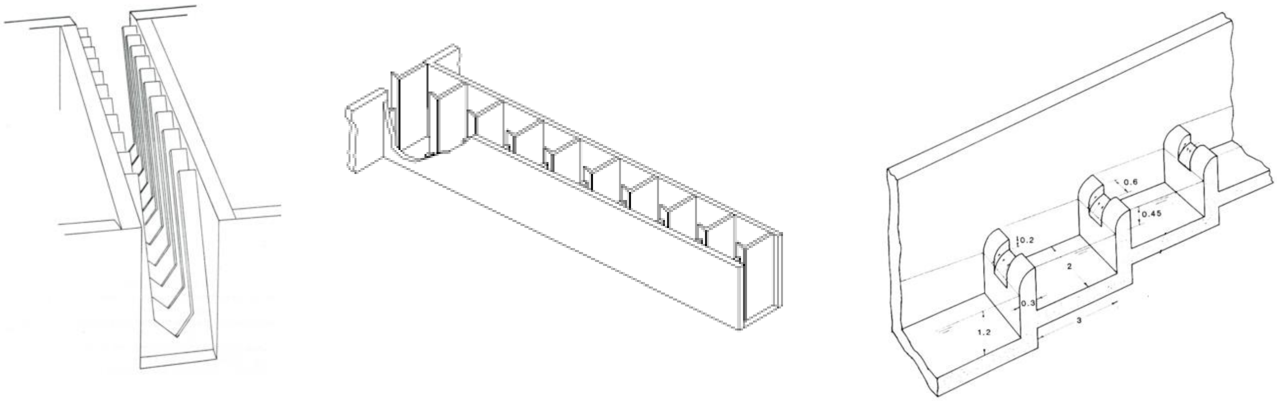
There is an abundance of low-head weirs within the Humber catchment due to the region's rich industrial heritage; out of the 60 watercourses discharging into the Humber Estuary, the only river which has a natural gravity outfall is the River Hull (Nunn and Cowx, 2012; Nunn *et al.,* 2007). Nunn *et al.* (2008) provided indirect evidence for the negative relationship between the number of these low-head barriers in rivers in the Ouse catchment and successful migration to upstream spawning grounds; this study showed that *Lampetra* ammocoete densities in the River Swale, a relatively unaltered river, were higher and consisted of multiple age classes in comparison to ammocoetes within highly impounded rivers, such as the Rivers Ure and Derwent. These findings complement the results of a study conducted in the Ballinderry catchment, Northern Ireland, where *Lampetra* ammocoete abundance was negatively correlated with the number of barriers downstream (Goodwin *et al.,* 2008). Although there is a possibility that these results reflect localised larval mortaility, there is direct evidence from telemetry studies that differences in the accessibility of spawning habitat may be the causal factor for variability in larval recruitment (Greaves *et al.,* 2007; Jang *et al.,* 2004; Lucas *et al.,* 2009).

Lucas *et al*. (2009) found that only 10 out of 57 acoustic tagged river lamprey in the tidal Ouse successfully ascended Barmby Barrage, the first migration barrier found at the Derwent's confluence, despite in some cases evidence of multiple visits to the barrier. Six barriers are present along the lower 50 km of the River Derwent: the tidal barrage at Barmby, and five low-head (2-3 m high) weirs at Elvington (sluice gates), Stamford Bridge, Buttercrambe, Howsham and Kirkham (Chapter 2). During the same study, they released 66 upstream migrating river lamprey less than 4 km above Barmby Barrage, and found that only 64% of lamprey passed Elvington Sluices (21.3 km upstream of Barmby), and only 17% (of the original cohort) passed Stamford Bridge weir (32.6 km upstream of Barmby). Furthermore, no radio-tagged upstream migrating river lamprey (n = 34) were successful in ascending all five weirs, and the final locations of lamprey were strongly associated with areas immediately below weirs (Jang *et al.,* 2004).The demonstrable cumulative effect of low-head barriers in the lower Derwent on upstream migrating river lamprey is of great concern, given that 98% of suitable spawning habitat in the Derwent occurs >50 km upstream of the Derwent's confluence and the five low-head weirs. On average, just 1.8% of spawners in the Derwent were found upstream of these barriers (Lucas *et al.,* 2009). It is suggested that over 80% of spawning in the Derwent occurs below Stamford Bridge weir, which renders the population extremely susceptible to interference and habitat damage (Jang and Lucas, 2005). Whether the spawning site immediately below Stamford Bridge is sufficient to maintain the population is unclear; river lamprey do not exhibit homing (Tuunainen 1980), therefore 'straying' adults which were spawned in other tributaries in the Humber may help to support the Derwent subpopulation (Lucas *et al.,* 2009). Regardless of this, it is imperative that there are effective mitigation schemes to help restore connectivity in the tributaries of the Humber, particularly in the lower Derwent given that it is an SAC for river lamprey and must therefore ensure free access to spawning areas under the Habitats Directive. Furthermore, the distribution of river lamprey in the Trent is severely limited by Cromwell weir and there is an urgent need to provide free passage at this site to promote the rehabilitation of this species in this river (Greaves *et al.,* 2007).

1.6.1.1. Fishways and barrier removal

Given that all member states in the European Union are obligated to achieve at least 'Good Ecological Status' in all surface waters by 2015 (WFD, 2000), restoring connectivity in lotic systems is essential. The most desirable method to restore connectivity in many cases is to remove the barrier altogether (Humphreys and Gough, 2012). In the Umatilla River, Oregon, Pacific lamprey passage improved substantially from 32% to 81% after the removal of in-stream structures at Boyd's hydroelectric dam (Jackson and Moser, 2012). However, barrier removal may conflict with hydropower generation initiatives and water abstraction schemes, and can also have short-term and long-term ecological impacts, such as increased sediment loads, erosion and spread of disease (Bednarek, 2001; Hurst *et al.,* 2012).

If barrier removal is impractical, the most appropriate solution to improve longitudinal connectivity is to install a fishway facility (or multiple facilities, depending on the size of the barrier and/or the fish community), which may either be built into the existing barrier or constructed as a bypass channel (Clay, 1995; Katopodis and Williams, 2011). There are several different fishway designs, although they are commonly grouped into either nature-like (rock ramps, slopes and bypass channels) or technical (pool-type, baffled, and slot; Figure 1.6) designs (FAO, 2002).



(a) (b) (c)

Figure 1.6. Common technical fishway designs: a) plain Denil, b) single vertical slot, c) pool and weir pass (after Armstrong *et al.,* 2010; Katopodis, 1992)

The installation of a fishway does not necessarily guarantee free passage of fish. In order for fishways to be effective for target species, the hydraulic conditions at the entrance, exit and within the fishway must be suitable in order for fish to be attracted to, and successfully pass through, the fishway with minimum delay to their migration (Williams et al. 2012). Fishway research has historically been biased towards salmonids and clupeids (Clay, 1995; Williams *et al.,* 2012) and only recently has passage criteria for lampreys been assessed in the field (Johnson *et al.,* 2012; Laine *et al.,* 1998; Moser *et al.,* 2011) and in laboratory conditions (Kemp *et al.,* 2011; Russon *et al.,* 2011; Russon and Kemp, 2011a). However, most studies of fishway efficacy for lampreys have concentrated on climbing species, including Pacific lamprey (see Chapter 2, section 2.1). The assessment of fishway efficiencies for river lamprey has been very limited; to date, no quantitative field studies of fishway efficiencies for river lamprey have been undertaken in the UK. As a result, it is unclear whether the fishways installed in rivers in UK, and elsewhere in Europe, are providing free passage for anadromous river lamprey. Although studies in Europe have revealed that low-gradient vertical slot fishways may offer a suitable solution for river lamprey passage (Adam, 2012; Laine *et al.,* 1998), this design is very rare in UK waters due to its high construction costs (Armstrong *et al.,* 2010). In the Ouse catchment, Humber River Basin, the most common fishway designs appear to be pool passes and plain/Alaskan Denils (Fig. 1.7), although these are of unknown efficiency for upstream migrating lamprey species. Lucas *et al.,* (2009) found that the use of the fishway at Elvington (pool and weir design) on the River Derwent was unimportant

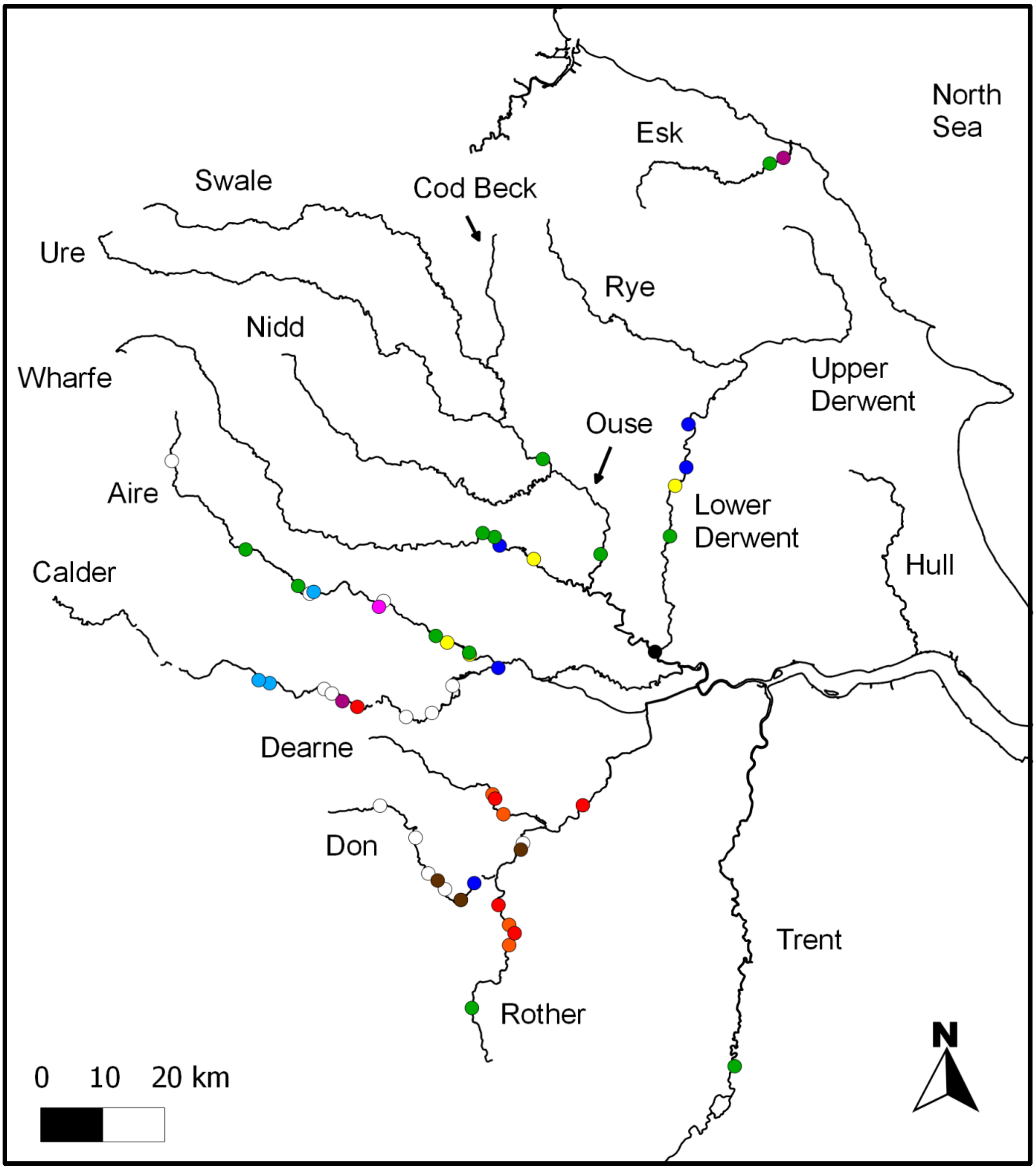


Fig 1.7. Location (coloured circles) of different fishway designs within the Ouse catchment and the tidal Trent, Humber River Basin. Colours represent different fishway designs: green = pool and weir pass; yellow = Denil; brown = Alaskan Denil; royal blue = Larinier pass; pink = bypass channel; light blue = easement; red = rock ramp; orange = eel pass; purple = multiple passes; black = operational change; white = complete/partial collapse. Data courtesy of Steve Chambers, 2013. Data is incomplete and may be subject to changes.

and that lamprey were instead dependent upon high river flows to traverse barriers. Therefore, there is a critical need to evaluate the utility and efficacy of these fishway designs for river lamprey, and since the median cost of construction of recent fishways in UK rivers is in the order of £100 000 (M.Lucas pers. comm.), it is important that such fishways are fit for purpose.

1.6.2. COMMERCIAL EXPLOITATION

The majority of the world's fisheries are in decline (FAO, 2010; Dudgeon *et al.,* 2006; Myers and Worm, 2003). In 2008, the global capture fisheries production was approximately 90 million tonnes, of which 10 million tonnes were from inland waters (FAO, 2010). This was considered to be an underestimation of the actual harvest, as small-scale artisanal and recreational fisheries were not incorporated into the calculation (Cooke *et al.,* 2011). Although inland fisheries are rarely considered in discussions regarding the decline of global fisheries, they constitute a major source of food and income for hundreds of millions of rural households (Allan *et al.,* 2005; Welcomme *et al.,* 2010). However, overexploitation continues to threaten this valuable resource and has been responsible for the decline of several freshwater species (Allan *et al.,* 2005). The European river lamprey is representative of a commercially valuable fish species that has been subject to extensive exploitation, and is one of the most widely exploited species of lamprey (Renaud, 1997; Sjöberg, 2011; Thiel *et al.,* 2009).

River lamprey have been subjected to a long history of exploitation in Europe, dating back at least to Roman times (Sjöberg, 2011). Famously, King Henry I was suggested to have died from eating an excess of lamprey whilst visiting Normandy in 1135, although it is unclear whether river lamprey or sea lamprey were responsible for his death (Kelly and King, 2001; Renaud, 1997). Today, the exploitation of river lamprey for human consumption is mostly restricted to countries surrounding the Baltic Sea, including Finland, Sweden, Russia, Estonia, Latvia and Lithuania (Kesminas and Švagždys, 2010; Sjöberg, 2011; Thiel *et al.,* 2009). However, all available evidence suggests that that recent catches of river lamprey are significantly lower than historic catches. For example, in Estonia catches have fallen from 41-102 t between 1928–1938 to 10.4 t in 1996 (Saat *et al.,* 2002) and current catches in Lithuania are ten times lower than those in the interwar period (Kesminas and

Švagždys, 2010). Similar declines in annual river lamprey catches have occurred in Latvia, Finland and Sweden (Birzaks and Abersons, 2011; Sjöberg, 2011; Tuunainen *et al.,* 1980). Although decreases in river lamprey landings have most commonly been attributed to river regulation and habitat degradation (Birzaks and Abersons, 2011; Kainua and Valtonen, 1980; Saat *et al.,* 2002; Thiel *et al.,* 2009; Tuunainen *et al.,* 1980), it is suggested that intensive exploitation was primarily responsible for the disappearance of river lamprey in the lower Vistula River, Poland, in the late 1950s (Witkowski, 1992); annual catches fell from 100 t, between 1930 and 1938 and after World War II, to just a dozen kg per year. Furthermore, finclipping of upstream river lamprey migrants in two Finnish rivers revealed high levels of exploitation, with fishing mortalities estimated at 65% and 80% (Valtonen, 1980).

Since the late 19th century, commercial fishing of river lamprey in Britain targeted populations in the River Severn, River Thames, and the Derwent, Trent and Ouse subcatchments of the Humber River Basin (Buller and Falkus, 1994; Maitland, 2003; Masters *et al.,* 2006). Typically, river lamprey caught in these waters were sold as bait for the North Sea long-line fishery, targeting cod *Gadus morhua* and turbot *Psetta maxima*, and not to meet human gastronomic demands (Masters *et al.,* 2006; Renaud, 2011). According to Renaud (2011) up to 450 000 adults were used as bait by the English fishing fleet on a yearly basis in the 19th century. Buller and Falkus (1994) also describe how a Victorian Thames fisherman caught 120 000 “lamperns” (river lamprey) in a single night, and that Dutch fishermen bought “lamperns” from Teddington to be used as long-line bait. Day (1884) stated that river lamprey from Britain were sold to Dutch fishermen for between £3 and £5 per thousand individuals.

There are several accounts of river lamprey being caught in significant numbers in the Humber River Basin during the late 19th and early 20th century. On the River Trent, 3 000 river lamprey were caught in a single night at Averham weir, and over 10 000 river lamprey were caught in one night on the Trent and sold for £10 per thousand individuals (Jacklin, 2006; Spicer, 1937). Smith (1912) also describes how he and a friend caught 400 river lamprey on a stretch of low-lying grassland near the River Derwent after a flood event and they were offered to the local people, although a portion were reserved for consumption. The River Ouse, however, maintained a substantial commercial river lamprey fishery between 1908-1914 (Masters *et al.,* 2006). Here, river lamprey were caught in a single wicker basket placed at the downstream end of a lamprey race at Naburn weir, and the live catches were sent by the thousand to The Netherlands to be used as long-line fishing bait (Appleby and Smith, 2000; Masters *et al.,* 2006). Catch data from 1910-11 indicates that 54 500 river lamprey were captured in this fishery, although this represents a particularly high exploitation rate at the time; for instance, 25 500 river lamprey were caught in 1913-14 (Masters *et al.,* 2006). It is not known whether this historic fishery was operating at a sustainable level, although Masters *et al.* (2006) suggests exploitation could have been high given that lamprey were funnelled through a physical bottleneck. As the North Sea long-line fishery was replaced by the trawl fishery *c.*1915, this lamprey fishery, and other lamprey fisheries in Britain, fell into disuse (Lanzing, 1959).

In the late 1980s and early 1990s, river lamprey started to be caught again, as by-catch in a licenced eel fishery, in the tidal reaches of the rivers Trent and Ouse (Masters *et al.,* 2006; P.Bird pers.comm.). These lamprey were, and still are, sold to tackle shops in Britain, having become popularised as a successful bait for northern pike. Although modern catches in the Ouse (below Naburn weir) appear to be significantly lower than those from historical fisheries, with a low annual catch of 9 083 individuals in 2000-01, for instance, the modern fishery is deemed to be operating at a minimum relative exploitation level of 9.9% (Masters *et al.,* 2006). However, recently it has been confirmed that there is at least one other fisher trapping adult river lamprey on the Ouse, therefore the exploitation level on the River Ouse is expected to be much higher than previously thought. Currently, river lamprey are also trapped in the tidal reaches of the Trent (Greaves *et al.,* 2007), although catches are significantly lower than those from the Ouse (section 1.5). It is likely, therefore, that commercial fishing in the Ouse and the Trent has negatively affected the river lamprey population in the Humber to some extent. Given that these fisheries are in the vicinity of the Humber Estuary SAC, in which river lamprey are a listed feature and which must be maintained at or restored to ‘favourable condition’ for this species, a re-evaluation of the scale and impact of these fisheries is urgent.

1.6.3. IMPINGEMENT AND ENTRAINMENT

High levels of entrainment and impingement (i.e. prolonged contact with screen) at intake screens in power station and public water supply abstractions can represent a significant threat to fish populations (Calles *et al.,* 2010; Hadderingh *et al.,* 1983; Hadderingh and Jager, 2005; Turnpenny, 2006). Monitoring of intake screens at both South Humber Bank Power Station (Stallingborough, UK) and Eems Power Station (Netherlands) revealed that 35 species (differing at the two sites) became impinged during study periods (Hadderingh and Jager, 2005; Proctor and Musk, 2001). It is well documented that lampreys are susceptible to impingement and entrainment at abstraction sites due to their elongated shape, their poor swimming capabilities and lack of avoidance to accelerating flows (Rose and Mesa, 2012; Russon and Kemp, 2011a). Both entrainment and impingement can lead to fatigue, damage and mortality of lampreys, as is evident with Pacific lamprey and river lamprey (Moursund *et al.,* 2003; Proctor and Musk, 2001; Rose and Mesa, 2012; Starke and Dalen, 2004). For river lamprey, impingement and entrainment can occur at different stages of their life cycle (APEM, 2008), although they appears to affect downstream migrating juveniles to a greater extent (Frear and Axford, 1991; Proctor and Musk, 2001).

Only a few studies exist which document the impingement and entrainment levels of river lamprey within the Humber river system. Proctor and Musk (2001) evaluated the extent of impingement on a variety of estuarine fish at South Humber Bank Power Station, including river lamprey, and found an impingement rate of 482 lamprey per 24 hrs in June, 2000. This month witnessed lamprey impingement at its highest, with lamprey representing 8.99% of the total number of impinged fish. These were likely to have been emigrating sub-adults, early in the parasitic growth phase. On a similar scale, 16 019 lamprey were found to be impinged at intake screens between 1990-91 at Moor Monkton water abstraction works, River Ouse (Frear and Axford, 1991). However, identification of lamprey was not always resolved at the species level, and current levels of river lamprey impingement at Moor Monkton are suggested to be negligible due to the instalment of fine mesh screens (APEM, 2008; Frear and Axford, 1991). On the River Derwent, assessments of Elvington and Loftsome Bridge public water supply abstractions between 2004 and 2006 suggested that approximately 1 709 and 239 river lamprey became impinged at their intake screens, respectively (Dawes, 2006). Furthermore, it was calculated that the maximum, residual entrainment loss of river lamprey transformers in the Derwent at Elvington water treatment works equated to 3.4% of the transformer population (APEM, 2009). However, there is a high degree of uncertainty regarding the size of the transformer population in the Derwent, or indeed in other rivers within the Humber, therefore this estimate should be treated with care. More recently, the entrainment impact at a small-scale hydropower scheme on river lamprey ammocoetes and transformers in the Derwent has been evaluated (Bracken and Lucas, 2012). The scheme, located at Howshaw, consists of a three-bladed Archimedes screw, and the damage rate of lamprey was estimated at 1.5%. Although this figure is low, the cumulative impact of multiple small-scale hydropower schemes within a catchment may be significantly higher (Bracken and Lucas, 2012).

Levels of impingement and entrainment at abstraction works on the River Trent seem to be lower than those on the rivers Derwent and Ouse. A study conducted at Keadby Power Station, River Trent, found just two adult river lamprey impinged at the intake screen (Jacklin, 2006). The sharp contrast in figures may be a result of differing sampling period durations, as intake screens at Keadby Power Station were only checked on 14 occasions, in comparison to 57 occasions at Moor Monkton, for example. However, it is also likely to be indicative of the comparatively low river lamprey population within the River Trent (Greaves *et al.* 2007). There is an increasing need to evaluate the impact of entrainment and impingement on lamprey at abstraction sites in the Humber, particularly at large power stations within the Humber Estuary SAC. However, the initiation of these studies will largely depend upon the cooperation of power station companies with environmental authorities.

1.7. SUMMARY AND RESEARCH DIRECTION

This chapter has reflected upon the various anthropogenic factors which have been responsible for the decline of lamprey populations worldwide, namely river engineering and obstruction, habitat degradation, pollution and exploitation (Kelly and King, 2001; Mateus *et al.,* 2012; Renaud, 1997; Sjöberg, 2011; Thiel *et al.,* 2009). All of these threats have contributed to the decline of European river lamprey populations in many European watersheds and, although there are signs that this species is recovering in some river systems, recent annual catches are markedly lower than historic annual catches across the continent (Birzaks and Abersons, 2011; Kesminas and Švagždys, 2010; Masters *et al.,* 2006; Sjöberg, 2011; Thiel *et al.,* 2009; Witkowski, 1992).

The Humber River Basin, north-east England, has historically held one of the UK's most important anadromous river lamprey populations (Jang and Lucas, 2005; Masters *et al.,* 2006). In the early 20th century, these populations were commercially exploited, in particular in the Ouse and Trent (Jacklin, 2006; Masters *et al.,* 2006), but the biggest risk to their viability was probably chronic industrial pollution. Although pollution levels within the Humber River Basin have fallen in recent years, three main threats to river lamprey remain in the short to medium term; river regulation and poor longitudinal connectivity between key habitats (Lucas *et al.,* 2009; section 1.5.1), commercial fisheries (Masters *et al.,* 2006; section 1.5.2) and impingement and entrainment at water intakes at power stations and public water supply abstractions (Proctor and Musk, 2001; section 1.5.3). Given that river lamprey are a listed feature in the Humber Estuary and lower Derwent SACs, it is important that a) these potential threats to the integrity of these sites are well understood and b) the effectiveness of mitigation schemes, such as fishway installations, are evaluated, in order to better inform and develop effective management strategies.

One of the key issues to address is the unknown efficacy of fishways for river lamprey that are found within their distributional range, for instance those fishways located in the Humber River Basin. Low-head weirs have limited the dispersal and migration of river lamprey in the Humber (as have large scale dams in continental Europe (Mateus *et al.,* 2012; Tuunainen *et al.,* 2980)) and there is evidence that individuals of this species are dependent upon high flow periods, rather than available fishways, to negotiate these barriers (Lucas *et al.,* 2009). Hence, the suitability of existing fishways in the Humber, and indeed elsewhere in Britain and Europe, for river lamprey is called into question. The most common fishways found in the Humber and elsewhere in Britain are of technical designs (e.g. Denils, pool passes), which were originally intended to provide free passage for economically important species, such as salmonids (Clay, 1995). To date, there have been no quantitative studies to assess the efficiencies of these fishways for lampreys in the UK, although recent studies using experimental flumes have begun to develop passage criteria for river lamprey (Kemp *et al.,* 2011; Russon *et al.,* 2011; Russon and Kemp, 2011a). To complement these laboratory studies, Chapter 2 seeks to:

1) Evaluate *in situ* the efficacy of two conventional, technical fishways of different designs (plain Denil and pool and weir) for upstream migrating river lamprey, using Passive Integrated Transponder (PIT) telemetry.
2) Investigate the patterns of visitation to both fishways in the context of environmental factors, such as river flow, fishway discharge and water temperature.
3) Understand how the fishways' hydraulic conditions relate to observed attraction and passage efficiencies.
4) Offer recommendations as to which types of fishway are likely to be most successful for this non-climbing lamprey species.

An additional concern for the river lamprey population in the Humber is the presence of commercial fisheries operating in the tidal Ouse and the tidal Trent, which have been targeting lamprey since the late 1980s and early 1990s (Masters *et al.,* 2006; P.Bird pers.comm.). One fishery in the tidal Ouse was deemed to be operating at a minimum relative exploitation level of 9.9%, and it is clear that at least one other fisher has been operating on the same river stretch (Masters *et al.,* 2006). Furthermore, recent changes in UK legislation have led to the regulation of these fisheries by competent authorities (see Chapter 3, section 3.2), therefore a reappraisal of exploitation levels in the Humber is greatly needed. The lamprey caught in these fisheries are sold as pike bait to tackle shops and recreational anglers in Britain. However, the scale and structure of the river lamprey bait market in Britain, as well as the knowledge and views of key stakeholders involved, has not been examined. This is essential in order to appreciate how important river lamprey are to different stakeholders and to indicate potential conflicts between conservation authorities and stakeholders that may arise through river lamprey fishery regulations. Consequently, Chapter 3 seeks to:

1) Reassess the exploitation level of lamprey fisheries operating in the Humber River Basin.
2) Determine the scale and structure of the river lamprey bait market in Britain.
3) Understand the degree to which the bait market is dependent upon the Humber stock and determine whether river lamprey are being sourced from outside of Britain or are being exported from Britain.
4) Investigate the views and attitudes of key stakeholders in the river lamprey bait market.

Although an overview of the impacts of impingement and entrainment of lamprey in the Humber has been provided (section 1.6.3), these issues are not investigated in further detail in this thesis due to time and spatial constraints.

Chapter 2: Extreme inefficiency of two conventional, technical fishways used by European river lamprey

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2.1. ABSTRACT

In recent years, fishways have increasingly been designed and installed with the intention to not only provide economically important fishes, such as salmonids, with free passage at barriers, but also for other elements of the migratory fish community. However, in Europe and North America, large numbers of conventional technical fishways exist, for which the efficacy and suitability for non-salmonid species is often inadequately known. Using Passive Integrated Transponder (PIT) telemetry, this study evaluated the efficacy of two such conventional, technical fishways (pool and weir and plain Denil baffle) over the upstream migration and spawning seasons. For lamprey that entered the fishways, 0.0% and 5.0% passage efficiencies were recorded for Denil and pool and weir fishways, respectively, over the entire study period. The pool and weir fishway exhibited poor attraction efficiency (42.6%) compared to the Denil fishway (91.8%), and lamprey took significantly longer to locate the pool and weir fishway, probably as a result of ineffective attraction flow. Most lamprey detected at the fishway entrances were recorded within 24 h of release and returned mostly during high flow events on up to 12 separate dates over a 150 day period. Under these conditions, these fishways were unsuitable for river lamprey. Emphasis is placed upon the increased need for a thorough consideration of the entire migratory fish community during the inception of fishway designs, and that post-construction, strategic evaluation of fishways should be actively supported and encouraged to advance the provision of effective multi-species fishways.

2.2. INTRODUCTION

If appropriately designed and suitably sited, fishway facilities can alleviate habitat fragmentation and provide free passage for multiple species (Clay, 1995; Larinier and Marmulla, 2004; Gough *et al.,* 2012). The construction of fishways at man-made barriers has been used as an ecological restoration tool for more than 300 years, with rapid advances in fishway technology occurring from the mid-20th century (Clay, 1995). The efficacy of a fishway for upstream migrants is largely determined by its hydraulic conditions (e.g. velocity, turbulence), both at the tailrace and within the fishway. Water velocities and bulk flow must be high enough to sufficiently attract fish to the fishway entrance and to enter, whilst water velocity and other hydraulic features, such as shear stress, need to be low enough to allow successful passage (Keefer *et al.,* 2011; Williams *et al.,* 2012). However, the behaviour (i.e. willingness to enter and move through the fishway) and swimming capabilities of fish vary greatly; it is essential that this is accounted for when designing and implementing fishways if they are to pass a broad range of fish with different swimming modes (Noonan *et al.,* 2012; Russon and Kemp, 2011b; Williams et al. 2012).

In its infancy, fishway technology was heavily skewed towards providing salmonids, and to a lesser extent, clupeids, with free passage during their upstream migration through the use of low gradient pool passes (Clay, 1995; Larinier and Marmulla, 2004; Williams *et al.,* 2012). From the early 1900s fishways became more elaborate, steep and compact in design to minimise construction expenditure, and there are now numerous different fishway designs, typically grouped into either technical (pool-type, baffled, and vertical slot) or nature-like (rock ramps and bypass channels) designs (Katopodis and Williams, 2012). Only in recent years have these designs been evaluated, on site or in laboratories, for less economically important or less well-understood taxa (e.g. Cypriniformes, Anguilliformes, Percfiformes, Characiformes) (Bunt *et al.,* 1999; Keefer *et al.,* 2011; Laine *et al.,* 1998; Lucas *et al.,* 1999, 2000; Makrakis *et al.,* 2011; Russon and Kemp, 2011a, 2011b; Thiem *et al.,* 2012; White *et al.,* 2011). Improved understanding of the behaviour and passage ability of a wider range of species is needed, through laboratory and field studies, if we are to move further towards effective multi-species fish passage provision.

Despite suffering major declines worldwide, in many cases due to damming and river alteration, lampreys have been relatively overlooked during the evolution of fishway engineering (Kemp *et al.,* 2011; Lucas *et al.,* 2009; Moser *et al.,* 2002a;

Renaud, 1997). Most research concerning lamprey passage has originated in North America: firstly, in detailing the efficacy of large fishway facilities at hydropower dams in the lower Columbia River for threatened Pacific lamprey *Lampetra tridentata* (Jackson and Moser, 2012; Johnson *et al.,* 2012; Keefer *et al.,* 2009, 2010, 2011; Moser *et al.,* 2002a, 2002b, 2011), and secondly in investigating the capabilities of the sea lamprey *Petromyzon marinus*, an invasive species in the North American Great Lakes, to negotiate barriers, in order to develop preventative measures to block their upstream migration (Hanson, 1978; Hunn and Youngs, 1980; Katopodis *et al.,* 1994). However, differences in the size, swimming capabilities and behaviour of lamprey species and migratory forms warrant care in extrapolation between species. Pacific lamprey possess the ability to climb steep ramps and vertical structures via cycles of propulsion, through axial undulation, and oral disc attachment (Kemp *et al.,* 2009; Reinhardt *et al.,* 2009; Zhu *et al.,* 2011). This has led to the installation of Pacific lamprey passage structures at Bonneville Dam fishway, Columbia River Basin, consisting of aluminium ramps and rest boxes; passage efficiency for Pacific lamprey increased to 90-100% (Moser *et al.,* 2011; Reinhardt *et al.,* 2009). Similar climbing ability occurs also in southern hemisphere pouched lamprey *Geotria australis* (McDowall, 1988). However, there is no evidence to suggest that European lampreys, such as the river lamprey *Lampetra fluviatilis* and, indeed, Great Lakes sea lamprey, are capable of such climbing behaviour (Reinhardt *et al.,* 2009; Kemp *et al.,* 2011; Russon *et al.,* 2011). Instead, at obstructions, they rely on a burst swim – attach – rest mode of locomotion, though they will also swim through thin water films, including around rocks and other structures (Lucas *et al.,* 2009; Kemp *et al.,* 2011; Russon *et al.,* 2011).

Recent field and laboratory studies have begun to assess passage criteria for European river lamprey (Kemp *et al.,* 2011; Laine *et al.,* 1998; Lucas *et al.,* 2009; Russon *et al.,* 2011; Russon and Kemp, 2011a). However, more information is required not only to evaluate behaviours and swimming performance under laboratory conditions to guide suitable fishway designs (e.g. Kemp *et al.,* 2011), but also to test, under field conditions, the effectiveness of fishway designs, old or contemporary, for lamprey and/or other non-salmonid species. This approach is needed in order to move towards effective passage solutions for migratory fish communities, rather than a few economically important target species, such as salmonids. Using Passive Integrated Transponder (PIT) telemetry, this study evaluated the efficacy of two conventional, technical fishways of different designs (pool and weir, plain Denil) for the European river lamprey during their adult spawning migration, and patterns of visitation to each fishway were analysed in the context of environmental factors.

2.3. METHODS

2.3.1. STUDY SITE

The study was conducted from November 2011 to April 2012 on the lower Yorkshire River Derwent (Fig. 2.1), north-east England, a low gradient reach (*c.* 0.3 m km^{-1}) within the Humber river system (mean flow 250 m^3 s^{-1}) with SAC status in which

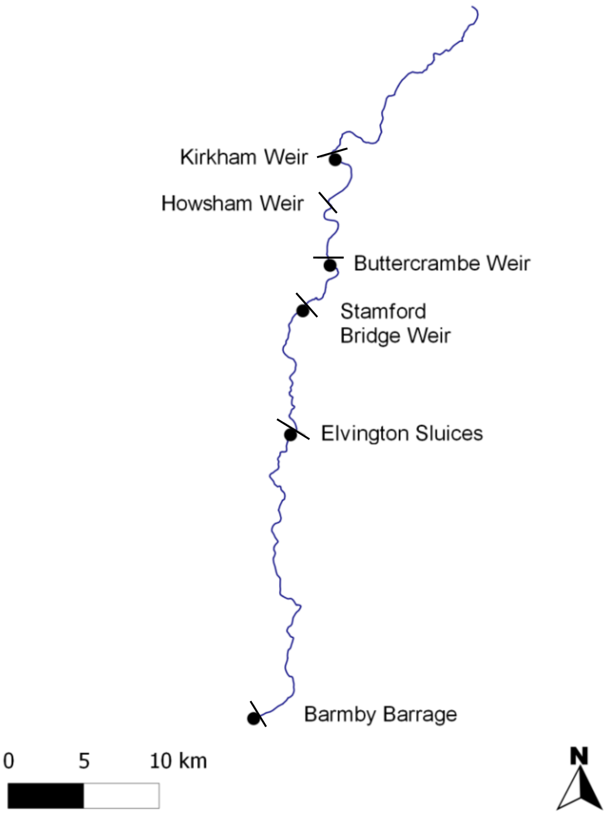

Figure 2.1. Map of the lower Derwent, Yorkshire. Black lines represent barriers, circles represent fishways

river lamprey are a primary feature. The lower Derwent has mid-channel depths of about 2-6 m and an average daily flow of 16.6 $m^3 s^{-1}$ (Lucas *et al.,* 2009). The Fish community is dominated by riverine cyprinids and does not currently sustain significant anadromous salmonid populations (Whitton and Lucas, 1997). The Derwent drains the North Yorkshire Moors, flowing from north to south before joining the Yorkshire River Ouse which combines with the Trent to form the Humber Estuary, the largest coastal plain estuary on the east coast of Britain. The Humber Estuary, also an SAC for river lamprey, provides feeding grounds for parasitic stage river lamprey and, along with widespread, suitable larval and spawning habitat in the Humber tributaries, such as the Derwent, offers suitable habitat for lifecycle completion (Lucas *et al.,* 2009). The Humber is considered to sustain one of the most important river lamprey populations in the UK (Jang and Lucas, 2005). The lower Derwent was selected because, despite being a designated SAC, it represents one of the most impounded rivers in the Yorkshire Ouse catchment, featuring a tidal barrage at its mouth and five low head barriers (<3 m) along the lower 60 km (Lucas *et al.,* 2009) (Fig. 2.1). The study was conducted at the two downstream-most freshwater barriers, Elvington Sluices (Fig. 2.2) and Stamford Bridge (Fig. 2.3), both of which have conventional, technical, high-gradient fishway installations that are of a design type for salmonids (pool and weir fishway and Denil baffle fishway, respectively).

Figure 2.2. Elvington Sluices. The white outline indicates the location of the pool and weir fishway entrance. Photograph taken on 14/01/2012

Figure 2.3. Stamford Bridge weir. The white outline indicates the location of the Denil fishway entrance. Photograph taken on 07/10/2011.

2.3.2. FISHWAYS

Elvington Sluices (river kilometre (rkm) 24.3; Fig. 2.2) consists of two gravity operated, undershot, radial gates spanning the 35 m wide river channel. The sluice gates automatically open further with increased river flow and are situated on top of a *c.*11 m long, 20° sloping weir face. The pool and weir fishway entrance is located at the base of the weir face on the right hand bank, perpendicular to the main river channel (Fig. 2.2), and exits at the bypass canal which runs parallel to the main river channel. The fishway was constructed in 1937. The fishway consists of fourteen pools, each 3 m x 2.8 m and 1.5 m deep, and are connected by sloping ramps in an alternating configuration (Fig. 2.4). Each ramp is 122 x 120 cm and these extend into their associated upstream and downstream pools, reducing each pool's volume to *c.*10.5 m^3. Each ramp has a 20 cm head loss, giving an overall fishway gradient of 13.3%. The fishway is 6% submerged (the first pool) when river discharge is <8 m^3 s^{-1} (Q_{70}), 10% submerged at 10-12 m^3 s^{-1} (Q_{60}-$_{50}$), 50% submerged at 20-25 m^3 s^{-1} (approximately Q_{30-20}) and 100% submerged at >40 m^3 s^{-1} (<Q_7), approximately.

Stamford Bridge (rkm35.6; Fig 2.3) has a three tier, vertical mill weir with a head loss of 2-2.5 m during typical flows. The plain Denil fishway entrance is located adjacent to the weir on the right hand bank and is installed parallel to the main river flow (Fig. 2.3). The plain Denil fishway, constructed in 1996 was intended to enhance connectivity for multiple species, including non-salmonids (Lucas *et al.,* 1999, 2000), since rheophilic freshwater fish species are abundant through the lower and middle Derwent but anadromous salmonids were (Whitton and Lucas, 1997), and remain, rare. It has a total length of 13.5 m, a flume width of 92cm, eighteen V-notched baffles (equally spaced every 50 cm) and has a gradient of 21% in the 10-m long baffled zone. Depth in the fishway increases as tailwater levels rise and the fish pass is completely inundated at approximately Q_7.

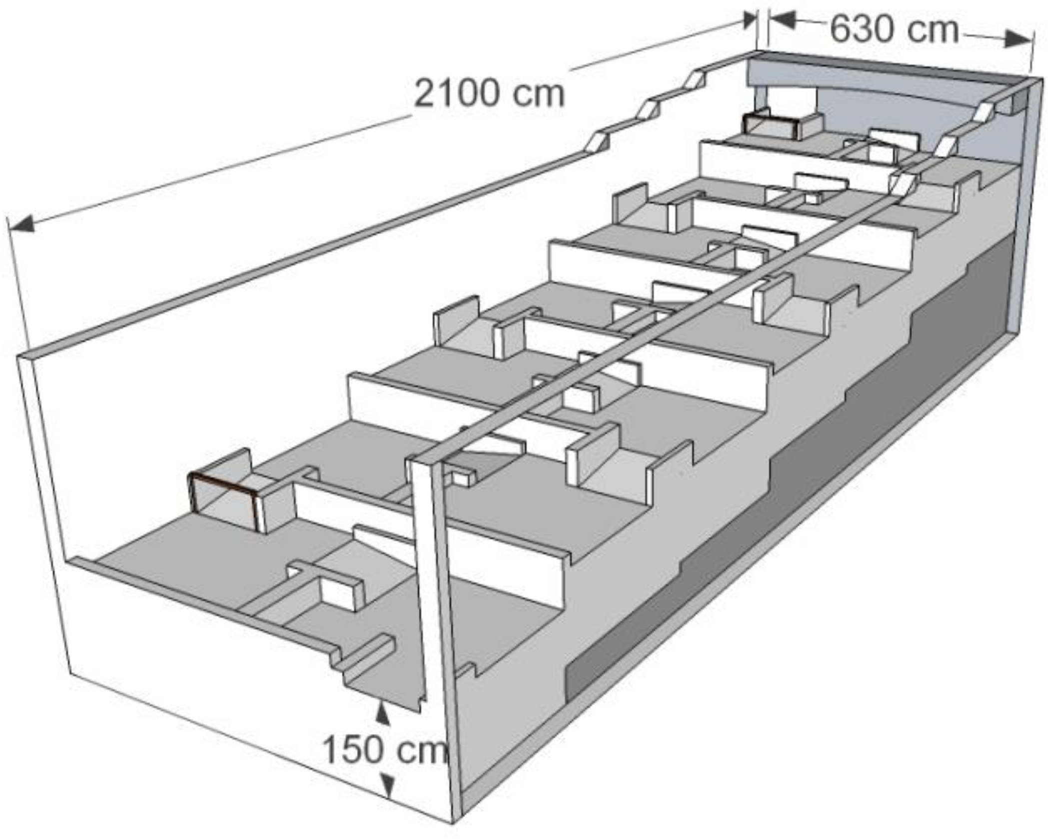

Fig. 2.4. Elvington pool and weir fishway design, consisting of 90° alternating ramp orientation. Note the location of PIT antennae at ramp 2 and the exit ramp.

2.3.3. LAMPREY TAGGING AND PIT TELEMETRY

Passive Integrated Transponder (PIT) telemetry is a cost-effective tool for fish detection and the small size of the tags minimises any adverse effects on swimming performance (Lucas and Baras, 2000). However, PIT telemetry is often confined to studying movements through or over a detection coil, often installed across streams or in structures such as fishways, thus limiting its application for large scale tracking (Castro-Santos *et al.,* 1996; Lucas and Baras, 2000). The use of PIT detection systems has become much more prevalent in freshwater studies since the 1990s to monitor a diverse range of fish species (Castro-Santos *et al.,* 1996; Lucas *et al.,* 1999; Aarestrup *et al.,* 2003; Calles and Greenberg, 2007), and studies have successfully PIT tagged adult Pacific lamprey (Cummings *et al.,* 2008; Keefer *et al.,* 2010a; Keefer *et al.,* 2010b), juvenile Pacific lamprey (Mueller *et al.,* 2006) and even sea lamprey ammocoetes (Quintella *et al.,* 2005).

In this study, pass-through half duplex (HDX) Passive Integrated Transponder (PIT) antennae (Castro-Santos *et al.,* 1996) were installed at the entrance and exit of each fishway in order to assess: a) attraction and passage efficiency, and b) patterns of visitation to each fishway. Attraction efficiency was defined as the proportion (%) of released lamprey detected at the fishway entrance, and passage efficiency was defined as the proportion (%) of lamprey detected at the fishway entrance that were subsequently detected at the fishway exit. Attraction efficiency in this study is a minimum estimate, as piscivorous fish, birds and mammals are abundant on the river (Whitton and Lucas 1997) and take lamprey during their migration (M. Lucas unpublished observations). Lamprey for the study were trapped 1 km below the tidal limit of the River Ouse (Masters *et al.,* 2006), as lamprey catch per unit effort is higher there than in the Derwent tributary of the Ouse (Lucas *et al.,* 2009; Masters *et al.,* 2006). River lamprey do not exhibit natal homing behaviour and are strongly rheotactic (Tuunainen *et al.,* 1980), with prior studies showing that migrating river lamprey taken from the Ouse and released in the lower Derwent exhibit no difference in rates of upstream migration from those caught and released in the Derwent (Lucas *et al.,* 2009). Lamprey were transported to either or both sites, PIT tagged and released 60-100 m below each barrier.

Lamprey without visible external injuries were sedated (MS-222, 0.1 g L^{-1}), their total body length (BL_{total}) measured to the nearest 0.5 cm, and tagged by surgical implantation into the body cavity under U.K. Home Office Licence. Tagged lamprey were electronically scanned to confirm that tags were functional and record each tag's unique identification code. All lamprey were allowed to fully recover before release (*c.* 30 mins). PIT tags (HDX, Texas Instruments model RI-TRP-RRHP, 134.2 kHz) measured 23 x 3.65 mm and weighed 0.6 g in air. Tags were detected by HDX (Texas Instruments) readers, with separate but synchronised readers interrogating the lower and upper antennae in the fishway eight times per second. Tag detection data (identity, date, time) for each antenna were stored on a flash memory card housed in a logger and periodically downloaded onto a portable laptop. At the pool and weir fishway, the entrance PIT antenna (130 cm x 80 cm) was installed at the second ramp from the entrance, as the first was permanently submerged (and hence could be bypassed). The exit PIT antenna (130 cm x 80 cm) was installed at the exit (14^{th}) ramp. At the Denil fishway, the entrance antenna (92 cm x 240 cm) spanned the fishway and was located 120 cm into the fishway flume (115 cm before the first baffle), whilst the exit antenna (92 cm x 140 cm) spanned the upstream exit. Tag ranges of 40-50 cm were achieved for all antennae. Logging equipment was housed within a weather-proof storage unit and powered by two 110 Ah 12V leisure batteries in parallel, at each site. Before and after each battery change and data download (every 5 ± 2 days), a test tag was placed through each antenna loop to check that the equipment was functioning correctly. PIT equipment was operational from 30 Nov 2011 to 16 Apr 2012 at Elvington Sluices and 17 Nov 2011 to 16 Apr 2012 at Stamford Bridge, and, due to occasional battery failure, was operational for 99.4% and 94.8% of the time, respectively.

A total of 275 lamprey were PIT tagged and released (134 at Stamford Bridge; 141 at Elvington Sluices) between Nov 2011 and Feb 2012 (Table 2.1 and 2.2) during the middle period of adult migration (Masters *et al.,* 2006). Lamprey were released at both sites (1-2 h between releases) on four occasions, 30 Nov 2011, 06 Dec 2011, 16 Dec 2011 and 09 Jan 2012 (referred to as 'pair released' lamprey), allowing for finer comparison of fishway visitation patterns. The BL_{total} (cm) of lamprey released at Stamford Bridge (mean ± SD, 37.2 ± 2.1) and Elvington Sluices (36.8 ± 2.8) did not differ significantly ($t(308) = 1.355$, $P = 0.176$). Similarly, BL_{total} of lamprey which were pair released did not differ between sites (two-way ANOVA; $F_{1,219} = 0.009$, $P = 0.927$), yet BL_{total} of lamprey pair released on the four different dates significantly differed (two-way ANOVA; $F_{3,219} = 3.972$, $P = 0.009$), with lamprey released on 16 Dec 2011 and 09 Jan 2012 being significantly larger than lamprey released on 30 Nov 2011 (Tukey $P = 0.035$; $P = 0.039$, respectively). There was no interaction between release date and site (two-way ANOVA; $F_{3,216} = 2.028$, $P = 0.111$).

2.3.4. FLOW MEASUREMENTS, ENVIRONMENTAL FACTORS AND ANALYSIS

All velocity measurements were taken using an electromagnetic velocity meter (Valeport, model 801). Fishway discharge was calculated as:

$Q = AV$

where Q is fishway discharge (m^3 s^{-1}), A is the cross-sectional area of flow (m^2) and V is the mean water velocity (m s^{-1}). Fishway discharge values were then converted to a percentage of base river flow to compare the extent of attraction to each fishway. Fishways in the UK and USA typically have attraction flows of between 5-10% of the total discharge at a barrier (Williams *et al.,* 2012), although Larinier and Marmulla (2004) consider 1-5% suitable for smaller rivers, and many are constructed with these lower attraction flows. In order to assess levels of turbulence within the pools during low and high discharges, power dissipation per unit pool volume was also calculated, according to Larinier (2002), as:

$Pv = \rho\ g\ Q\ DH/V$

where Pv is volumetric dissipated power (W m^3), ρ is density of water (1000 kg m^3), g is acceleration due to gravity (9.81 m s^2), DH is head difference between pools (m) and V is volume of water in pool (m^3). To better understand the range of water velocities and turbulence at key areas within each fishway, velocity measurements were taken at four ramps within the pool and spill fishway at 60% depth (Fig. 2.5a), and in line with the first (from downstream) baffle (Fig. 2.5b) and between the first and second baffle in the Denil fishway (Fig. 2.5c). Lack of access prevented further measurements to be taken within the Denil fishway.

Fifteen minute and mean daily river flow records for the River Derwent were obtained from the Environment Agency's gauging station at Buttercrambe, 5 km upstream of Stamford Bridge weir; no significant tributaries enter the river between there and Elvington, 16 km downstream. Discharge values for the River Derwent were calculated using Buttercrambe gauged daily river flow time series data from 1973-2011 (NERC, 2012). Water temperature was measured at 0.5 h intervals using an automatic logger (Tinytag, TG-4100) at Stamford Bridge. Linear regression analyses were conducted to test the effect of mean daily river flow and mean daily water temperature on lamprey visitation to both fishway entrances. Prior to modelling, data collected on release dates were removed and daily lamprey counts at each fishway entrance were transformed as $\log_{10}(x + 1)$. Fishway figures were drawn using Google SketchUp (Version 8.0) and statistical analyses were carried out using SPSS (Release 19.0.0).

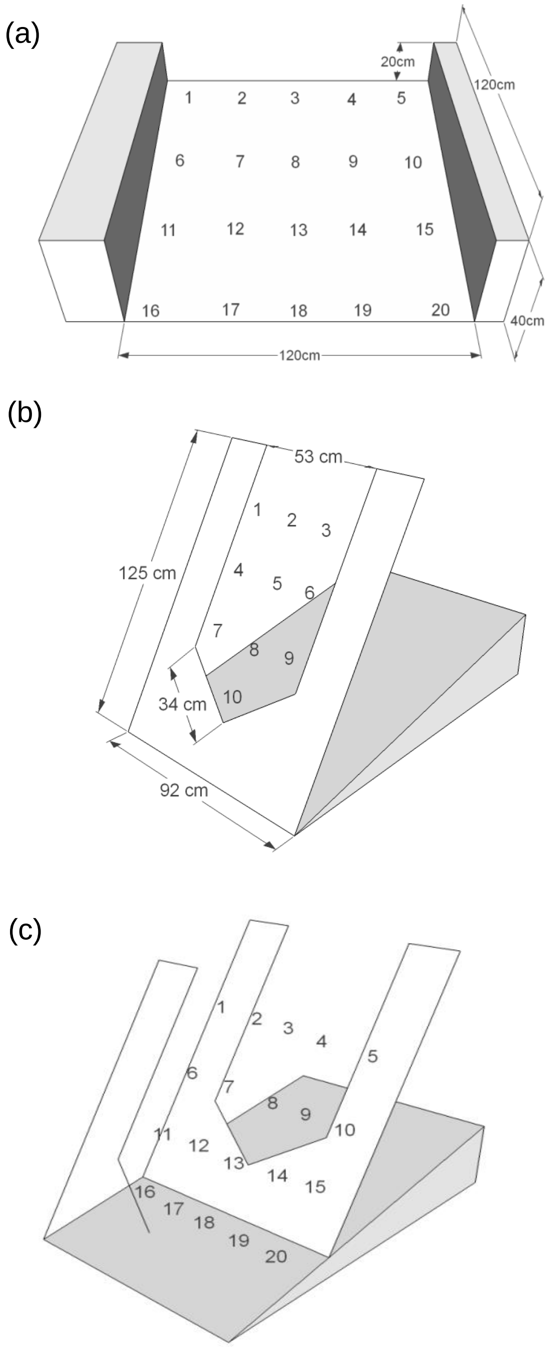

Figure 2.5. Schematics showing the location of velocity measurements taken facing into the prominent flow. a) dimensions of pool and weir ramps, with 20 measurements taken at each of ramps 4 (4th from entrance), 5, 6 and the exit ramp; b) dimensions of baffles within the Denil baffled pass, with 10 measurements taken in line with the baffle 1 (1st from entrance); c) 20 measurements taken between baffles 1 and 2 of the Denil pass. See section 2.3.4 for further details.

2.4. RESULTS

2.4.1. ATTRACTION AND PASSAGE EFFICIENCY

Despite 123 out of 134 lamprey (91.8%) released below Stamford Bridge weir entering the Denil fishway, none passed successfully over a 150 day period (Table 2.1). In comparison, 60 out of 141 lamprey (42.6%) released below Elvington Sluices entered the pool and weir fishway, with only three lamprey (5.0%) passing successfully over a 137 day period (Table 2.2). Lamprey that did pass varied in BL_{total}, in the time taken to pass, and passed at different times of day with varying mean daily flows and water temperatures, but sample size was too small for analysis. Only one of the three lamprey that passed the pool and weir fishway was detected upstream at the Denil fishway entrance. However, thirteen lamprey (9.2%) released below Elvington Sluices not recorded as having passed the pool and weir fishway were detected 11 km upstream at the Denil entrance, all but two of which were detected within 24 h of flow exceeding 30.7m^3 s^{-1} (Table 2.2; Fig. 2.6b). It is highly likely that these lamprey passed through the open sluice gates whilst the river was in flood. There was no evidence to suggest that the BL_{total} of lamprey released below Elvington Sluices that passed Elvington Sluices differed significantly from those released that had failed to pass Elvington Sluices (*t*-test, t_{11} = -0.425, P = 0.679).

In all, 76.4% of lamprey (94 of 123) released at Stamford Bridge that located the Denil fish fishway did so within 24 h of release, whilst 60.0% of lamprey (36 of 60) released at Elvington Sluices that located the pool and weir fishway did so within the same time period. Overall, lamprey took significantly less time to locate Stamford Bridge fish pass (median time = 1.5 hours) than Elvington fish pass (median time = 4.7 hours) (Mann-Whitney; U = 2263.0, Z = -4.242, P < 0.001). However, comparisons of median location time between pair-released lamprey (30 Nov 2012; 06 Dec 2012; 16 Dec 2012; 09 Jan 2012) revealed that only lamprey released at Stamford Bridge on 16 Dec 2012 and 09 Jan 2012 took less time to locate the Denil fishway than lamprey released at Elvington took to locate the pool and weir fishway on the same day (Mann-Whitney; U = 98.0, Z = -2.012, P = 0.044; Mann-Whitney; U = 58.0, Z = -2.021, P = 0.043), though sample sizes were smaller.

There was a significant difference in the time taken for lamprey released on the five separate dates at Stamford Bridge to locate the Denil fishway (Kruskal Wallis; H = 20.69, d.f. = 4, P < 0.001). Post hoc pairwise comparisons of release dates revealed

Table 2.1. Details of PIT tagged lamprey released below Stamford Bridge weir with attraction and passage efficiency figures for the Denil fishway

Date	*n*	Length, mean ± SD (cm)	Detected at Stamford Bridge fishway entrance	Detected at Stamford Bridge fishway exit	Detected at Elvington fishway entrance	Attraction efficiency (%)	Passage efficiency (%)
17-Nov-11	30	37.4 ± 1.9	29	0	0	96.7	0.0
30-Nov-11	27	36.9 ± 1.8	25	0	1	92.6	0.0
06-Dec-11	32	36.5 ± 2.6	28	0	0	87.5	0.0
16-Dec-11	20	38.0 ± 2.1	17	0	0	85.0	0.0
09-Jan-12	25	37.3 ± 2.1	24	0	0	96.0	0.0
Total	**134**	**37.2 ± 2.1**	**123**	**0**	**1**	**91.8**	**0.0**

Table 2.2. Details of PIT tagged lamprey released below Elvington Sluices with attraction and passage efficiency figures for the pool and weir fishway

Date	*n*	Length, mean ± SD (cm)	Detected at Elvington fishway entrance	Detected at Elvington fishway exit	Detected at Stamford Bridge fishway entrance	Attraction efficiency (%)	Passage efficiency (%)
30-Nov-11	27	36.1 ± 1.7	10	0	2	37.0	0.0
06-Dec-11	33	37.1 ± 1.9	15	0	1	45.5	0.0
16-Dec-11	35	37.4 ± 2.1	19	1	4	54.3	5.3
09-Jan-12	25	37.9 ± 2.5	9	1	4	36.0	11.1
03-Feb-12	7	35.4 ± 3.8	3	0	2	42.9	0.0
25-Feb-12	14	33.5 ± 4.9	4	1	0	28.6	25.0
Total	**141**	**36.7 ± 2.8**	**60**	**3**	**13**	**42.6**	**5.0**

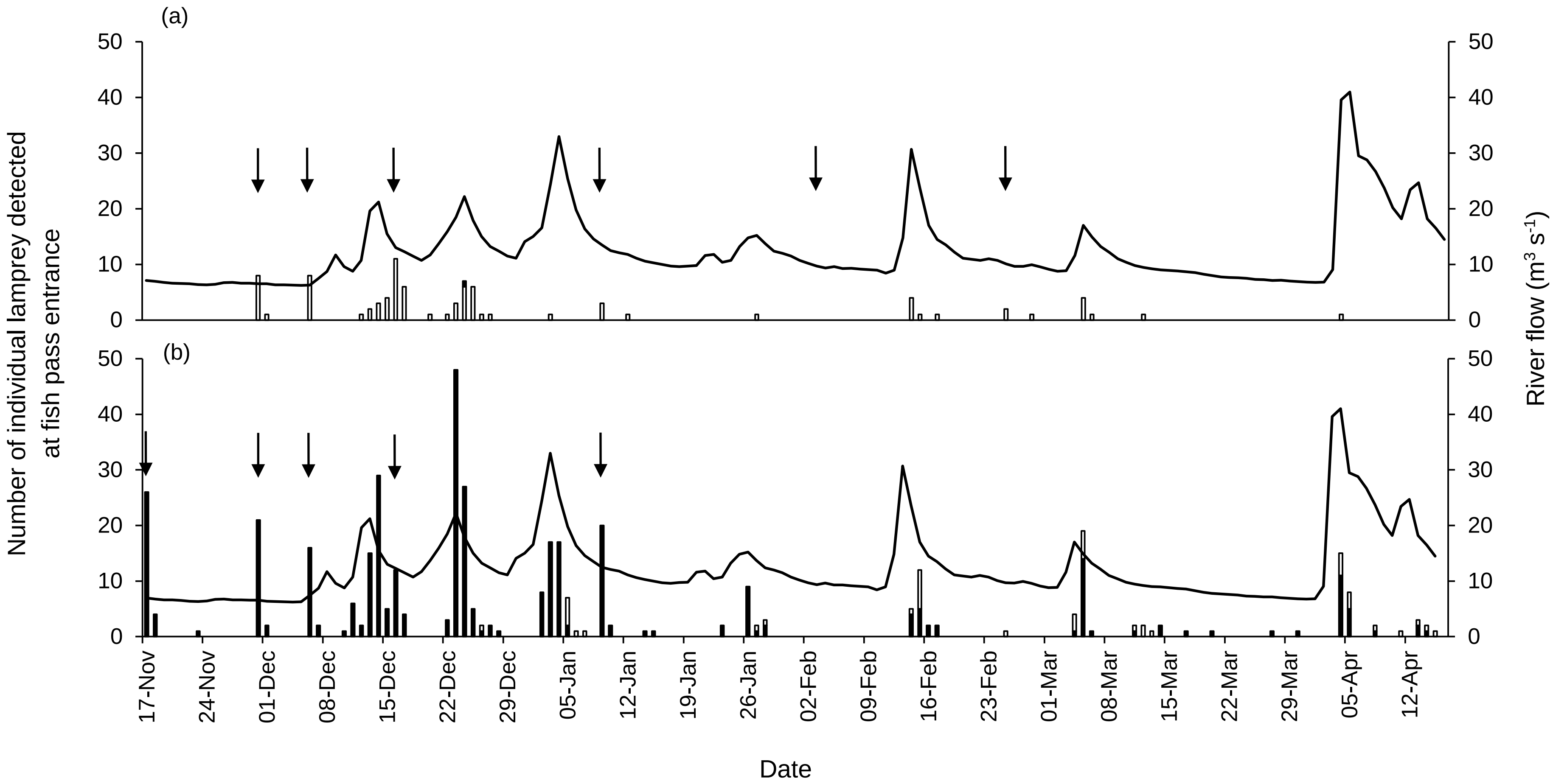

Figure 2.6. Number of lamprey detected at the entrance to a) Elvington Sluices, and b) Stamford Bridge fishways, in relation to river flow. Arrows denote release dates, white bars represent lamprey released below Elvington Sluices and black bars represent lamprey released below Stamford Bridge weir.

that lamprey released on 17 Nov 2011 took significantly less time to locate the Denil fishway than those released on 30 Nov 2011 and 09 Jan 2012 (Mann-Whitney *U* with Benjamini-Hochberg corrected significance at $P = 0.005$ and $P = 0.010$, respectively). This was most likely due to diel activity effects (see section 2.4.3), as it is well documented that river lamprey are strongly negatively phototaxic during their upstream winter migration (Sjöberg, 1977); lamprey were released at 16:50 on 17 Nov 2011, eight minutes after civil twilight, whereas lamprey were released at 15:30 and 15:40 on 30 Nov 2011 and 09 Jan 2011, 59 minutes and 105 minutes before civil twilight, respectively. Conversely, there was no significant difference in the time taken for lamprey released at Elvington Sluices on the first four release dates to locate the pool and weir fishway (Kruskal Wallis; $H = 4.908$, d.f. = 3, $P = 0.179$); all lamprey at Elvington Sluices were released after civil twilight. Not enough lamprey released on the final two release dates were detected and were thus excluded from analysis.

2.4.2. PATTERNS OF VISITATION

It is evident from Figure 2.6 that peaks in the number of lamprey detected at both fishways were highest on release dates and during high flow periods, although there were proportionally less lamprey detected at the pool and weir fishway than at the Denil fishway (Fig. 2.7). There was a significant positive relationship between lamprey visitation and mean daily river flow for both the Denil entrance (Linear regression, $F_{1,\ 145} = 54.72$, $P < 0.001$, $R^2 = 0.274$) and the pool and weir entrance (Linear regression, $F_{1,\ 131} = 14.05$, $P < 0.001$, $R^2 = 0.097$). Mean daily water temperature had no effect on lamprey visitation at either fishway entrance. Disregarding release dates, lamprey visitation was almost absent during low flow periods (e.g. mid-January, early-February, mid/late-March). The highest number of tagged lamprey recorded in a day (23/12/2011) at the Denil fishway was 48 lamprey (44.0% of lamprey released at the time) when daily flow was elevated (18.5 $m^3\ s^{-1}$) above preceding conditions. It is also important to note that lamprey that had not visited either fishway on the day of release entered fishways thereafter when river flow had risen markedly (Fig. 2.7), again indicating that lamprey visitation at both fishway entrances was positively correlated with river flow.

The majority of lamprey released at Elvington Sluices that successfully located the pool and weir fishway only visited on one occasion, with no lamprey visiting the fishway on more than four separate days (Fig. 2.8a). Conversely, the majority of

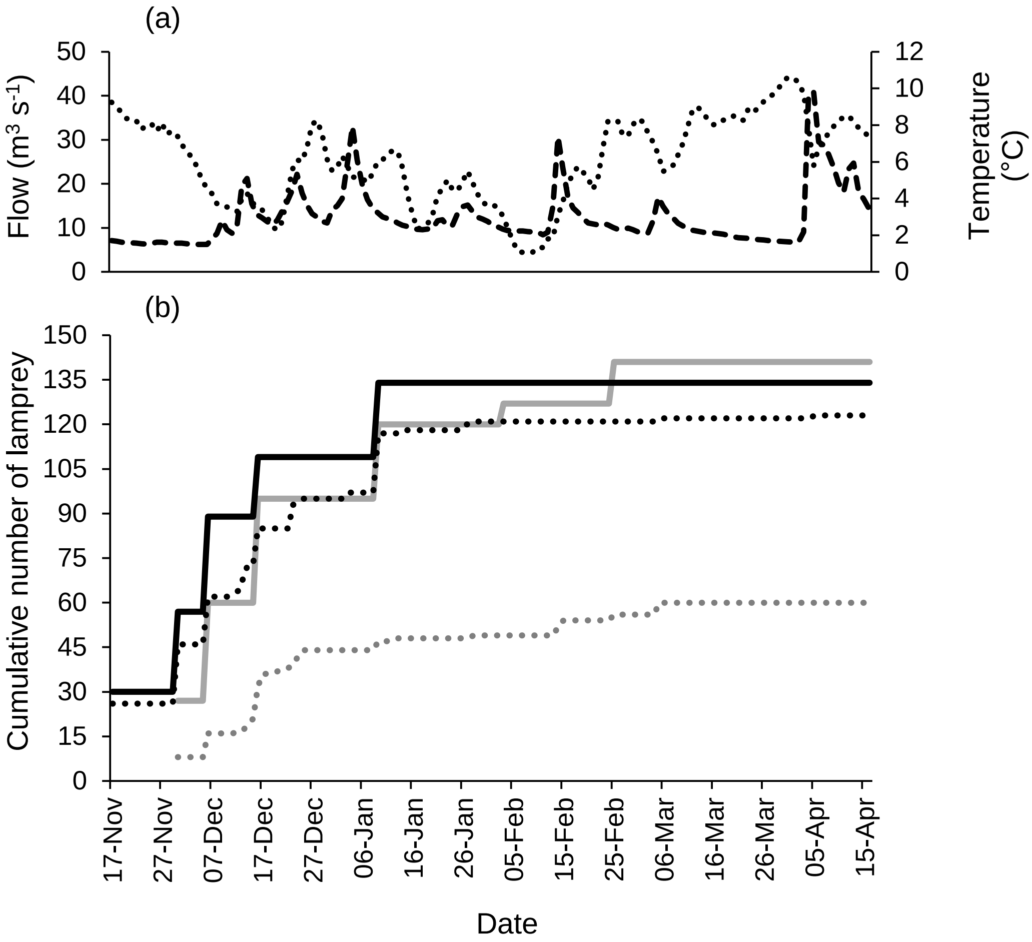

Figure 2.7. (a) Mean daily flow (dashed) and temperature (dotted) for the duration of the study. (b) Cumulative number of lamprey released (solid) and detected (dotted) at Elvington fishway entrance (grey) and Stamford Bridge fishway entrance (black) over the study period. Note that increases in the number of new lamprey being detected occur during release days and high flow events.

lamprey released at Stamford Bridge visited on multiple occasions, with almost one third (32.5%) of lamprey that had successfully located the Denil fishway visiting on four or more separate days and one doing so on 12 separate days (Fig. 2.8b). Figure 2.9 shows that a large number of lamprey at Stamford Bridge were still in the vicinity of the fishway entrance after several weeks, with twenty lamprey being detected after 10 weeks of release and four lamprey being detected 130-150 days after release. The mean minimum number of days in which individual lamprey were delayed at the Denil fishway was 36 days. The mean minimum delay period below the pool and weir fishway was calculated as 10 days, as the majority of lamprey released at Elvington were only detected 0-9 days after release (Fig. 2.9) and on one occasion only (Fig. 2.8a). During the study period river flows were sufficient to partially or wholly drown

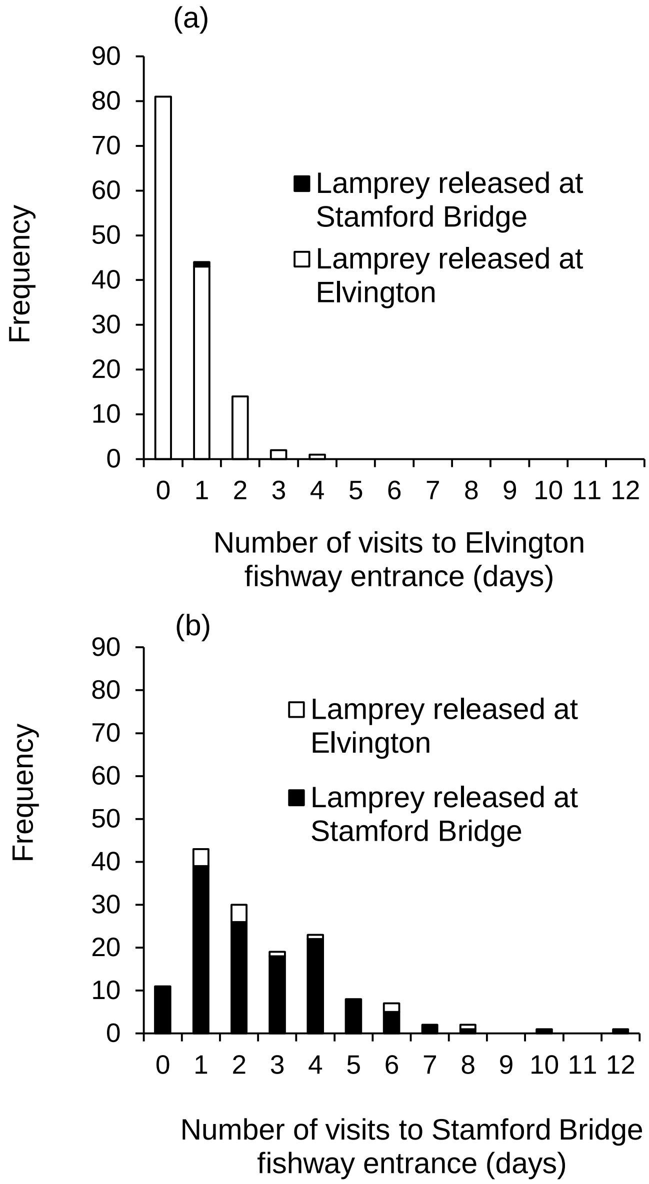

Figure 2.8. Number of daily visits lamprey made to a) Elvington fishway and b) Stamford Bridge fishway during the study period.

Elvington weir on three occasions (for example, see Fig. 2.10), but never sufficient to do so at Stamford Bridge weir, although the spate on 4 April 2012 (41 m^3 s^{-1}) came close to doing so; thus the potential route of passage upstream throughout the study at Stamford Bridge was via the Denil fishway.

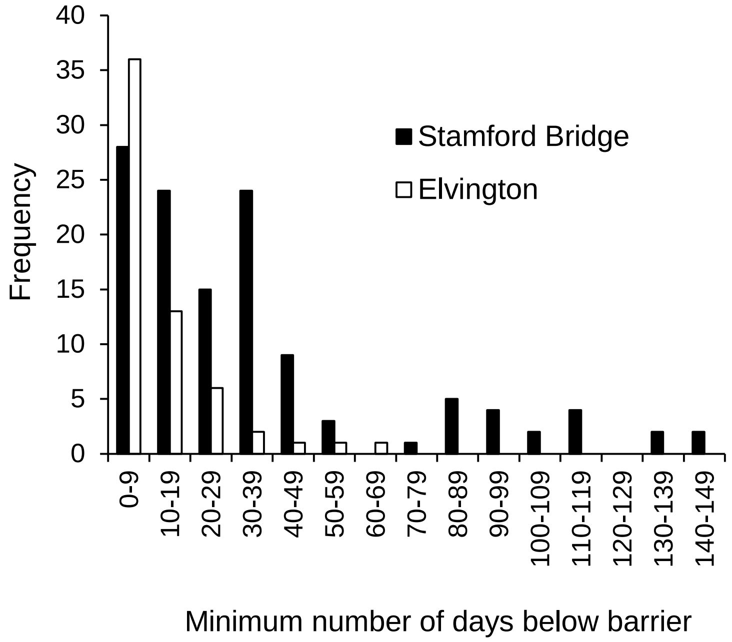

Figure 2.9. Minimum number of days in which individual lamprey were restricted behind each barrier (from day of release to the day of last detection) over the study period.

Figure 2.10. Elvington Sluices in flood conditions on 14/02/12 (mean daily flow 30.7 $m^3\ s^{-1}$).

2.4.3. DIEL ACTIVITY

Lamprey detections at Stamford Bridge were two-way categorised by diel activity at the entrance to the fishway (morning defined as 04:00 - 09:59h; afternoon as 10:00-15:59h; evening as 16:00-21:59h; night as 22:00-03:59h), and months when detected (November/December; January/February; March/April), and chi-square analysis revealed a highly significant association between these variables (X^2 = 40.22, d.f. = 6, $P < 0.001$). Evening activity was positively associated with November and December months (partial X^2 = 5.72), afternoon activity was positively associated with January and February months (partial X^2 = 5.29), whilst morning activity was strongly positively associated with March and April months (partial X^2 = 8.02). The only strongly negative association was between evening activity and March and April months (partial X^2 = 9.16). There were not enough detections at Elvington fishway entrance to conduct a similar chi-square analysis.

2.4.4. FLOW MEASUREMENTS

The pool and weir fishway discharge was 1.3 and 2.1% of river flow during elevated (*c.*18 m^3 s^{-1}, Q_{30} – near the long-term mean, but representing relatively high flows during the period of study) and low (*c.* 7 m^3 s^{-1}, Q_{75}) river flows, respectively. Discharge through the Denil fishway was 4.2% for elevated flow (*c.*18 m^3 s^{-1}), and 4.5% at low flow (*c.* 7 m^3 s^{-1}). Volumetric dissipated power in the pools at the pool and weir fishway was calculated as 22.1 W m^3 for low flow (*c.* 7m^3 s^{-1}) and 36.0 W m^3 for relatively high flow (*c.*18 m^3 s^{-1}). At the pool and weir fishway, velocities were lower at the upstream exit ramp than ramps 4, 5 and 6 located within the fishway (Table 2.3.). Velocities typically increased by 60% from measurements 1-5 and 6-10 at all ramps, and were, on average, highest at measurements 11-15 (Table 2.3). Mean velocity for the ramps within the fishway at measurements 16-20 (Fig. 2.5a) was 1.57 m s^{-1}, and the highest recorded velocity was 2.13m s^{-1} (measurement 16, ramp 6). Further velocity measurements and visual assessment of flow, using streamer tapes, within the pools, demonstrated a surface-streaming flow created by each ramp, as opposed to a plunging flow.

Table 2.3. Mean velocity (m s^{-1}), *V*, and standard deviation, SD, measurements at locations within both fishways (see Fig. 5). Grading from white to dark grey cells indicate measurements being taken from the edge to the centreline of given structures. Pool and baffle numbers are counted from the downstream entrance.

	Pool and Weir Fishway								**Denil Baffled Fishway**			
Measurement	**Ramp 4**		**Ramp 5**		**Ramp 6**		**Exit Ramp**		**Baffle 1**		**Baffle 1 – 2**	
	V	**SD**	***V***	**SD**	***V***	**SD**	***V***	**SD**	***V***	**SD**	***V***	**SD**
1	0.92	0.02	0.95	0.11	1.03	0.04	0.87	0.02	1.43	0.11	0.56	0.43
2	1.08	0.07	0.90	0.06	0.91	0.05	0.73	0.01	1.46	0.16	1.61	0.13
3	1.07	0.02	0.95	0.02	0.93	0.04	0.73	0.02	1.53	0.10	1.57	0.16
4	1.00	0.01	1.03	0.02	0.97	0.04	0.66	0.02	0.85	0.13	1.59	0.15
5	0.99	0.02	0.90	0.04	0.96	0.03	0.83	0.01	0.75	0.22	0.35	0.43
6	1.54	0.05	1.50	0.08	1.63	0.03	1.31	0.01	1.02	0.08	0.36	0.45
7	1.56	0.04	1.55	0.04	1.72	0.03	1.22	0.01	0.84	0.10	1.24	0.18
8	1.55	0.05	1.52	0.03	1.72	0.03	1.24	0.01	0.47	0.28	1.05	0.18
9	1.57	0.02	1.51	0.02	1.72	0.03	1.25	0.02	0.57	0.22	1.06	0.17
10	1.52	0.01	1.45	0.02	1.69	0.06	1.32	0.01	0.18	0.25	0.98	0.21
11	1.52	0.01	1.29	0.04	1.84	0.02	1.30	0.01			0.14	0.26
12	1.80	0.05	1.88	0.04	1.86	0.03	1.33	0.02			1.05	0.24
13	1.87	0.05	1.87	0.03	1.88	0.03	1.44	0.01			0.76	0.21
14	1.90	0.02	1.84	0.04	1.76	0.04	1.35	0.02			0.62	0.20
15	1.91	0.03	1.80	0.03	1.84	0.04	1.16	0.01			0.17	0.42
16	1.80	0.05	1.21	0.08	2.13	0.02	0.92	0.06			0.05	0.12
17	1.68	0.07	1.68	0.08	2.00	0.04	1.23	0.02			0.11	0.25
18	1.60	0.08	1.52	0.11	1.86	0.05	1.23	0.02			-0.11	0.12
19	1.71	0.05	1.70	0.05	1.83	0.06	1.24	0.19			0.06	0.18
20	1.41	0.03	1.54	0.18	2.00	0.07	1.12	0.65			0.22	0.08

In the Denil fishway, velocities in line with the baffle were highest nearest the water surface and at the edge of the baffle opening (1.53m s^{-1}; Fig. 2.3b, measurement 3) whilst lowest at the centreline towards the base of the baffle opening (0.18 m s^{-1}; Fig. 2.5b measurement 10) (Table 2.3). In between baffles 1 and 2 (from downstream entrance) flow was typically slower and more turbulent nearest the walls of the fishway due to the recirculation of flow caused by the side plates of baffle 1. Velocities increased from the base of the fishway slope to the water surface and velocities were typically highest near the centreline of the fishway (maximum recorded velocity 1.61m s^{-1}; Fig. 2.5c, measurement 2).

2.5. DISCUSSION

In this study, two high-gradient technical fishways typical of those found widely in European waters (Clay, 1995), the plain Denil baffled, and pool and weir, were found to be extremely inefficient for European river lamprey, with passage efficiencies of 0% and 5.0%, respectively. The fact that no lamprey were successful in passing the Denil fishway is particularly striking given that 91.8% of released lamprey entered the fishway, the majority within 24 h of release (indicating strong motivation to pass), and almost one third of which visited the fishway on four or more separate days. Similar repeated attempts to traverse fishways and obstacles have been documented for river lamprey (Lucas *et al.,* 2009; Russon *et al.,* 2011) and Pacific lamprey (Keefer *et al.,* 2011; Moser *et al.,* 2002a). In contrast, the pool and weir fishway exhibited relatively poor attraction efficiency (42.6%), the vast majority of detected lamprey visited the fishway on one occasion only and took a significantly longer period of time to locate the fishway. Furthermore, whilst peaks in lamprey visitation to both fishways on a given day were highest during high flow events, outside of release dates, significantly less lamprey visited the pool and weir fishway on a given day than the Denil fishway. These observations can be attributed to the pool and weir's low fishway discharge and the suboptimal, perpendicular orientation of the attraction flow in relation to the barrier; these factors have proved to be problematic for other fish species attempting to locate fishway entrances (Aarestrup *et al.,* 2003; Bunt, 2001; Gowans *et al.,* 1999; Keefer *et al.,* 2011; Laine *et al.,* 1998; Larinier *et al.,* 2005). The cumulative effect of the two barriers with ineffective fishways on tagged lamprey was stark; since the critical flow for lamprey passage over Stamford Bridge weir (when drowned), 44 $m^3 s^{-1}$ (Lucas *et al.,* 2009), equating to Q_5 over the whole calendar year, or Q_9 for the migration period of September to March, was never exceeded during the 2011-12 migration period, the total passage efficiency of all lamprey in passing both Elvington and Stamford Bridge barriers together was likely 0%.

Given that Lucas and Baras (2001) recommend a minimum fishway passage efficiency of 90-100% for diadromous species, the passage efficiency figures reported in this study are extremely low. A review of fishway performance by Bunt et al. (2012) found, from 19 monitoring studies comprising 26 anadromous and potamodromous species, that Denil fishways had a mean upstream passage efficiency of 51%, whilst pool and weir passes were the least efficient with a mean passage rate of 40%, although there was high variation amongst these values. However, Noonan et al. (2012), in a similar meta-analysis, found the converse situation, but both found consistently lower passage efficiency of weaker swimming temperate non-salmonids. Bunt et al. (2012) indicated that fishway type, slope and elevation change were core predictors of passage efficiency, while Noonan et al (2012) found taxonomic group, fishway type and fishway length to be key. Despite this, it is doubtful that low slope pool and weir and Denil fishways will offer an effective solution for migrating adult river lamprey. Despite the very steep gradient of the Denil pass in this study, low velocities were present behind baffles, but turbulence was high. In a combined Denil (slope, 16-21%) and vertical slot (slope 7%) fishway on the River Kemijoki, Finland, whilst nearly 1,000 adult salmonids passed the fishway over three years and a variety of cyprinids passed each year, no river lamprey were observed negotiating the Denil fishway, and limited progress was made through the vertical slot sections, although progress improved slightly with the installation of bristles at the bottom of the slots (Laine *et al.,* 1998). Whilst Pacific lamprey have been shown to ascend Denil fishways up to 20.1m long and 28.7% gradient, with a rate of up to 1 372 lamprey passing in 24 h (Slatick and Basham, 1985), the present study clearly demonstrates European river lampreys' inability to scale a 10-m long, 21% gradient baffled zone within a Denil fishway.

As previously shown by Lucas et al. (2009), the pool and weir fishway at Elvington was somewhat redundant during high river flows, with thirteen lamprey negotiating the barrier, most likely, through the undershot sluice gates. Lucas et al. (2009) demonstrated that acoustic-tagged lamprey were able to move through the sluice gates when mean daily flow exceeded 27m^3 s^{-1}, complementing our findings that 11 lamprey released at Elvington were detected 11 km upstream at Stamford Bridge Denil fishway within 24 h of river flow exceeding 30.7m^3 s^{-1}. However, whilst Lucas et al. (2009) indicated that 64% of all lamprey released downstream of Elvington, over a four year study period, successfully passed Elvington Sluices, here only 9.2% of lamprey released below Elvington Sluices, in a single year, were detected upstream of the barrier at the Denil fishway. In the former study the percentage of days for which mean daily river flow at the fish pass locality exceeded 27 m^3 s^{-1} for the four migration seasons ranged from 18.5-47.6%, whereas in the 2011-12 lamprey migration season this was only exceeded on 3.9% of days. This demonstrates that population attrition at barriers is more severe during prolonged low river flow periods, as confirmed with Pacific lamprey migration (Jackson and Moser, 2012). Because lampreys are fully semelparous, efficient passage at barriers and via fishways is particularly important. It should be noted that the minimum estimates of migration delays below the barriers made in this study are probably underestimates, particularly at the Denil fish pass at Stamford Bridge where critical flow for lamprey passage over the weir (when drowned), 44 $m^3 s^{-1}$ (Lucas *et al.,* 2009), was never exceeded over the study period, thus the delay could be regarded as the period from entry into the fish pass to the end of the study - a markedly longer period than the conservative measure of time between first and last detection, used here.

Impassability at Elvington Sluices is a particular problem since no suitable spawning habitat is located downstream of the barrier (Lucas et al., 2009). Given that 16 of 141 lamprey passed Elvington Sluices (three via fishway, 13 via sluice gates), it is estimated that a maximum of 125 lamprey (88.7%) failed to reproduce as a direct result of river impoundment and fishway failure. It is unlikely that the figure is significantly less than this, as Lucas et al. (2009) demonstrated that there was minimal decline in the number of lamprey detected from just above Elvington Sluices to below Stamford Bridge weir, and our findings show that the Stamford Bridge fishway exhibited a >90% attraction efficiency. Thus, any lamprey able to traverse Elvington Sluices are likely to be subsequently detected at the Stamford Bridge fishway. Despite there being available spawning habitat (450 m^2) below Stamford Bridge weir (Jang and Lucas, 2005), a large number of lamprey released below the barrier attempted to ascend the fishway on multiple occasions over the entire study period, including during pre-spawning and spawning period in late March to mid April. It is highly probable that detections at the fishway entrance during spawning period are an indicator of migratory behaviour, as opposed to movement during nest building, as spawning habitat is not available within the tailrace of the fishway (Jang and Lucas, 2005). This provides evidence that spawning-phase river lamprey, similar to spawning-phase pacific lamprey (Jackson and Moser, 2012) retain their strong rheotactic behaviour.

Prior studies assist in interpreting why the passage efficiencies at the two technical fishways for river lamprey were poor. It seems likely that within the pool and weir fishway, the high water velocities over the ramps and the lack of attraction flow generated by each ramp largely contributed to the failure of the fishway for river lamprey. Flume studies reveal that river lamprey are thigmotactic, moving in close proximity to the substrate and structured walls (Kemp *et al.,* 2011), similar to Pacific lamprey (Keefer *et al.,* 2011), and require adequate attraction flow to stimulate upstream migration. Furthermore, Piper *et al.,* (2012) revealed that upstream passage of European eel (another thigmotactic, benthic species) at eel ladders was two-fold higher when provided with a plunging attraction flow as opposed to a streaming attraction flow. However, each pool within the pool and weir fishway is provided with a streaming flow from an upstream ramp and the pool sub-surface hydraulics are characterised by slow, re-circulating eddies. With little attraction flow being provided to the pool substrate, it is likely that locating each ramp is difficult for river lamprey. Whilst fine-scale behaviour of sea lamprey locating surface weirs has been documented by Haro and Kynard (1997), the fishway pools in their study contained surface weirs and submerged orifices, therefore the flow profiles of our fishway pools are likely to differ.

European river lamprey have been demonstrated to achieve a maximum burst speed of 1.75 – 2.12 m s^{1} at a velocity barrier within an experimental flume, at a mean temperature of 12.6°C (Russon and Kemp, 2011a). These figures match closely to the recorded velocities over each ramp within the pool and weir fishway. Furthermore, Russon et al. (2011) noted that, in an experimental flume, river lamprey failed to ascend a crump weir, similar in geometry to the pool and weir ramps, with a maximum mean velocity at the weir face of 2.30 m s^{-1}, similar to the maximum mean velocity of 2.13 m s^{-1} recorded at the pool and weir ramps. However, as median water temperature in Humber rivers during the river lamprey migrating season is typically between 5 - 7°C (Masters *et al.,* 2006), significantly lower than in the flume studies, and maximum attainable swimming velocity decreases with temperature for fish (Wardle, 1980), river lamprey would find ascending the ramps in the fishway very difficult. In addition, the cumulative effect of attempting to traverse 14 ramps at maximum recorded burst speeds is liable to be significant; electromyogram telemetry of sea lamprey during movement through difficult passage areas suggested an increasing onset of fatigue after each burst movement (Quintella *et al.,* 2004).

At the Denil fishway, the inherent turbulence behind the baffles, high water velocities, the high gradient slope and the length of the fishway are likely to act as behavioural and physical impediments to ascent. Indeed, studies have shown that high gradient Denil fishways (e.g. ≥ 20%) are typically inefficient for other non-salmonid species (Lucas *et al.,* 1999; Mallen-Cooper and Stuart, 2007; Noonan *et al.,* 2011). In high velocity situations river lamprey use a "burst-attach-rest" mode of swimming (Kemp *et al.,* 2010). River lamprey have been observed using oral disc attachment on the downstream side of the baffle plates at the Denil fishway at Stamford Bridge, although none have been observed attached to baffles more than half way up the fishway (M. Lucas pers. obs.). The difficult transition from stationary attachment to progressing upstream in turbulent flow has been well documented in Pacific lamprey at bulkhead challenges (Keefer *et al.,* 2010), with many lamprey being unable to re-attach and being swept downstream. This has also been observed with river lamprey within the Denil fishway at Stamford Bridge (D. Bubb pers. comm.).

In reviewing results from field and laboratory studies, we suggest that low gradient vertical slot or nature-like fishways are likely to be most efficient for river lamprey, as well as providing passage to a large variety of other riverine taxa (Calles and Greenberg, 2007; Noonan *et al.,* 2011; Pratt *et al.,* 2009; Rodríguez *et al.,* 2006; Stuart and Berghuis, 2002). Preliminary evidence suggests that at a 1% slope, double vertical slot fishway with 10 cm drops between 9 m long basins and with a cobble bed, on the River Elbe, Germany, 88% of river lamprey successfully utilised the fishway (Adam, 2012). Furthermore, vertical slot fishways at Cobourg Brook and Big Carp River in Canada have been used to trap invasive Great Lakes sea lamprey, and have recorded passage efficiencies of 81-100% for this species (O'Connor *et al.,* 2003, 2004). Keefer *et al.,* (2011) also showed that Pacific lamprey exploited low-velocity side channels in an experimental fishway. High efficiencies recorded at vertical slot fishways for lamprey can be partly attributed to the provision of passage routes near the sides and substrate of the fishway. In addition, the rounding of entrances, turns or bulkhead challenges in fishways should be considered, as this modification has demonstrably improved entry success, increased passage efficiency and decreased passage time for Pacific lamprey (Keefer *et al.,* 2010; Moser *et al.,* 2002b). However, a serpentine (alternating) vertical slot configuration is not recommended, as this design can cause turbulent and confusing currents for lamprey (M. Moser pers. comm.).

Low to moderate gradient nature-like or rock-ramp fishways are likely to exhibit high passage efficiency for lamprey due to their suitable oral disc attachment sites, and heterogeneous flow conditions, whereby lamprey can exploit low velocity areas for refuge and passage. However, nature-like fishways have often been found to exhibit low attraction efficiencies (Bunt *et al.,* 2012) as the entrances were often located several tens of metres or more below barriers and/or had rather limited attraction flow. Therefore high passage efficiency in nature-like passes may be offset by an inability to locate the fishway unless suitably sited (Bunt *et al.,* 2012). Nevertheless, nature-like passes with gravel could also afford spawning habitat for lamprey.

Historically, pool and weir and Denil type designs were the chief candidates for installation at low-head barriers in the UK (Beach, 1984). Vertical slot fishways and nature-like fishways are rarely installed in England and Wales given their high construction cost (Armstrong *et al.,* 2010), and lack of space for installation, respectively. More recently, the Larinier super-active baffled fishway (Fig 2.11) has become a favoured technical pass design for multi-species communities in UK waters,

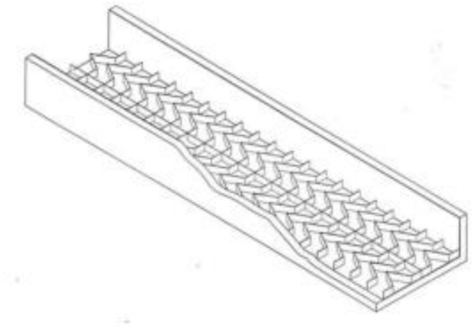

Figure 2.11. Larinier super-active baffled fishway design (after Armstrong *et al.,* 2010)

but these are of unknown efficiency for upstream migrating lamprey species. Furthermore, at some barriers in the UK, fishways have been retrofitted with smooth steel plates on the sides of the walls, with the intention this could promote river lamprey passage by providing resting/climbing surfaces, although the efficacy of such installations has not yet been examined. We therefore recommend that the effectiveness of steel structures to aid river or sea lamprey passage be tested empirically before it is considered further. Retrofitted plates with rows of cylinders or domes, of the type employed as upstream eel passes (Solomon and Beach, 2004), may also offer a specific lamprey passage solution for sloping weir faces, when submerged, but efficiency tests on these are absent for European lampreys. While they may aid serpentine crawling, they may inhibit sucker attachment and resting and can create undesirable high turbulence zones. Indeed, bollards of this type did not improve upstream passage efficiency for Pacific lamprey in an experimental fishway, and passage efficiency was lower when bollard spacing was reduced (Keefer *et al.,* 2011). It is therefore imperative that implementations of upstream passage solutions for river lamprey (and other non-climbing lamprey species) across its distributional range are scientifically well-informed in order to prevent installation of ineffective fishways for these species.

Overall, given the cost of fishway installation, we recommend careful thought and testing of fishway designs for river lamprey and similar species where barrier removal is not possible (the preferred option for river reach reconnection). Although the monitoring of fishways must inevitably be strategic, owing to limited resources, emphasis should be placed upon the long-term cost-effectiveness of thorough, scientific evaluation of fishway designs (i.e. assessing delay times, attraction and passage efficiencies), before and after installation, rather than ‘trial and error’ installation of fishways untested for target species, in order to advance the provision of effective multi-species fishways.

Chapter 3: A multifaceted investigation into the European river lamprey angling bait market in Britain: commercial catch and stakeholder attitudes

3.1. ABSTRACT

It is widely established that for conservation projects to succeed for exploited species, there needs to be a thorough understanding of the ecology of the species being conserved and the socio-economic role the species plays in society. Whilst the ecology of the European river lamprey and its socio-economic importance as a food resource in Europe is generally well understood, little information exists regarding their exploitation for angling bait, a phenomenon widespread in Britain. Given that the river lamprey is regarded as a threatened species across Europe, the exploitation of this species to satisfy recreational users represents a particularly challenging dilemma for conservationists. This chapter sought to gain a thorough understanding of the scale of lamprey exploitation for angling bait, the structure of the lamprey bait market in Britain, and to appreciate the knowledge and attitudes of some key stakeholders in the lamprey bait market (wholesale suppliers and fishing tackle shop managers). This study demonstrates that the lamprey bait market in Britain is mostly dependent upon lamprey stocks from mainland Europe (The Netherlands and Estonia) and that the contribution of lamprey from waters in Britain (principally the Humber River Basin) to the angling bait market has declined since changes in legislation, which granted powers to appropriate authorities to regulate river lamprey exploitation, were implemented in 2011. Recent historic catch per unit effort (CPUE) data for the Humber do not suggest a decline in stock levels of river lamprey. In total, it was estimated that *c.*9 tonnes of river lamprey were supplied to tackle shops and anglers in Britain between summer 2011 and summer 2012. Telephone questionnaires revealed that the vast majority of tackle shop managers were unaware of which species of lamprey they sold, where they had originated from, or whether they were threatened or not. However, most managers (77.0%) were in favour of a ban on the capture and selling of lamprey in Britain if they were considered to be threatened. Conversely, wholesale suppliers were far more knowledgeable about the lamprey they

sold than tackle shop managers, although in general they more indecisive over a ban. Quantitative analysis of tackle shop managers' responses revealed two factors which influenced their decision to support a ban. These were (1) how important they felt knowing if the lamprey they sell are threatened, and (2) the level of impact lamprey unavailability would have on their businesses. It appeared that those most impacted by lamprey unavailability were those who felt lamprey are an irreplaceable product. Overall, this study suggests that supplier managers would be most impacted by regulations in lamprey stocks in Britain or in mainland Europe, and hypothesises that anglers with a strong preference for using lamprey may also be strongly affected.

3.2. INTRODUCTION

Disparities often exist between the agendas of conservationists and stakeholders, particularly when stakeholders are consumptive users of a natural resource (Allan *et al.,* 2005; González, 2003; Thorbjarnarson, 1999; Tsounis *et al.,* 2010). Consumptive use may refer to either the exploitation of a resource for human needs (e.g. food) or for recreational purposes (e.g. angling, hunting, pet trade etc.) (Duffus and Dearden, 1990), and the latter use may be difficult to justify if the activity contributes to species decline. For example, the collection of ornamental fish in Hawaii for the aquarium trade has significantly reduced the abundance of targeted fish by up to 75% (Tissot and Hallacher, 2003). Similarly, trophy hunting was found to be the primary driver of declines in lion abundance in Tanzania, with lion harvests declining by 50% across the country between 1996 and 2008 (Packer *et al.,* 2010). Where a threatened species is exploited for recreational purposes, conservationists must develop a detailed understanding of how sustainable exploiting the resource is, the scale of exploitation (e.g. local, national, international) and the reasons for exploitation (e.g. consumers' ignorance towards the threat; resource is economically important). Whilst the first point is mostly an ecological concern, the other two issues are, for the most part, socio-economic concerns, and requires conservationists to engage with stakeholders in order to understand their attitudes towards the use of the species (Granek *et al.,* 2008; Hodgson *et al.,* 2000; Williams and Moss, 2001).

The worldwide exploitation of lamprey (see section 1.3.), a taxonomic group in which over half of its species are threatened (Kelly and King, 2001; Mateus *et al.,* 2012; Renaud, 1997), typifies the complexities inherent in conservation management. For instance, in many European countries, the anadromous river lamprey and sea lamprey are an economically important food resource and have generated significant income for many fishermen (Beaulaton *et al.,* 2008; Birzaks and Abersons, 2011; Sjöberg, 2011; Thiel *et al.,* 2009; Tuunainen *et al.,* 1980). Indeed, in Portugal an individual sea lamprey can be worth up to €45 in peak season (Andrande *et al.,* 2007). However, both species are of conservation concern in Europe, being listed as protected species under Annex III of the Bern Convention and requiring protection by member states of the European Union under the Habitats and Species Directive (92/43/EEC). Although, under Annex V of the Habitats and Species Directive, their taking in the wild and exploitation may be allowed and subject to management measures. Intensive exploitation, along with the synergistic effects of river engineering and habitat degradation, jeopardises the sustainability of both species across Europe (Birzaks and Abersons, 2011; Kainua and Valtonen, 1980; Kelly and King, 2001; Masters *et al.,* 2006; Mateus *et al.,* 2012). Therefore, fisheries managers have the dual role of satisfying stakeholders, whose businesses may heavily depend upon lamprey sales, whilst at the same time achieving conservation objectives and meeting international statutory requirements; this dilemma is pervasive amongst inland fisheries (Cowx *et al.,* 2010).

The management of lamprey populations has additional complexities, as many species have been widely recognised as effective bait for recreational angling. For example, Pacific lamprey populations are declining rapidly in North America (Clemens *et al.,* 2010) and their larvae have been used as sport-fish bait, mainly for the introduced smallmouth bass *Micropterus dolomieui* (Close *et al.,* 2002). To help reduce the threat of exploitation on Pacific lamprey populations, their use as sport-bait is now illegal in the states of Oregon, Washington and Idaho (Luzier *et al.,* 2011). Most accounts of lamprey being exploited for angling bait are brief (Close *et al.,* 2002; Renaud, 2011; Schultz, 1930; Vladykov, 1949, 1952), and little information exists detailing the extent of exploitation and the level of threat this activity has had on their populations. The most detailed documentation of lamprey exploitation for sport bait, pertains to the European river lamprey in Britain (Masters *et al*. 2006).

Masters *et al.* (2006) described that since 1995, adult river lamprey have been captured in the tidal Ouse, Humber River basin, and sold to fishing tackle shops in Britain, having become popularised as successful bait for northern pike. The authors were initially aware of one fisher operating on the Ouse and estimated that the fishery was operating at a minimum relative exploitation level of 9.9%. However, during the course of the study the authors discovered a second fisher capturing lamprey in the Ouse, although the scale of this fishery was unknown. The authors concluded that “an unregulated increase in commercial fishing appears to be the most immediate threat to the river lamprey population of the tidal Ouse”. During this time lamprey were legally caught as by-catch in an authorised eel fishery; lamprey were not recognised as a “freshwater fish” in the Salmon and Freshwater Fisheries Act (SAFFA), 1975, therefore lamprey fisheries could not be legally regulated by the Environment Agency. Although theoretically, control was possible by appropriate competent authorities in the vicinity of SACs, on the precautionary basis of protection of lamprey as a listed feature. However, the UK Marine and Coastal Access Act 2009 amended SAFFA to legislate for lamprey, and from Jan 2011 provisions were in place to allow the EA to authorise lamprey fisheries. In 2011 the two fishers operating on the tidal Ouse were issued authorisations to trap river lamprey, although temporal and total catch restrictions applied; traps could only be fished between 01 Nov and 10 Dec, up to 2301 lbs could be taken from the tidal Ouse (constituting 522 kg for each fisher), and catch data had to be reported to the Environment Agency. The total take of 2301 lbs reflects a 5% exploitation level in the Ouse, upstream of the River Wharfe (based upon a rounded estimated returning adult population of 200 000 individuals (Hopkins, 2008)), agreed by the Environment Agency and Natural England. The same authorisations were issued to the fishers in 2012. A reassessment of fisheries commercially targeting lamprey in the tidal Ouse is therefore due, given the recent change in legislation, the discovery of a second fisher and the availability of catch data beyond 2003 (the final fishing season reported by Masters *et al.* (2006)).

Although Masters *et al.* (2006) gave the size of annual river lamprey catches by a fisher in the tidal Ouse, which were subsequently sold to fishing tackle shops (ranging from 9 083 to 30 992 lamprey between 1995 – 2003), the scale and structure of the river lamprey bait market in Britain remains unclear. Firstly, the total number of wholesale suppliers of river lamprey in Britain, and more importantly how many river lamprey they sell per year and where they are sourced, is unknown. River lamprey caught in the tidal Ouse may represent just a small proportion of lamprey supplied to fishing tackle shops and pike anglers in Britain. Whilst a small number of lamprey have been caught in the River Trent in the past (Masters *et al.,* 2006), some river lamprey may have been caught in rivers elsewhere in Britain, or more likely, captured in other European waters and exported to Britain. If so, the source of river lamprey may not be as contained as previously thought and the demand for river lamprey in Britain may impact on other European river lamprey populations. Furthermore, although the use of adult river lamprey is principally restricted to Britain, it is plausible that wholesale suppliers in Britain export some of the river lamprey they obtain from rivers in Britain. This chapter will seek to address these issues and in so doing depict the magnitude of the river lamprey angling bait market in Britain.

Failing to take into account the knowledge and views of stakeholders, when attempting to conserve and regulate the system from which they derive benefits, can ultimately lead to the failure of conservation efforts (Dorow *et al.,* 2009; Arlinghaus *et al.,* 2002; Marshall *et al.,* 2007; Cowx *et al.,* 2010; Stankey and Shindler, 2006). This eventuality may arise because stakeholders are either reluctant to comply with regulations that have excluded their views (Gibson and Marks, 1995) or they perceive that conservation policies have placed a higher value on wildlife than their livelihoods (Chan *et al.,* 2007; Songorwa, 1999). Furthermore, stereotypical thinking may exist between both conservationists and stakeholders, as is apparent in angler-fishery management, which may reduce the potential for cooperation and result in stakeholders displaying rule-breaking behaviour (Arlinghaus, 2005, 2006). Subsequently, conservationists should not only seek to attain a thorough understanding of the system itself (in this case, the vitality of the river lamprey fisheries and the scale and structure of the river lamprey bait market), but should also engage with, and learn from stakeholders. Knowledge gained through investigating (a) how informed stakeholders are about the resource they use, (b) the potential impacts on stakeholders' businesses or livelihoods from regulating the resource, and (c) how amenable stakeholders are to proposed regulations of the resource, can better inform policy-making decisions and help predict the effects of conservation actions (Chan *et al.,* 2007; Danylchuk and Cooke, 2010; Dorow *et al.,* 2010; Granek *et al.,* 2008; Weladji *et al.,* 2003). In the case of the river lamprey angling bait market, key stakeholders include the fishers who catch river lamprey, river lamprey wholesale suppliers, fishing tackle shops who sell lamprey and recreational anglers who use river lamprey as bait. Gauging the knowledge and attitudes of all stakeholders is beyond the scope of this chapter. Instead, attention will be paid to wholesale suppliers and fishing tackle shops. This is because they constitute easy-to-reach stakeholders (lamprey fishers may be operating in several European countries) and, as they are the main internal stakeholders, the market structure and information on the supply and demand of lamprey in Britain can be determined. Furthermore, their businesses may depend strongly on river lamprey sales, and so they are likely to be among the most financially impacted by legislation affecting the supply of lamprey.

This multifaceted investigation into the river lamprey angling bait market in Britain had several aims. These were to re-evaluate the state of river lamprey fisheries which exist in Britain, to determine the size and scale of the river lamprey market in Britain, to understand the origin of the river lamprey being sold in Britain and to gauge the knowledge and attitudes of key stakeholders (wholesale suppliers and fishing tackle shops) within the river lamprey market in Britain to help inform conservation managers.

3.3. METHODS

The broad nature of this investigation into the river lamprey angling bait market in Britain required it to be conducted through several methods:

1) The collection and analysis of available commercial river lamprey catch data in Britain (Yorkshire tidal River Ouse only, see section 3.3.1)
2) Telephone Questionnaires
   i) A semi-structured telephone questionnaire targeted at river lamprey wholesale supplier managers in Britain, each having been identified by tackle shop managers (see sections 3.3.2.2 and 3.3.2.3)
   ii) A detailed, structured telephone questionnaire targeted at tackle shop managers listed in a river lamprey wholesale supplier's directory (known before investigation), based in Britain.
   iii) A brief, structured telephone questionnaire survey targeted at tackle shop managers listed in a major online telephone directory.

3.3.1. COMMERCIAL CATCH DATA

The only significant river lamprey commercial catch dataset in Britain in recent years pertains to river lamprey trapped below Naburn weir (53°54'N, 01°06'W) on the tidal Ouse, Yorkshire, between 1995 (the onset of the recent commercial fishery) and 2012. For this reason, this component of the investigation focused on river lamprey catches in the tidal Ouse only. The primary aims were (a) to understand the scale of seasonal (annual) catches of lamprey by fishers operating in the tidal Ouse, Yorkshire, (b) to compare the total catch and catch per unit effort (CPUE) of fishers operating in the tidal Ouse, before and after temporal and total catch restrictions were implemented in 2011 fishing season, (c) to examine the variation in CPUE within fishing seasons in the tidal Ouse, (d) to examine the variation between fishing seasons in the tidal Ouse, and (e) to determine whether there has been a decline in mean seasonal CPUE between 2000 and 2012, from when the most detailed catch data exist, that might suggest a decline in lamprey abundance in the tidal Ouse.

From Jan 2011 temporal and total catch restrictions were applied to lamprey fisheries in the tidal Ouse. Before 2011, river lamprey were typically trapped between October and January, reflecting the main period of upriver migration in that location

(Masters *et al.,* 2006), although since (and including) 2011 lamprey can only be trapped between 1st November to 10th December in the tidal Ouse. In this chapter, trapping lamprey from year x through to year $x + 1$ is referred to as fishing season x e.g. trapping from Oct 2000 to Feb 2001 is referred to as the 2000 season. Catch data from the tidal Ouse were collected either directly from the fishers or from the Environment Agency. Although the submission of lamprey catch data to the Environment Agency has been a statutory requirement since 2011 season onward, any submission of catch data for seasons before 2011 was voluntary. Consequently, catch data from fishers in the tidal Ouse before 2011 is incomplete.

There are two fishers operating in the tidal Ouse who have fished for lamprey, using either fyke nets and/or unbaited, two-funnel eel traps (Masters *et al.,* 2006), since 1995. Over the period 1995-1999 one fisher (henceforth referred to as Fisher A) used a combination of fyke nets and traps, although from 2000 onwards Fisher A used traps only. However, Fisher A upgraded ten of his traps from uncovered to black netlon covered in 1999, as he believed they fished more effectively, and had upgraded all of his traps to black netlon covered by 2011. Whether the second fisher (henceforth refered to as Fisher B) has ever altered his fishing gear is unclear. While Fishers A and B use the same 3 km river reach for fishing, they use different sites (one each), the locations of which have remained the same for Fisher A since 2000, and for Fisher B for all data obtained. Fisher A was able to provide total catch data (lbs or kg) for fishing seasons 1995-2008, 2011 and 2012, although finer scale information was provided for seasons 2000-2008, 2011 and 2012, with the catch (lbs or kg) and number of traps fished for each date the traps were lifted being recorded. This allowed CPUE values to be calculated for each date the traps were lifted as mean weight per trap, and could be converted to mean number of lamprey per trap per day using a mean weight for an individual lamprey of 101.2g (as shown in Masters *et al.,* 2006). Catch data from Fisher A for 2009 fishing season could not be located by either the fisher or the Environment Agency. Furthermore, there was a closed season in 2010 for eel fishing (May 2010 to Feb 2011 for eels of 12 cm or less, and all other eels from Oct 2010 to March 2011), under the Eels (England and Wales) Regulation 2009 (no. 3344), therefore no lamprey were caught by Fisher A in 2010 season; the traps to catch lamprey, authorised to target eel, had to be removed for the season. Fisher A has actively co-operated with the Environment Agency for several years now. Catch data provided by the Fisher B included total catch data (lbs) for fishing seasons 2004, 2005, 2011 and 2012, and included the catch (lbs) and number of traps fished for each date the traps were lifted. CPUE values for each date the traps were lifted could, therefore, be calculated for all four seasons. Although Fisher B has been trapping lamprey for a similar number of seasons to Fisher A, catch information from seasons other than 2004, 2005, 2011 and 2012 was not documented.

3.3.2. TELEPHONE QUESTIONNAIRES: DESIGN AND ANALYSIS

Questionnaires are being increasingly used in ecological research as they often provide the best means of obtaining quantitative and qualitative data on human behaviour, particularly when seeking to understand the knowledge and attitudes of stakeholders (White *et al.,* 2005). The telephone interview method was selected because it can yield high response rates, can allow views to be expressed in detail, the contact details of interviewees were, in this case, easily accessible online, and it allows the collection of data over a wide geographic area (Bourque and Fielder, 2003; White *et al.,* 2005). Three separate telephone questionnaires were generated, targeted towards wholesale supplier managers (section 3.3.2.1), fishing tackle shop managers listed in a known river lamprey wholesale supplier's directory (section 3.3.2.2) and tackle shop managers listed in a major online directory (section 3.3.2.3). Although the size and content of the three questionnaires varied, a few similar procedures applied to all. Firstly, all respondents were first asked whether their company supplies or sells lamprey; if so the manager was requested for a full interview, if not the enquiry was ended. Respondents were not specifically asked about river lamprey at this stage, as respondents were asked in the questionnaire whether they knew which species of lamprey they sell in order to assess how knowledgeable they were about them (section 3.3.2.1 and 3.3.2.2). Managers were able to request a suitable time and date to be contacted if they were too busy to complete the questionnaire. Occasionally, respondents asked for the questionnaire to be emailed for them to complete in their own time. No self-administered questionnaires were sent as this might have provided the opportunity for respondents to research the conservation status of lamprey, potentially affecting respondents' responses. Furthermore, comparing results between self-administered questionnaires and telephone questionnaires can be problematic and unreliable (Dillman *et al.,* 1996).

Although a brief, general explanation was provided as to the purpose of the questionnaire (Appendix 2), any mention of lamprey being considered a threatened species in Europe (Mateus *et al.,* 2012; Renaud, 1997) was deliberately avoided to prevent biasing respondents' views. Furthermore, interviewer bias was not an issue as all telephone interviews were conducted by the same individual. Respondents were assured that all answers would remain completely anonymous and confidential, informed that the anonymous data may be pooled and written for a scientific publication, and that answering questions was voluntary. Sensitive questions (defined by Tourangeau and Yan (2007) as those that potentially stimulate a socially undesirable response) were asked towards the end of each questionnaire (section 3.3.2.1 and 3.3.2.2), so as to minimise the risk of respondents terminating the questionnaire partway through (Marshall, 2005).

Likert scales were occasionally used in the wholesale supplier questionnaire (section 3.3.2.1) and the tackle shop manager questionnaire (3.3.2.2). For example, respondents were asked "*if lamprey were no longer available to sell, would this have no impact, a slight impact, a moderate impact or a strong impact on your company?"* Similarly, respondents were asked *"how important is it for your company to know if the lamprey that you sell come from a threatened or non-threatened population: very important, important, slightly important or not important?"* To prepare these variables for chi square analyses, response categories were merged to satisfy Cochran's rule, stating that ≥80% of expected values in an $r \times c$ table should be five or more, and no expected values should be less than 1 (Cochran, 1954). Therefore, the response categories "moderate impact" and "strong impact" were merged to form a "moderate/strong impact" response category. "Very important" and "important" were merged to form an "important" response category, and "slightly important" and "not important" were merged to form a "not/slightly important" response category; results were interpreted with consideration to these merged response categories.

Tackle shop managers (3.3.2.2) and supply managers (section 3.3.2.1) were also asked whether they agree, disagree or find it difficult to say, to various statements (Appendices 2 and 3), a common procedure found in other stakeholder surveys (Anderson *et al.,* 2007; Arlinghaus 2006; Dorow *et al.,* 2010; Marshall *et al.,* 2007). For example, whether they agree, disagree or find it difficult to say, that *"there should be a ban on the capture and selling of lamprey in Britain if they are considered to be threatened".* Although a ban on the capture and selling of lamprey is currently an unrealistic scenario, responses to this statement would reveal how accepting stakeholders would be towards a very restrictive conservation measure.

There is evidence to suggest that particular phrasing of statements can encourage a response bias (Petrinovich and O'Niell, 1996). It is possible, for example, that respondents might passively agree with a ban if the lamprey they sell are considered to be threatened, as this is, arguably, the more socially desirable response. To test this, tackle shop managers (3.3.2.2) were randomly given the statement *"there should be a ban…"* or the inverse statement *"there should not be a ban…"* and asked whether they agreed, disagreed or found it difficult to say. Results were analysed using chi square analysis to assess whether statement phrasing elicited a response bias.

3.3.2.1. Wholesale supplier telephone interview

The central aims of this component of the investigation were to understand (a) the scale and structure of the river lamprey supply market in Britain, (b) to estimate the amount of river lamprey supplied to tackle shops and anglers in Britain over a one year period, (c) to understand the origin of the river lamprey being supplied, and (d) to understand managers' attitudes towards the supplying of river lamprey. These aims were achieved by telephone interviewing all river lamprey wholesale suppliers in Britain identified by tackle shop managers (section 3.3.2.2 and 3.3.2.3). One wholesale supplier of river lamprey in Britain was known before the investigation (henceforth referred to as Supplier A). However, other suppliers had to be identified in order to be interviewed. Suppliers other than Supplier A were identified by '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 and Waldorf, 1981). To accomplish this, tackle shop managers in Britain were sampled from two separate sampling frames (section 3.3.2.2 and 3.3.2.3) and, if they sold river lamprey, were asked to identify which supplier(s) supplied their lamprey. Every supplier identified by the snowball sampling procedure was then contacted and asked whether they supplied lamprey. If so, managers were first asked if they sourced their lamprey themselves, or whether they obtained their lamprey from another wholesale supplier of lamprey in Britain (and if so, which supplier). This information was used to determine the river lamprey supply market structure in Britain. Managers who sourced the lamprey themselves, and subsequently supplied to either other suppliers, tackle shops or anglers, were then asked to participate in the telephone interview, as they represent the key stakeholders in the river lamprey supply market (Fig. 3.6).

Respondents were asked to answer up to 26 questions and the original questionnaire can be found in Appendix 3. The study began on 11 Dec 2012 and concluded on 11 Jan 13. The questionnaire was made up of four sections; whilst all sections contained closed questions, the final two sections allowed wider opinions to be expressed. The first section of the questionnaire asked for details regarding the nature of their lamprey sales e.g. when their business began supplying lamprey, who lamprey were supplied to and for what reason, and whether lamprey were exported from Britain. Respondents were also asked whether they knew which species of lamprey they sold, and if so which species? The second section asked for information regarding the extent of their lamprey sales, in particular how many lamprey were supplied from summer 2011 to summer 2012. This period was decided upon because both the pike fishing season (especially between October and mid-March, but year round in several geographical areas e.g. Scotland, Ireland) and lamprey commercial fishing season fall within the bounds of this period, and respondents were only asked to recall the amount of lamprey supplied during the most recent 12 month period to increase the reliability of their answers. The third interview section sought to identify the origin of the lamprey they sold, if known, and whether they believed these lamprey originated from a threatened or non-threatened population. The final section examined the impact that lamprey unavailability would have on their business. This section concluded by asking whether they would personally alter their 'selling behaviour' with regards to lamprey (i.e. sell less or stop altogether) or not, or agree to a ban on the capturing and selling of lamprey in Britain, if they are considered to be threatened.

3.3.2.2. Tackle shop telephone questionnaire: Supplier A sampling frame

This study consisted of a more extensive (i.e. more respondents, more questions asked), structured telephone questionnaire targeted towards tackle shop managers selling lamprey directly to anglers. One of the main lamprey wholesale suppliers in Britain (Supplier A), who supplies 427 tackle shops in Britain with angling bait products, was known before the investigation. Supplier A permitted the use of their directory containing contact details of the 427 tackle shops. The manager stated that their business supplies lamprey to the majority of their tackle shop customers, therefore sampling from this sampling frame (directory of 427 tackle shops) would ensure a high probability of calling tackle shop managers selling lamprey. Further tackle shops were contacted from a separate, larger sampling frame (online directory of businesses) to understand in greater detail the extent of lamprey sales in Britain (section 3.3.2.3).

The Supplier A sampling frame was stratified by region in Britain (Scotland, North England, East England, West England/Wales and South England (Fig. 3.1; Appendix 1)) and tackle shops were randomly sampled from these five strata. Stratified random sampling was used to discern whether the amount of lamprey stocked by tackle shops differed between regions as a proxy for indicating whether the demand for lamprey by anglers differed between regions. It was deemed suitable to obtain 30 full responses from tackle shop managers from each region, to achieve a total of 150 responses for analysis. However, there was a shortfall in responses from Scotland due to the relatively small number of tackle shops supplied by Supplier A in this region; in total, 137 full responses from tackle shops were achieved. The study started on19 July 2012 and concluded on 22 August 12.

Due to the high number of tackle shops being contacted, far exceeding the number of suppliers contacted, many of the questions were closed, to allow for quantitative analysis, and the original questionnaire can be found in Appendix 2. The majority of data from respondents who could only partially complete questionnaires was not incorporated into analyses, except for data pertaining to the number of lamprey stocked by these respondents between summer 2011 and 2012; these data

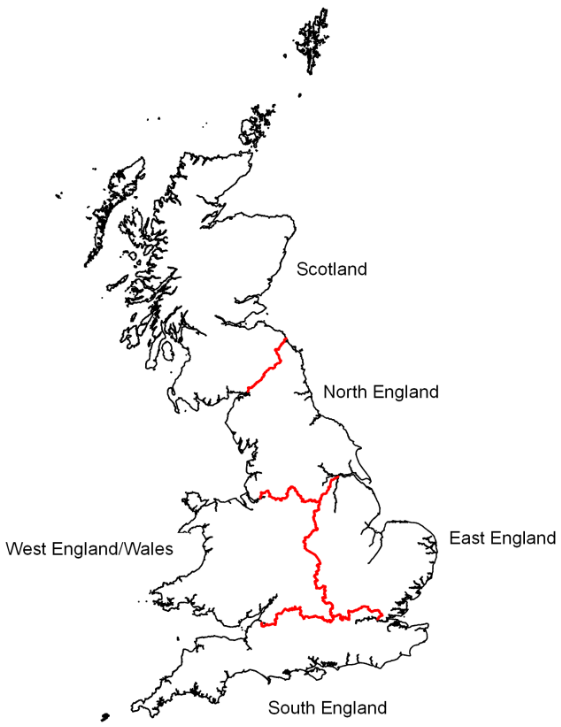

Figure 3.1. The division of Britain into five regions (Scotland, North England, East England, West England/Wales and South England) from which tackle shops were selected through stratified sampling.

were pooled with data from respondents who fully completed the questionnaire to test for regional differences in lamprey sales, and to estimate the number of lamprey sold by tackle shops within the Supplier A sampling frame. The key aims of this questionnaire were to (a) understand the nature and extent of lamprey sales in the managers' shops, (b) to understand the impact that lamprey unavailability might have on their businesses, (c) to understand whether or not managers were knowledgeable about the lamprey that they sell, and (d) to understand whether managers show concern for the conservation status of the lamprey that they sell, and whether they would personally alter their 'selling behaviour' with regards to lamprey, or agree to a ban on the capturing and selling of lamprey in Britain, if they are considered to be threatened. Respondents were asked to answer up to 50 questions, and similar questions were asked to those in the suppliers' questionnaire to allow for comparisons to be made between these two stakeholders (Appendix 2).

Furthermore, this questionnaire sought to understand (a) which variables influenced tackle shop managers' decisions to continue, or alter, their selling 'behaviour' if informed the lamprey they sell are from a threatened population, and (b) which variables influenced their agreement, disagreement, or indecision with a ban on the capture and selling of lamprey in Britain if they are considered to be threatened. Chi square tests of independence or logistic regressions were performed to reveal which variables had a significant effect on management decisions.

Potentially significant independent variables included:

1) How important it is for the company to know if the lamprey they sell are from a threatened or non-threatened population; it is hypothesised that managers who feel it is important to know are, or strive to be, 'conservation conscious', and would be more likely to alter their selling 'behaviour' or agree to a ban, and vice versa.
2) The number of years the company has sold lamprey; it is hypothesised that managers who have a long history of selling lamprey would be less likely to alter their selling 'behaviour' or agree to a ban, and vice versa.
3) The number of lamprey stocked by the company over a one year period (summer 2011 to summer 2012); it is hypothesised that managers who sold a relatively large number of lamprey would be less likely to alter their selling 'behaviour' or agree to a ban, and vice versa.
4) How 'replaceable' the manager believes lamprey are as a bait; it is hypothesised that managers who feel lamprey are an 'irreplaceable'

product would be less likely to alter their selling 'behaviour' or agree to a ban, and vice versa.

5) The impact of lamprey unavailability on the company; it is hypothesised that managers most impacted would be less likely to alter their selling 'behaviour' or agree to a ban, and vice versa.

3.3.2.3. Tackle shop telephone questionnaire: Online directory sampling frame

It was necessary to contact other tackle shop managers from a separate sampling frame to realise in greater detail the extent of lamprey sales in Britain. The *Yellow Pages* online telephone directory (www.yell.com) was selected because it was regarded as one of the most comprehensive telephone directories in Britain. "Fishing Tackle" in "England", "Wales" and "Scotland" was searched for on the website, after which 1 614 tackle shops were found in the results; these tackle shops made up the *Yellow Pages* sampling frame. The website displays 15 companies per results page, and a maximum of 10 results pages are provided for any searches, thus only 150 of the 1 614 tackle shops could be displayed. Therefore, tackle shops were first stratified by postcode district (accessed from www.list-logic.co.uk) and a tackle shop was randomly selected from a randomly selected postcode district. For example, if the postcode district "CV34" (Warwick, Warwickshire) was randomly selected from the list of postcode districts, a search was made in the online *Yellow Pages* for "Fishing Tackle" in "CV34", yielding seven results. This way, details of all tackle shops in the sampling frame were accessible. A tackle shop was then randomly selected from these results and contacted. In total 200 tackle shops were successfully contacted, between 02/10/2012 and 06/11/2012. There may have been some sampling bias, as there are a greater number of postcode districts in urban areas, although there are also likely to be a greater number of tackle shops in urban areas, therefore the bias is considered to be minimal.

The aims of this element of the study were to (a) estimate the number of tackle shops in the *Yellow Pages*, (b) estimate the number of lamprey being sold by tackle shops listed in the *Yellow Pages,* over a one year period, and (c) generate information about the number of other lamprey wholesale suppliers operating in Britain. These aims were achieved by asking tackle shop managers, confirmed to sell lamprey, two questions: *"How many lamprey did you sell from summer 2011 to summer 2012?"* and *"Which supplier(s) supply your lamprey?"*

3.4. RESULTS

3.4.1. COMMERCIAL CATCH IN THE TIDAL OUSE

Before temporal and catch licence restrictions were enforced in 2011, catch data from 2000–2008 fishing seasons indicate that lamprey in the Ouse were fished from as early as 9th Sep (2006 season, Fisher A) up to 21st Feb (2000 season, Fisher A) (Table 3.1), and the number of traps and days fished varied between seasons. Before 2011, total catch (kg) of river lamprey caught by Fisher A varied moderately between fishing seasons (1995-2008), ranging from 834.2 kg in the 2005 fishing season (equivalent to ~ 8 243 lamprey, with an average weight of 101.2g (Masters *et al.,* 2006)) to 2 810.5 kg (~ 30 998 lamprey) in 2003 fishing season (Fig. 3.2). Mean seasonal total catch (kg) for Fisher A for fishing seasons 1995–2008 was 1 841.5 ± 625.8 kg (± SD), equivalent to ~ 18 197 ± 6 184 lamprey. Relatively low catches from Fisher A were recorded for the 2000, 2005 and 2008 fishing seasons during the unrestricted fishing period (Fig. 3.2).

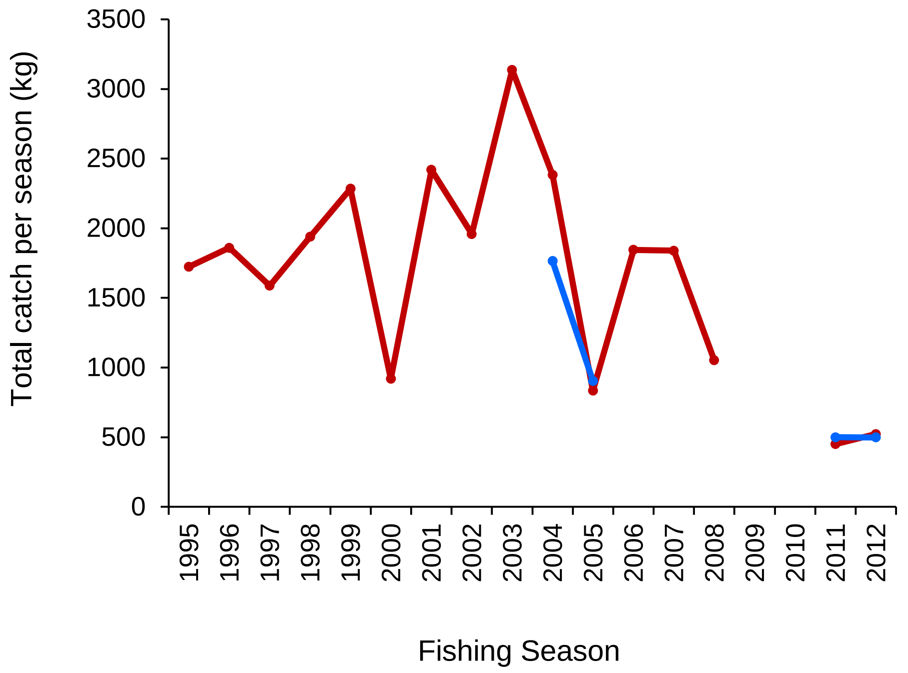

Figure 3.2. The total catches of river lamprey (in kg) by Fisher A (red) and B (blue) for seasons 1995 – 2008 (lamprey caught as by-catch in licenced eel fishery) and seasons 2011 – 2012 (lamprey caught in an authorised lamprey fishery with temporal and allowable catch restrictions) in the tidal Ouse, Yorkshire.

Table 3.1. Dates fished for both fishers for each season. U denotes data unavailable, and C denotes fishery closure due to Eels Regulation, 2009.

Fisher	Season	Dates fished	Number of occasions traps lifted (days)
A	1995	U	U
	1996	U	U
	1997	U	U
	1998	U	U
	1999	U	U
	2000	8th Oct – 21st Feb	7
	2001	6th Oct – 16th Jan	11
	2002	10th Oct – 11th Jan	8
	2003	19th Oct – 20th Jan	13
	2004	29th Oct – 27th Dec	7
	2005	U – 2nd Jan	5*
	2006	9th Sept – 28th Jan	10
	2007	3rd Oct – 30th Jan	9
	2008	1st Oct – 23rd Jan	14
	2009	U	U
	2010	C	C
	2011	6th Nov – 13th Dec	4
	2012	6th Nov – 10th Dec	4
B	2004	1st Oct – 30th Jan	20
	2005	1st Oct – 24th Jan	7
	2011	U – 11th Dec	7*
	2012	1st Nov – 25th Nov	4

G

*The date the traps were set was unknown, therefore mean CPUE could not be calculated for the first occasion (day) the traps were lifted.

Before 2011, total catch (kg) of river lamprey caught by Fisher B ranged from 904.5 kg (~ 8 937 lamprey) in 2005, 8.4% more than Fisher A's total catch for 2005, to 1 764.9 kg (~17 443 lamprey) in 2004, 25.9% less than Fisher A's total catch for 2004 (Fig. 3.2.). Thus, mean seasonal total catch (kg) for Fisher B for fishing seasons 2004 and 2005 was 1 334.7 ± 608.4 kg (± SD), equivalent to ~ 13 189 ± 6 012 lamprey. However, Fisher A's median CPUE (i.e. median of the mean CPUE values for each date the traps were lifted) for 2004 and 2005 was 22.0 and 8.4 lamprey trap^{-1} day^{-1}, respectively, markedly greater than Fisher B's median CPUE for 2004 and 2005 of 3.0 and 3.4 lamprey trap^{-1} day^{-1}, respectively. Median CPUE values were calculated because catch data were not normally distributed and sample sizes (number of days traps were lifted within each fishing season) were low (Table 3.1).

In contrast, the total catch (kg) of lamprey by both fishers showed little variation between the 2011 and 2012 fishing seasons when temporal and catch licence restrictions were imposed (Fig. 3.2.). Fisher A caught 450.5 kg of lamprey in 2011 and 552 kg in 2012. However, 30 kg of lamprey were returned to the river in 2012, thus the remaining total catch landed was 522 kg (although the median CPUE value for the season included the 30 kg of lamprey returned to the river in the calculation). Fisher B caught a minimum of 499.4kg of lamprey in 2011, as an unspecified amount of lamprey were returned to the river, and caught 589.7 kg of lamprey in 2012. However, 89.7 kg were returned to the river in 2012, therefore the remaining total catch landed was 500.0 kg. As the total allowable catch for each fisher in the Ouse is currently set at 522 kg, it is unclear as to why Fisher B returned more lamprey to the river than was necessary. In contrast to seasons 2004 and 2005, Fisher A's median CPUE for 2011 and 2012 was just 2.0 and 2.1 lamprey trap^{-1} day^{-1}, respectively, whilst Fisher B's median CPUE for 2011 and 2012 was higher at 3.9 and 6.5 lamprey trap^{-1} day^{-1}, respectively.

The extent to which CPUE varies within fishing seasons for each fisher was examined, and the date in which CPUE is expected to be highest for each fisher for any given fishing season was estimated. Two Gaussian curves were independently fitted to CPUE data from Fisher A from all fishing seasons (2000–2008 and 2011–2012; Fig. 3.3a) and Fisher B from all fishing seasons (2004, 2005, 2011, 2012; Fig. 3.3b). The expected CPUE on date t in season j for either fisher was given as:

$$y(t) = \bar{y} z_j e^{-\left(\frac{(t-\bar{t})^2}{2s^2}\right)}$$

where $\bar{y}$ is the maximum CPUE in 2000 season (Fisher A) or 2004 season (Fisher B), $\bar{t}$ is the day in which CPUE is highest, s is a measure of the spread in CPUE and z_j is the relative difference in CPUE from season to season where z_{2000}= 1 (Fisher A) or z_{2004} = 1 (Fisher B). The curves were fitted to the data using maximum likelihood assuming the variation in the data about the mean had gamma distributions (see Richards, 2008). For Fisher A, the model predicts that $\bar{t}$, the date in which CPUE is expected to be highest, is 14th December, for any given fishing season, with an expected CPUE of 11.28 lamprey per trap for that day (Fig. 3.3.a). For Fisher B, the model predicts that $\bar{t}$ is 8th December, for any given fishing season, with an expected CPUE of 9.95 lamprey per trap for that day (Fig. 3.3.b).

Kruskal Wallis tests were performed to ascertain whether CPUE varied between fishing seasons for each fisher, however seasons with less than five CPUE

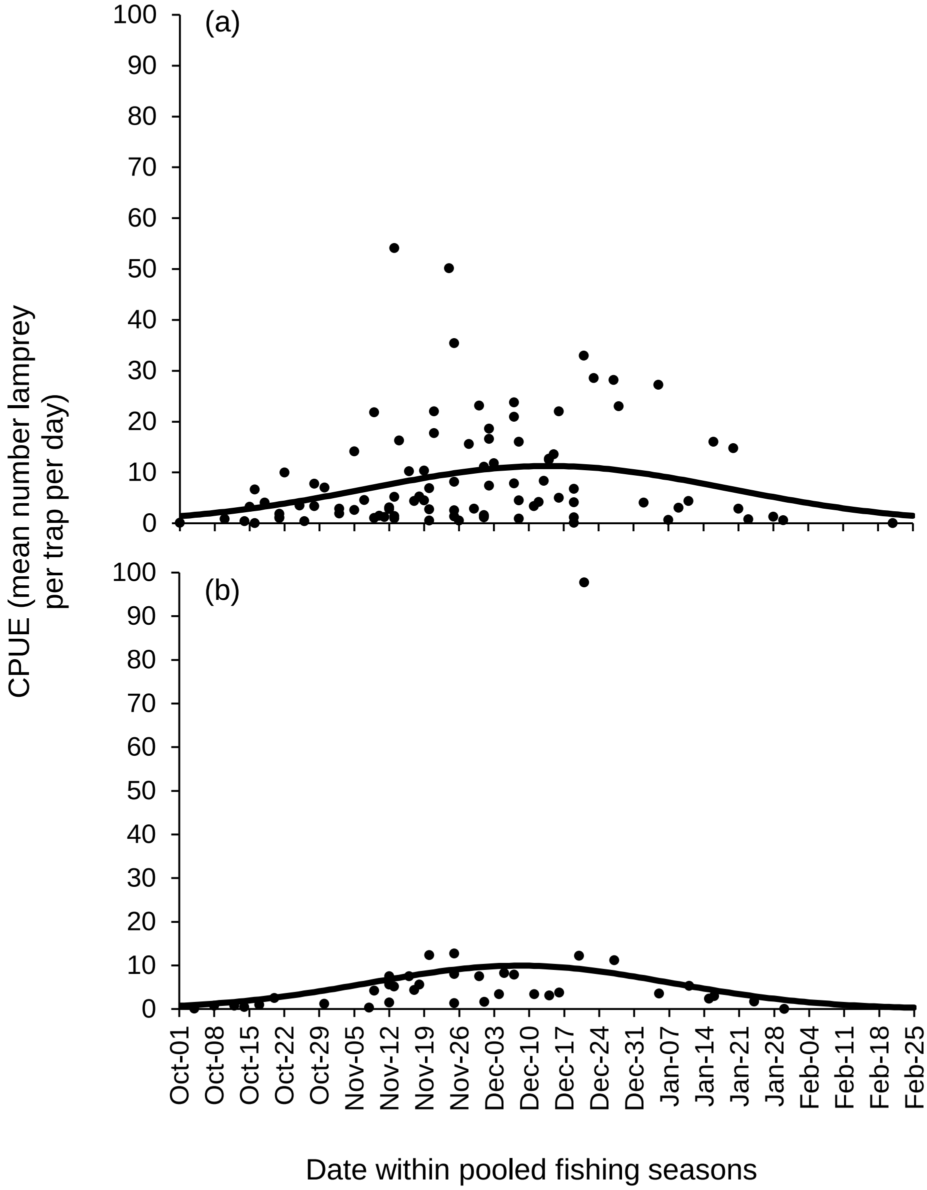

Figure 3.3. Scatterplots of catch per unit effort (CPUE, mean number of lamprey per trap per day) against pooled fishing season date: a) pooled data from seasons 2000 – 2008 and 2011 – 2012 for Fisher A's catch on the tidal Ouse, and (b) pooled data from seasons 2004, 2005, 2011 and 2012 for Fisher B's catch on the tidal Ouse. Gaussian curves fitted to the pooled data are shown (▬): $(t) = \bar{y}\bar{z}e^{-\left(\frac{(t-\bar{t})^2}{2s^2}\right)}$ where z_j is replaced by the mean of z_j.

values (i.e. seasons in which traps were lifted on less than five occasions) were excluded from analysis; this included CPUE data for seasons 2005, 2011 and 2012 (Fisher A) and CPUE data for season 2012 (Fisher B). Subsequent analysis showed that CPUE varied significantly between fishing seasons for Fisher A (Kruskal Wallis; $H = 27.315$, d.f. = 7, $P < 0.001$) (Fig. 3.4.). Post hoc pairwise comparisons of fishing

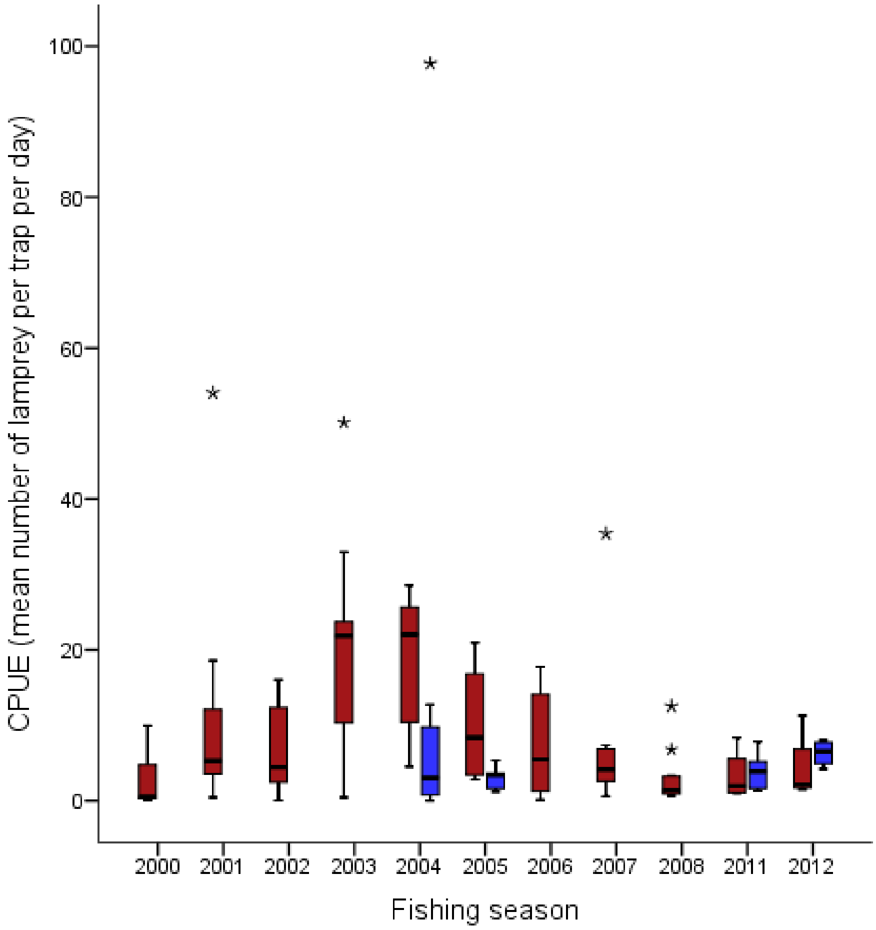

Figure 3.4. Box plots of catch per unit effort (CPUE, mean number of lamprey per trap per day) for Fisher A (red) and B (blue) for 2000–2008 and 2011–2012 fishing seasons. Thick black lines denote the median, boxes the interquartile range, T-bars the 95% confidence limits and asterisks the outliers in the data.

seasons revealed that CPUE was significantly higher during the 2003 season (median of 21.8 lamprey trap^{-1} day^{-1}) than both the 2000 (median of 0.5 lamprey trap^{-1} day^{-1}) and the 2008 seasons (median of 1.4 lamprey trap^{-1} day^{-1}) (Mann Whitney *U* with Benjamini-Hochberg corrected significance at P = 0.0054 and P = 0.0036), and significantly higher during the 2004 season (median of 22.0 lamprey trap^{-1} day^{-1}) than the 2008 season (Mann Whitney *U* with Benjamini-Hochberg corrected significance at P = 0.0018). The maximum recorded CPUE for Fisher A was 54.1 lamprey trap^{-1} day^{-1} between 11th – 13th Nov 2001 (Fig. 3.4).

For Fisher A's catch data between 2000–2012 fishing seasons, when only eel traps were used, the mean CPUE (weighted by number of traps fished*) for each

*Fishers sometimes removed a proportion of their traps during fishing seasons.

season was calculated (referred to henceforth as mean seasonal CPUE). There was no evidence to suggest a significant relationship between mean seasonal CPUE and year of fishing season (Linear regression, $F_{1,9}$ = 0.821, P = 0.388, R^2 = 0.084; Fig. 3.5).

With the limited data available, there was no evidence to suggest that CPUE varied between seasons for Fisher B (Kruskal Wallis; H = 0.177, d.f. = 2, P = 0.915) (Fig. 3.4). The maximum recorded CPUE for Fisher B was substantial at 97.7 lamprey trap^{-1} day^{-1} between 20th – 21st Dec 2004 (Fig. 3.4). This is the largest single CPUE value (and indeed, single catch) ever documented for the River Ouse since lamprey fisheries established in 1995.

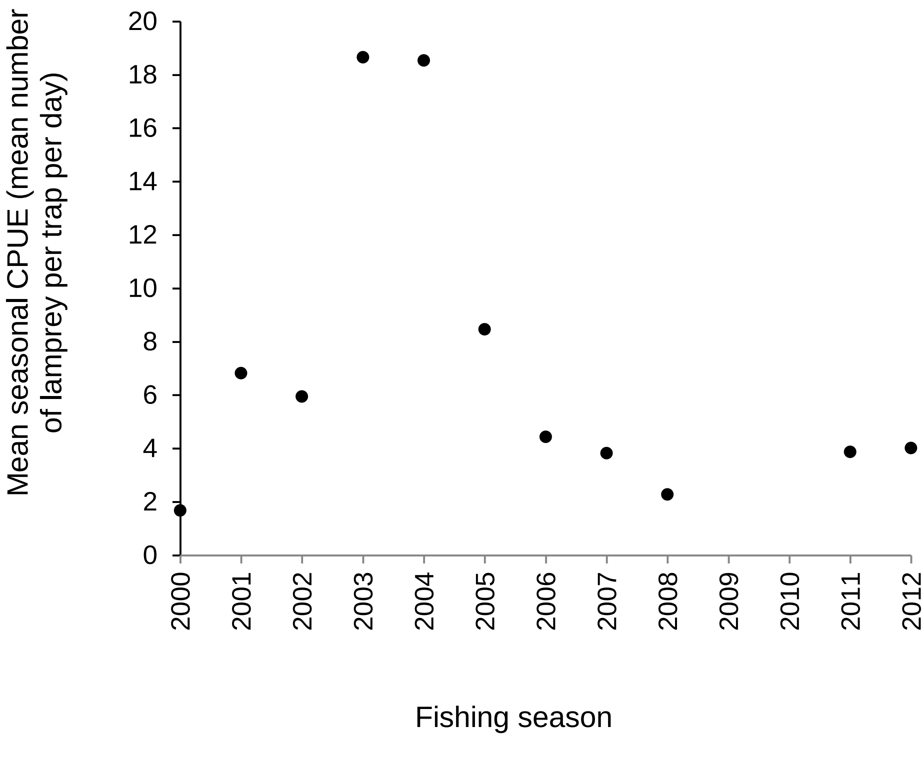

Figure 3.5. A scatterplot of mean seasonal CPUE (mean number of lamprey per trap per day) against fishing season for Fisher A's catch data. There was no significant relationship between variables (see section 3.4.1).

3.4.2. WHOLESALE SUPPLIER TELEPHONE INTERVIEW

Twenty four wholesale suppliers of lamprey, all based in Britain, were collectively identified by tackle shop managers (section 3.4.3.1 and 3.4.4), after which their contact details were searched for online and they were contacted by telephone. However, the contact details of two suppliers could not be found during online searches, five suppliers could not be contacted after numerous attempts, and six suppliers who were successfully contacted confirmed that they did not sell lamprey. It is likely, however, that the suppliers who could not be contacted hold, if at all, a minor stake in the British lamprey bait market, as only 5.7% of tackle shop managers in the yellow pages sampling frame said they used by these suppliers. Of the remaining 12 suppliers* who were successfully contacted and confirmed to sell lamprey, 11 (91.7%) agreed to answer questions (Suppliers A – K, Fig. 3.6). It was established that nine were direct suppliers of lamprey i.e. sold directly to tackle shops or anglers, whilst two (Suppliers C and F, Fig. 3.6) were indirect suppliers i.e. distributed lamprey to other suppliers. Whilst six (Suppliers F - K) obtained lamprey from other suppliers in Britain, five (Suppliers A - E) obtained lamprey directly from either fishers operating in the Humber River system, Britain, Billingsgate fish market, or imported lamprey from The Netherlands or Estonia (Fig. 3.6).

Suppliers A - E gave an approximation as to the number of lamprey supplied by their company between summer 2011 and summer 2012, which totalled to an estimated 9.01 tonnes (Fig. 3.6). The majority of lamprey supplied in Britain between 2011 – 2012 originated from The Netherlands, cautiously estimated at 6 100 kg of lamprey. It is likely the figure is lower than this, as Supplier D was only able to provide an approximated maximum number of lamprey their company supplied, and Supplier E could only state to the best of their knowledge that the large majority of lamprey from Billingsgate fish market, Britain, originated from The Netherlands, and that lamprey were only sourced occasionally from Britain. It was not known which river system the lamprey from The Netherlands originated from, although Supplier C stated their river lamprey had been caught as by-catch in an eel fishery operating in The Netherlands. Suppliers A and B both sourced lamprey from fisheries operating in the Humber River Basin, estimated to be in the region of 1 307 kg in total.

*11 remaining suppliers plus another supplier (C) identified during the suppliers' questionnaire.

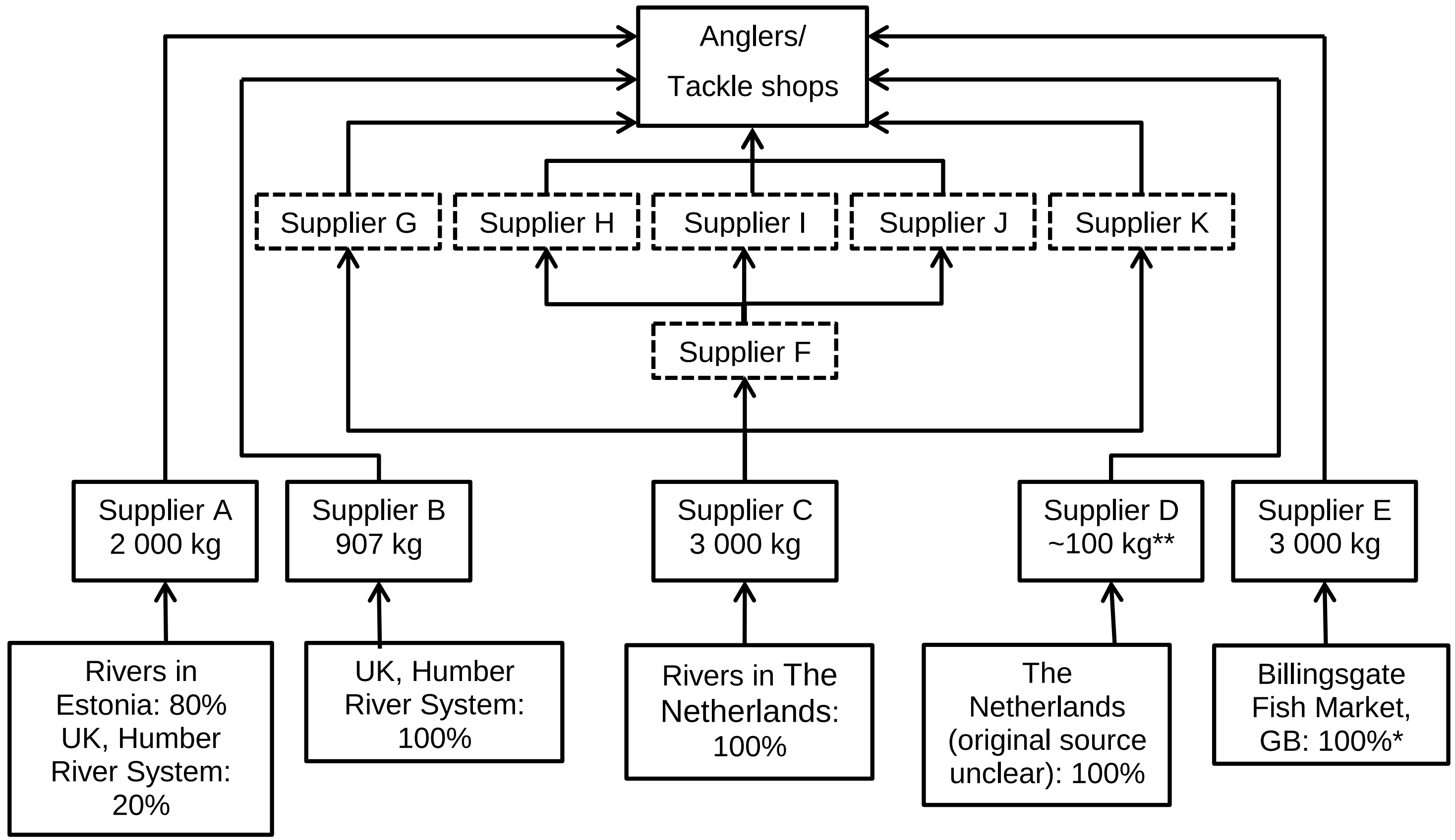

Figure 3.6. A schematic showing the river lamprey bait market structure in Britain. Suppliers A – E (bold boxes) obtained lamprey from either Britain, The Netherlands or Estonia, whilst suppliers F – K (dashed boxes) obtained lamprey from other suppliers. Suppliers C and F were indirect suppliers of lamprey i.e. only supplied lamprey to other suppliers. Arrows denotes the movement of lamprey products. *Supplier E suggested that lamprey from Billingsgate fish market were sourced from The Netherlands and Britain. **The number of lamprey was provided by Supplier D, which was converted to a weight based on an individual river lamprey weighing on average approximately 100g from The Netherlands (Lanzig, 1959).

However, the vast majority (80%) of lamprey supplied by Supplier A originated from Estonia, equivalent to approximately 1 600 kg*, although again the river system of origin was not known.

Suppliers A – E were asked further questions to gain a deeper understanding of the river lamprey bait market in Britain and to determine their attitudes towards the lamprey that they sell. To ensure anonymity, the answers to the questions are not attributed to the respondents. The earliest a supplier had been selling lamprey was 1980 and they were suggested to have originated from The Netherlands. All suppliers supply lamprey as frozen bait principally for pike angling, although lamprey are used as bait for other fish species (see section 3.4.3.1). Two suppliers have in the past also supplied lamprey to research institutions in France and Britain. One supplier has begun supplying their lamprey to aquariums and zoos for animal nutrition, partly to replace the supply of European eel, although this contributes to just 3% of their sales. Aside from one supplier having exported a small proportion of their lamprey to France for research purposes in the past, no supplier exports their lamprey. Whilst all suppliers supplied lamprey to either tackle shops or other wholesale suppliers, two suppliers also sold lamprey directly to anglers. One supplier has stopped stocking lamprey after a trial period of three years because there was a lack of customer interest in their lamprey.

Suppliers were relatively knowledgeable about the lamprey that they sold. Four of the five suppliers gave the name of the lamprey species they sell (all river lamprey), and all were aware of which country they originated from (Fig. 3.6). However, three of the five suppliers were unaware of which river or river system their lamprey were sourced from, and another supplier was only aware of where a proportion of their lamprey were sourced. Two suppliers believed the lamprey that they sell are from a non-threatened population, and one supplier was unsure whether they are from a threatened population or not. The remaining two suppliers understood that they are of conservation concern but regulations are in place to help protect the species, and indeed one supplier manager has been actively involved in regulating the fishery from which they source their lamprey.

Two suppliers claimed there would be no impact on their business if the lamprey that they sell became unavailable; for these suppliers, river lamprey only

*Supplier A confirmed that lamprey sourced from Estonia in 2011 and 2012 were the same weight as lamprey sourced from the Humber River system, although before then lamprey sourced from Estonia were typically between 60 – 70g.

constitute a small percentage of their sales. However, one supplier claimed it would impact their business moderately, whilst two suppliers claimed it would strongly impact their business; in fact, one supplier wished to expand by saying that lamprey unavailability would have a very strong impact on their business. Four suppliers disagreed that there are other available products to sufficiently replace lamprey, whilst the remaining supplier was unsure. One supplier mentioned that the most suitable replacement would be eel, although they felt this species was threatened more so than the river lamprey, and more expensive, so this would not constitute a sufficient replacement. Four suppliers stated they would discontinue their sales of lamprey if they were informed they were from a threatened population, with one supplier saying it would not make sense to continue sourcing lamprey from a threatened population, and another mentioning they would source their lamprey elsewhere. The remaining supplier declared they would be the first to ensure the fishery was operating in a sustainable way if the lamprey population was considered to be under threat. One supplier agreed that there should be a ban on the capture and selling of lamprey if they were considered to be threatened, one supplier was unable to comment, and the remaining three suppliers found it difficult to say. The common reason given for finding it difficult to say was that before they could make an informed decision they would need to be provided with rigorous scientific evidence confirming the lamprey they sourced were threatened.

3.4.3. TACKLE SHOP TELEPHONE QUESTIONNAIRE: SUPPLIER A SAMPLING FRAME

There were a total of 427 tackle shops registered in Supplier A's sampling frame (Table 3.2). A total of 289 tackle shops were contacted, of which 251 sold lamprey (86.9%). The 95% confidence interval for the proportion of shops selling lamprey was 3.9%, therefore it is estimated that between 83.0% and 90.1% of tackle shops in the Supplier sampling frame sold lamprey, equivalent to between 354 and 387 tackle shops (Table 3.2). For those shops that sold lamprey, a total of 137 telephone questionnaires were completed, reflecting a completed response rate of 54.6%, and telephone interviews lasted for 9 ± 4 minutes (mean ± SD) (Table 3.3). However, a further 60 respondents were willing to complete the survey, but due to time constraints they either partially completed the questionnaire (13.5%) or requested to be contacted again (10.4%), often on multiple occasions. Therefore,

Table 3.2. Estimations of the number of lamprey sold by tackle shops from the Supplier A and online directory sampling frame between summer 2011 and summer 2012.

	Supplier A sample frame	Online directory sample frame	
Total no. tackle shops	427	1 281	
Total no. contacted	289	200	
Amount that sell lamprey (proportion as %)	251 (86.9)	106 (53.0)	
95% confidence interval of proportion	± 3.9%	± 6.9%	
Estimated total no. tackle shops that sell lamprey (min - max)	354 - 387	590 - 768	
Median no. lamprey sold by tackle shops for 2011-2012	120	60	**Total**
Estimated no. lamprey sold 2011-2012 (min - max)	42 480 - 46 440	35 400 - 46 080	**77 880 - 92 520**

Table 3.3. Details of response rates from tackle shops (Supplier A sampling frame) in each region in Britain. The number of tackle shops which sell and do not sell lamprey are also provided.

	Sells Lamprey					**Does Not Sell Lamprey**
Region	Full Response (%)	Partial Response (%)	Call Back Request(s) (%)	Response Refusal (%)	Total	Total
Scotland	16 (66.7)	6 (25.0)	0 (0.0)	2 (8.3)	24	4
North England	31 (51.7)	2 (3.3)	8 (13.3)	19 (31.7)	60	5
East England	30 (46.2)	13 (20.0)	5 (7.7)	17 (26.2)	65	9
West England/Wales	30 (54.5)	3 (5.5)	10 (18.2)	12 (21.8)	55	9
South England	30 (63.8)	10 (21.3)	3 (6.4)	4 (8.5)	47	11
All Regions	137 (54.6)	34 (13.5)	26 (10.4)	54 (21.5)	**251**	**38**

a total of 197 respondents (78.5%) were happy to cooperate with the survey (Table 3.3). Only 4 respondents terminated the questionnaire partway through.

3.4.3.1. Respondents' characteristics and lamprey sales

Almost one half of tackle shop managers were over 50 years of age (48.9%) and 96.4% were male. Respondents had been managers for 14.3 ± 11.8 years (mean ± SD), had 2.1 ± 2.3 employees and 34.6% of stores sold online as well as in store. Shop location in relation to the coast significantly influenced whether shops sold lamprey (X_2 = 10.10, d.f. = 1, *P* = 0.001), with far more shops within 5 km of the coast not selling lamprey than one would expect by chance (partial X_2 = 5.79). It is highly likely that the species of lamprey sold by all shops was European river lamprey, as the vast majority of respondents claimed their lamprey were between 8 and 20 inches, typical of river lamprey, and for those who claimed their lamprey were below 8 inches were all supplied by a wholesale supplier known to only sell river lamprey. Although one respondent claimed they had been selling lamprey for 60 years, lamprey sales in tackle shops generally emerged 16 – 20 years ago (early-mid 1990s) (Fig. 3.7.), and most respondents had been selling lamprey for 10.2 ± 6.9 years. All respondents sold

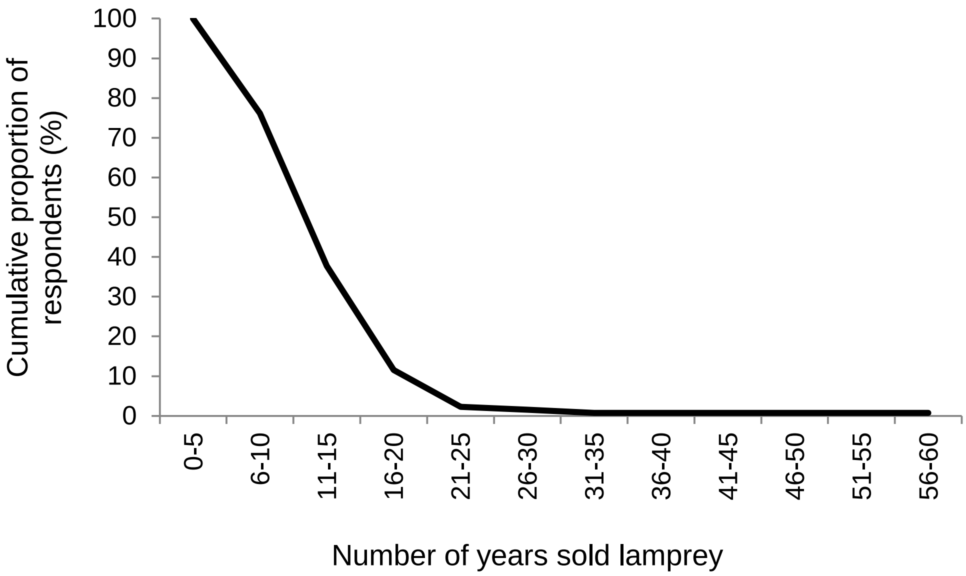

Figure 3.7. Number of years over which respondents (Supplier A sampling frame) have been selling lamprey

lamprey as frozen bait, either sectioned or whole, for pike angling. However, 17 respondents claimed they also sold lamprey as sea bait, with mackerel *Scomber scombrus* and conger eel *Conger conger* as target species, and 4 respondents had also sold lamprey for the introduced wels catfish *Silurus glanis* or chub *Squalius cephalus* in the past. When asked which was their most popular frozen bait, only one respondent stated lamprey; the most popular frozen baits were mackerel (40.0% of shops), squid (13.3%), roach *Rutilus rutilus* (12.4%) and smelt *Osmerus eperlanus* (11.4%).

Sales of lamprey were highest from October to mid-March, in association with the typical pike fishing season, for 84.6% of shops. However, in Scotland 37.5% claimed sales were the same all year round and 12.5% claimed sales were highest during summer; pike fishing continues throughout the summer in Scotland as there is no close season for coarse fishing. During their highest selling periods, the majority of shops (75.9%) had at least one customer buying lamprey per week and 18.0% of shops had at least one lamprey customer per day. Responses were mixed when asked about the popularity of lamprey over the last five years, with 24.8%, 32.3% and 42.9% of respondents remarking that the popularity of lamprey with their customers had decreased, increased and remained the same, respectively (Fig 3.8). However, a large majority of respondents (80.0%) stated that the ease with which customer demand for lamprey could be met had remained the same over the past 5 years, whilst 3.1% and 16.9% of respondents claimed it had become easier and harder, respectively (Fig 3.9). Interestingly, 11 respondents, all of whom bought from Supplier

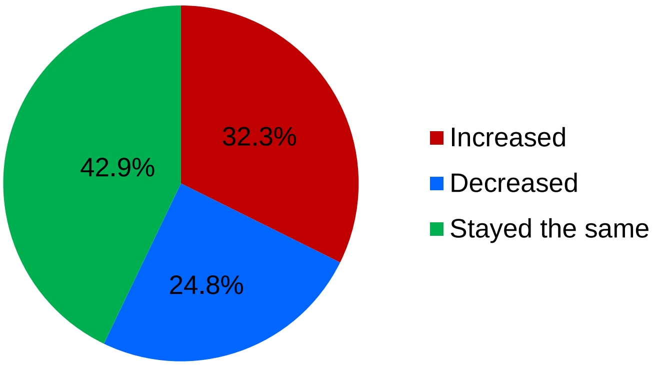

Figure 3.8. The percentage of respondents (Supplier A sampling frame) claiming the popularity of lamprey over the past 5 years has increased, decreased or stayed the same.

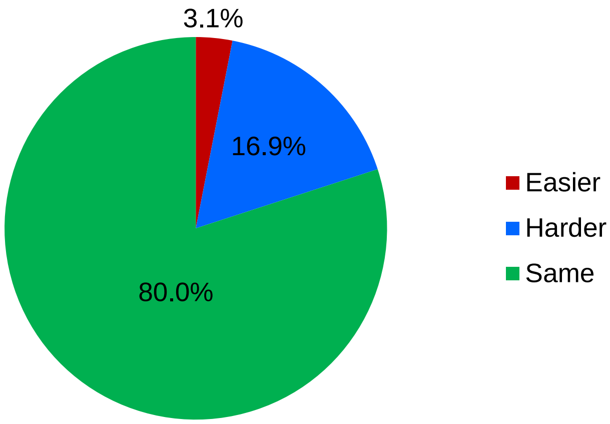

Figure 3.9. The percentage of respondents (Supplier A sampling frame) claiming that the ease with which customer demand for lamprey could be met had become easier, harder or remained the same.

A who sources their lamprey from the Humber River Basin and Estonia, said that there had been a shortage of lamprey one to two years ago, coinciding with the close season for eel fishing in 2010 and catch restrictions on lamprey trapping from 2011 in the Humber.

All respondents obtained their lamprey from a British based supplier, and there was no evidence to suggest that tackle shops personally fished for lamprey. As expected, the majority of respondents (65.2%) were supplied by Supplier A, although 20.7% of respondents were supplied by multiple suppliers, including Supplier A, 11.1% were supplied by suppliers other than Supplier A, and 3.0% chose not to comment (Fig. 3.10). In total, 19 separate suppliers of lamprey were identified by respondents. Summing the amount of lamprey stocked by each respondent suggests that 37 666 lamprey were stocked by respondents between summer 2011 and summer 2012. A strong difference in the number of lamprey stocked in shops between regions was found (Kruskal Wallis: H = 16.615, d.f. = 4, P = 0.002) (Fig. 3.11). Post hoc pairwise comparisons revealed that tackle shops in South England stocked significantly less lamprey between 2011 and 2012 than North England and East England (Mann-Whitney U with Benjamini-Hochberg corrected significance at P = 0.005 and P = 0.010, respectively), and tackle shops in West England/Wales also stocked significantly less lamprey in 2011 and 2012 than North England and East England (Mann-Whitney U with Benjamini-Hochberg corrected significance at

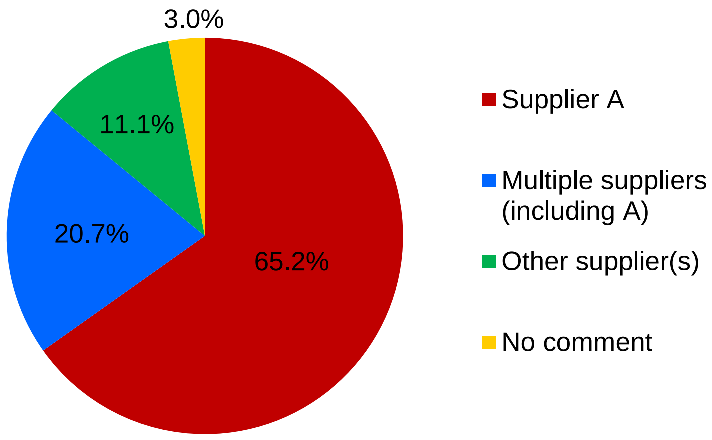

Figure 3.10. The percentage of tackle shops supplied by Supplier A, multiple suppliers (including Supplier A), or supplier(s) not including Supplier A.

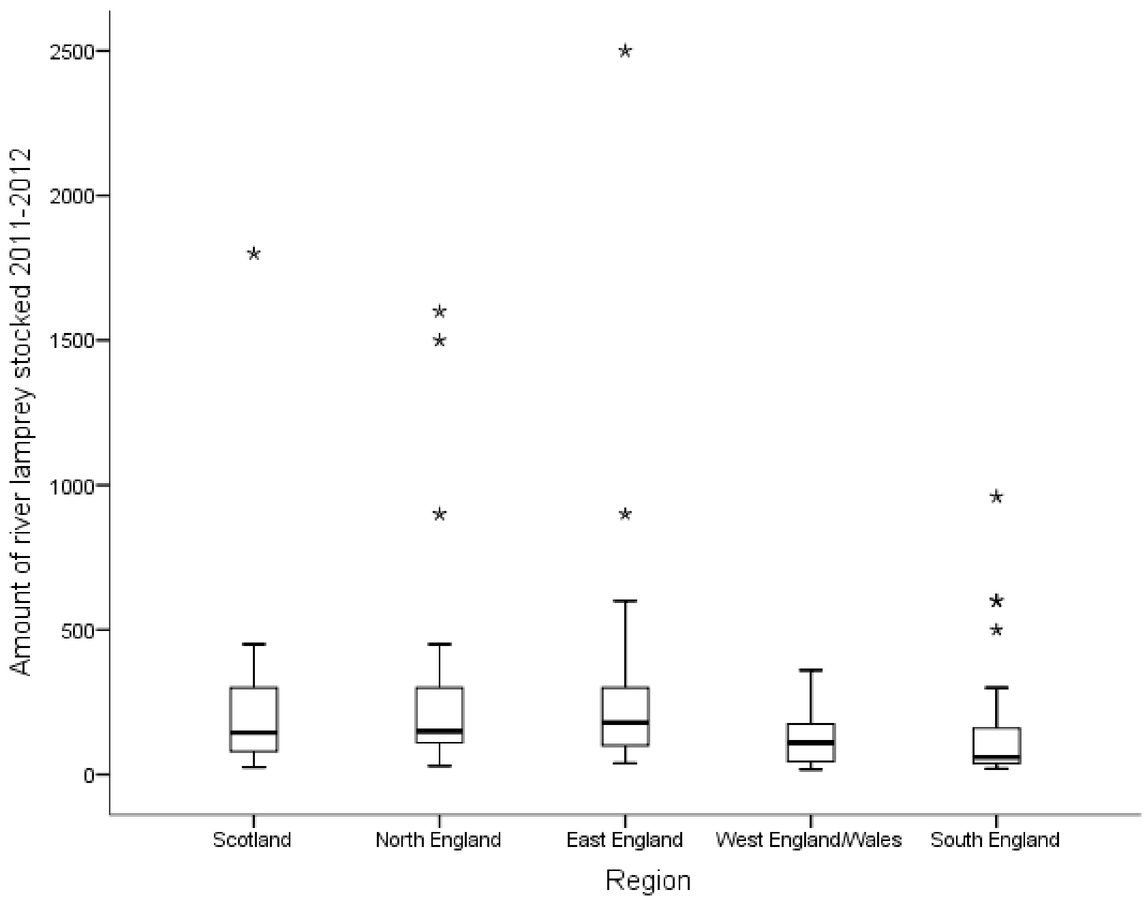

Figure 3.11. Box plots of the amount of individual lamprey stocked by tackle shops (Supplier A sampling frame) in each region between summer 2011 – 2012. Thick black lines denote the median, boxes the interquartile range, T-bars the 95% confidence limits and asterisks the outliers in the data. An extreme outlier (5000 lamprey stocked by a shop in East England) was removed from the figure to improve the clarity of the box plots.

P = 0.015 and *P* = 0.020, respectively). The median number of lamprey stocked by tackle shops between summer 2011 to summer 2012 was 120, and shops ranged from selling 18 lamprey to 5 000 lamprey within this period. Using the median value of 120 lamprey stocked by tackle shops from the supplier's sampling frame, and assuming between 354 and 387 of the tackle shops sold lamprey (section 3.4.3), it is projected that between 42 480 and 46 440 lamprey were stocked from summer 2011 and summer 2012 by tackle shops from the supplier's sampling frame (Table 3.2).

3.4.3.2. Respondents' knowledge about the lamprey that they sell

Figure 3.12 demonstrates that 98.5% of Supplier A respondents were unaware of which species of lamprey they sold, 85.3% were unaware of where the lamprey that they sold originated from, and 69.3% were unaware of whether the lamprey that they sold came from a threatened or non-threatened population; 5.1% and 25.6% believed

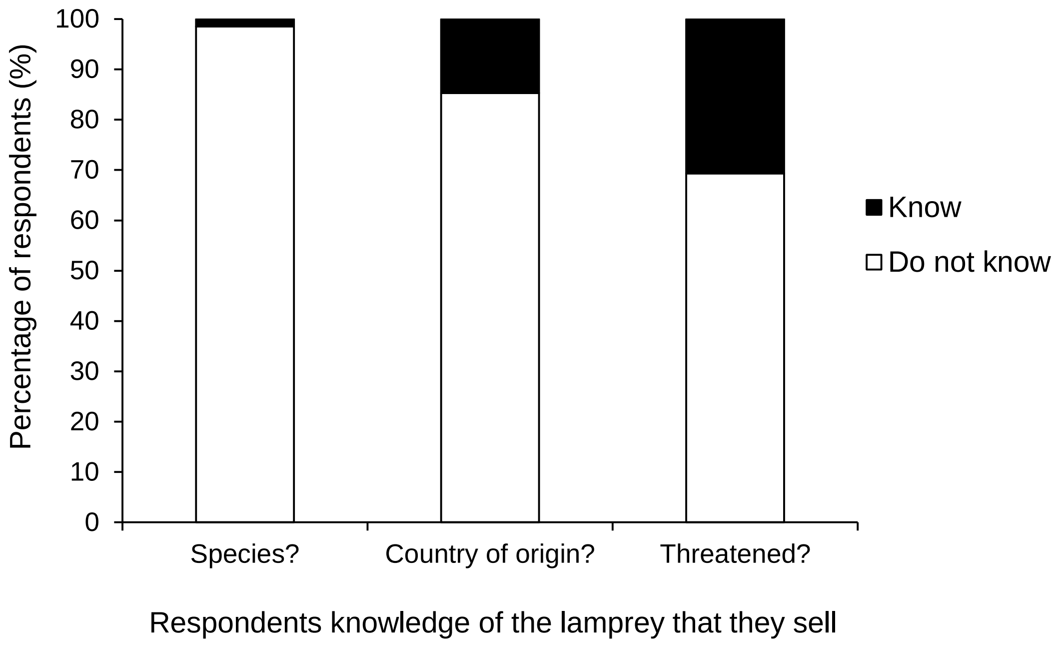

Figure 3.12. The percentage of respondents (Supplier A sampling frame) who know or do not know the species of lamprey that they sell, the country from which they originated, and whether they are from a threatened or non-threatened population.

the lamprey they sold came from a threatened and non-threatened population, respectively. Furthermore, it is likely that some respondents who claimed to know the origin of the lamprey they sold were mistaken, as eight different countries of origin were suggested (including countries in which European river lamprey are absent, such as Canada, Spain and Iceland) by different respondents, despite all of whom being supplied by the same wholesale supplier. Only one respondent knew which river the lamprey that they sold originated from (River Trent, England, see section 3.5.2), although five respondents said they believed the lamprey that they sold were from a sustainably farmed population.

3.4.3.3. Impact on business due to lamprey unavailability

The majority of respondents (56.3%) believed that if lamprey were unavailable to sell it would have no impact on their business, whilst 29.6%, 11.1% and 3.0% believed it would have a slight, moderate or strong impact on their business, respectively (Fig. 3.13). When asked if, in the event that lamprey were unavailable to sell, there would be other available products to sufficiently replace them, the vast majority of respondents (77.9%) said yes, 14.7% said no and 7.4% found it difficult to say (Fig. 3.14). All respondents who said yes stated other frozen baits as suitable replacements for lamprey, with native cyprinids, eel, smelt, mackerel and “bluey”

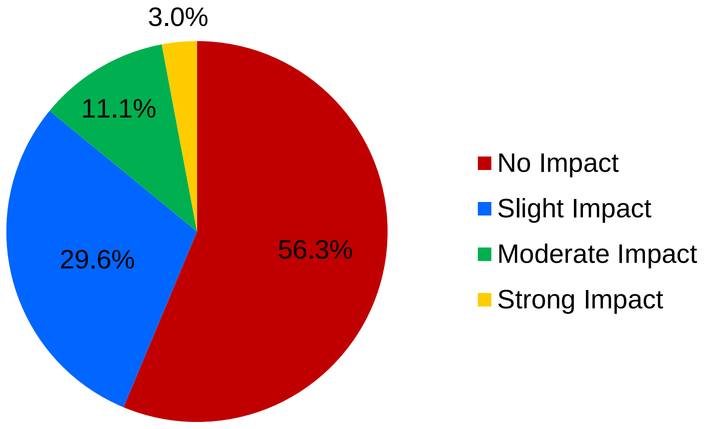

Figure 3.13. The impact of lamprey unavailability on respondents’ (Supplier A sampling frame) businesses

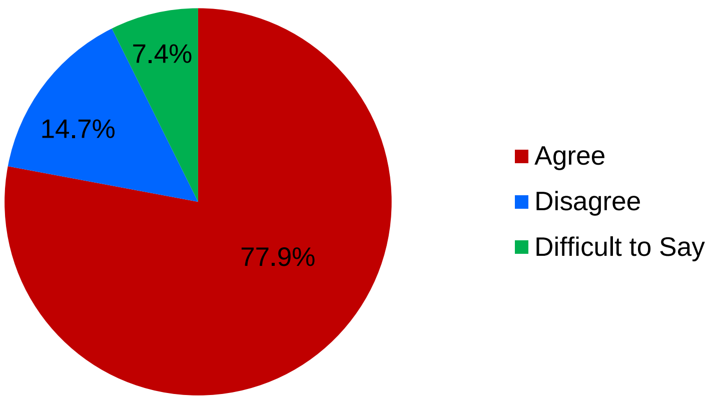

Figure 3.14. The percentage of respondents (Supplier A sampling frame) who agreed, disagreed or found it difficult to say that there are other available products which could sufficiently replace lamprey.

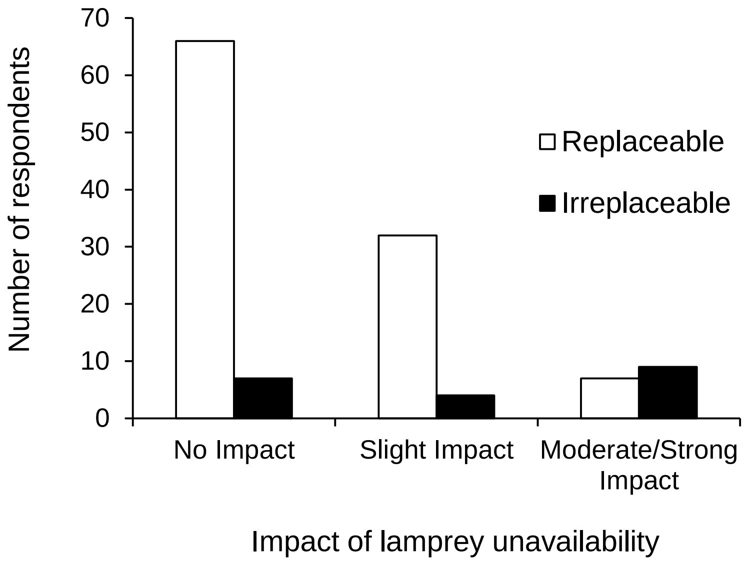

Figure 3.15. The distribution of responses regarding the perceived 'replaceability' of lamprey vs the impact of lamprey unavailability on respondents' (Supplier A sampling frame) businesses

(Pacific saury, *Cololabis saira*) being most commonly specified. No respondents suggested artificial lures, although they were not prompted to explain whether they felt artificial lures offered a suitable alternative to lamprey bait. There was no relationship between the number of lamprey stocked by respondents between 2011 and 2012 and the impact of lamprey unavailability (no impact/impact) on business (logistic regression: β = 0.001, SE = 0.001, d.f. = 1, P = 0.141). However, there was a highly significant association between the perceived 'replaceability' of lamprey (replaceable/irreplaceable) and the impact of lamprey unavailability on their business (X_2 = 22.16, d.f. = 2, P < 0.001), with a significant number of respondents who claimed lamprey are an irreplaceable bait stating that they would be impacted by lamprey unavailability (partial X_2 = 16.20; Fig. 3.15).

3.4.3.4. Respondents' attitudes towards personally altering, or legislatively preventing, sales of lamprey

When asked how important it is knowing whether the lamprey they sell originate from a threatened or non-threatened population, 71.0% of respondents said it was either very important or important, whilst 29.0% said it was slightly or not at all important (Fig 3.16). Only 16.2% of respondents would continue to sell the same amount of lamprey if they were reliably informed they were from a threatened population, whilst the majority of respondents said they would alter their selling "behaviour", either by reducing the amount they sell (21.5%) or stopping the sales of lamprey altogether (62.3%; Fig 3.17). Of the respondents issued the statement "*there should be a ban on the capture and selling of lamprey in Britain if they are considered to be threatened*" (n = 68), 56 agreed (yes to ban), 2 disagreed (no to ban) and 10 found it difficult to say. Of the respondents issued the inverse statement "*there should not be a ban on the capture and selling of lamprey in Britain if they are considered to be threatened*" (n = 66), 9 agreed (no to ban), 47 disagreed (yes to ban) and 10 found it difficult to say.

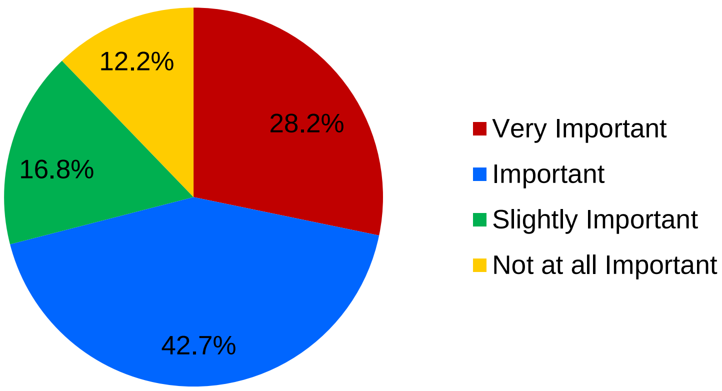

Figure 3.16. How important respondents (Supplier A sampling frame) felt about knowing if the lamprey they sell come from a threatened or non-threatened population.

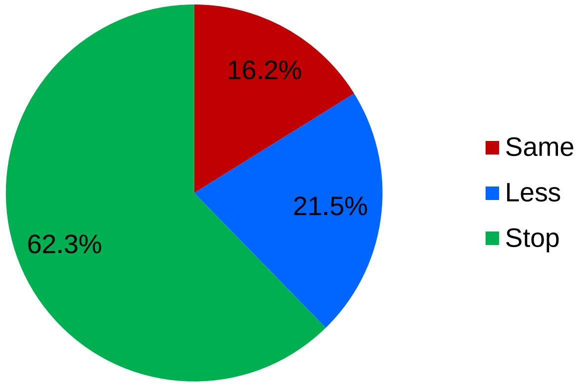

Figure 3.17. The overall percentage of respondents (Supplier A sampling frame) who would continue to sell the same amount of lamprey or alter their selling 'behaviour' (sell less or stop all together) if they were informed the lamprey they sell are from a threatened population.

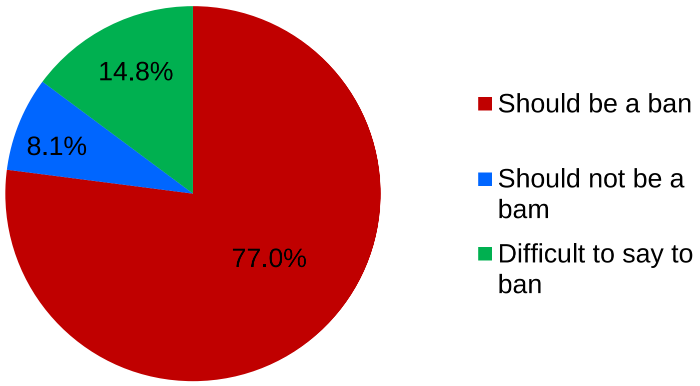

Figure 3.18. The overall percentage of respondents (Supplier A sampling frame) who said there should be a ban, should not be a ban, or found it difficult to say to a ban.

Therefore, overall 77.0% of respondents said there should be a ban, whilst 8.2% said there should not be a ban and 14.8% found it difficult to say (Fig. 3.18.). Analysis of responses suggested that statement phrasing did not influence respondents' decisions regarding a ban (X^2 = 5.21, d.f. = 2, P = 0.074). However, when respondents who were indecisive towards a ban were removed from analysis, a significant response bias was discovered (X^2 = 5.29, d.f. = 1, P = 0.022), with a significantly low number of respondents disagreeing with the statement "*there should be a ban*" (partial X^2 = 3.00).

Respondents' decision to alter their selling "behaviour" was significantly associated with how important they felt it is knowing if the lamprey that they sell are threatened (X_2 = 9.35, d.f. = 1, P = 0.002; Fig. 3.19). Respondents claiming it is slightly or not at all important decided they would keep selling the same amount of lamprey if they were informed they were threatened (partial X_2 = 4.86). The impact of lamprey unavailability on the respondents' businesses, the number of lamprey stocked by respondents between 2011 and 2012 and the number of years over which respondents had been selling lamprey had no effect on their decision to alter their selling "behaviour".

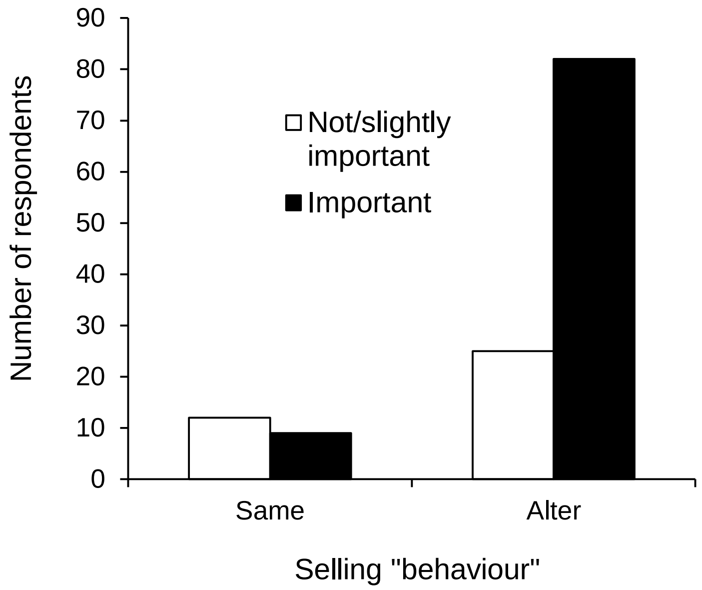

Figure 3.19. The distribution of responses regarding the importance of knowing if threatened or non-threatened vs decision to either sell the same amount of lamprey or alter (reduce/stop) their selling of lamprey.

Whether respondents were in agreement or indecisive about a ban on the capture and selling of lamprey in Britain if they are considered to be threatened was highly dependent upon the impact of lamprey unavailability on their business (X_2 = 12.48, d.f. = 2, P = 0.001) and how important they felt it is knowing if the lamprey that they sell are threatened (X_2 = 8.02, d.f. = 1, P = 0.004; Fig 3.20). Respondents

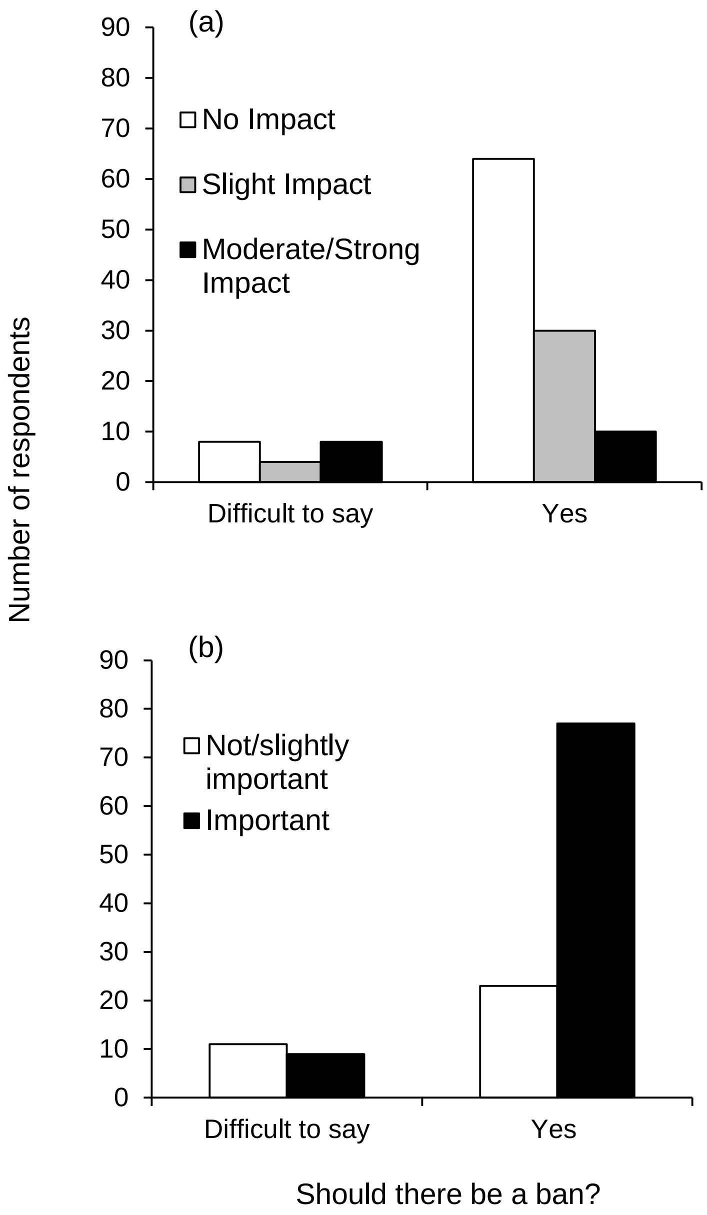

Fig. 3.20. The distribution of responses regarding (a) the impact of lamprey unavailability on respondents' businesses and (b) the importance of knowing if the lamprey they sell are threatened or non-threatened, vs. respondents' decision regarding a ban.

whose businesses would be most impacted by lamprey unavailability, and those claiming it is slightly or not at all important knowing if the lamprey that they sell are threatened, were more indecisive over a ban than expected. The number of lamprey stocked by respondents between 2011 and 2012 and the number of years over which respondents had been selling lamprey had no effect on their decision regarding a ban. Not enough respondents disagreed with a ban for this response to be incorporated into analyses. Table 3.4. summarises the significant factors influencing respondents' answers in this section.

Table 3.4. The variables influencing respondent's (Supplier A sampling frame) decisions regarding their selling "behaviour" and a ban. Ticks show a significant relationship between variables, crosses show no significant relationships were found, and dashes show that analyses could not be performed as Cochran's rule was not satisfied (section 3.3.2.)

	Dependent variables	
Independent variables	Selling behaviour	Decision on Ban
Importance of knowing if threatened	✓	✓
Number of years selling lamprey	×	×
Number of lamprey stocked 2011 - 2012	×	×
Perceived 'replaceability' of lamprey	-	-
Impact of lamprey unavailability on business	×	✓

3.4.4. TACKLE SHOP TELEPHONE QUESTIONNAIRE: ONLINE DIRECTORY SAMPLING FRAME

A total of 1 614 fishing tackle shops in Britain (excluding Northern Ireland) were found during an online *Yellow Pages* search. However, 333 tackle shops within the Supplier's sampling frame also featured in the Online Yellow Pages search, and were therefore removed from the Online Yellow Pages sampling frame to avoid duplication; this reduced the sampling frame to 1 281 tackle shops (Table 3.2). A total of 200 tackle shops were contacted, of which 106 sold lamprey (53.0%). The 95% confidence interval for the proportion of shops selling lamprey was 6.9%, therefore it is estimated that between 46.1% and 59.9% of Britain tackle shops registered in the Online Yellow Pages sampling frame sold lamprey, equivalent to between 590 and 768 tackle shops (Table 3.2).

For the shops that sold lamprey, 96.2% (n = 102) agreed to participate in the survey. The selling of lamprey was strongly associated with the shops' location in relation to the coast (X_2 = 9.53, d.f. = 1, P = 0.002), with more shops within 5 km of the coast not selling lamprey than one would expect by chance (partial X_2 = 3.36). Nineteen respondents were unable, or chose not to, state which supplier provided their shop with lamprey. Of the remaining 83 respondents, 19 separate suppliers were identified, although the supply market was concentrated, with nine providers (A, B, D, E, G – K; Fig. 3.6) supplying 85.2% of respondents. Totalling the amount of lamprey stocked by each respondent suggests that 10 753 lamprey were stocked by respondents between summer 2011 and summer 2012. The median number of lamprey stocked between 2011 and 2012 was 60, and shops ranged from stocking 10 lamprey to 2 000 lamprey within this period. Using a median of 60 lamprey stocked by tackle shops, and assuming between 590 and 768 tackle shops sold lamprey, it is projected that between 35 400 and 46 080 lamprey were stocked from summer 2011 and summer 2012 by British tackle shops registered in the Online Yellow Pages (Table 3.2). Combining this figure with the number of lamprey stocked by tackle shops in the Supplier A sampling frame (section 3.4.3.1.), it is estimated that a total of between 77 880 – 92 520 lamprey were supplied by tackle shops in both sampling frames. If an average weight of 100g for lamprey from the Humber River system (Masters *et al*. 2006), The Netherlands (Lanzing, 1959) and Estonia (see section 3.4.2) is taken, this constitutes a total weight of 7.79 – 9.25 tonnes of lamprey per annum.

3.5. DISCUSSION

3.5.1. COMMERCIAL LAMPREY FISHERIES IN THE TIDAL OUSE

Although total seasonal catches by Fisher A from 2004 onwards have not exceeded those reported by Masters *et al.* (2006), the presence of Fisher B in the tidal Ouse since at least the mid-1990s, and his large seasonal catches presented in this chapter, suggests that lamprey exploitation levels in the tidal Ouse have been higher than previously documented. For example, Fishers A and B collectively captured ~40 980 (4 147.2 kg) and ~17 180 lamprey (1 738.6 kg) during the 2004 and 2005 seasons, respectively, with the former catch considerably exceeding the maximum seasonal catch of 30 992 lamprey from the tidal Ouse (2003 season) reported by Masters *et al.* (2006). Furthermore, before catch restrictions were imposed in 2011, Fisher B’s total seasonal catches were between 74.1 and 108.4% of Fisher A’s total catches for the same seasons, suggesting that Fisher B may have always operated at a similar scale to Fisher A since lamprey fisheries established in 1995. Indeed, Fisher B landed the highest single catch recorded in the tidal Ouse since 1995, at an estimated 2 931 lamprey between 20th – 21st December, 2004 (CPUE of 97.7 lamprey trap^{-1} day^{-1}). However, it is interesting to note that Fisher A fished far more efficiently (i.e. higher median seasonal CPUE) than Fisher B in 2004 (~7x more efficient) and 2005 (~2.5x more efficient) season, although since 2011 Fisher B has fished more efficiently than Fisher A. The shift in fishing efficiency between fishers is unclear, although it may relate to potential changes in fishing gear type or fishing location by Fisher B.

In the recent past, a third fisher had operated a lamprey fishery in the Ouse, catching between 800 - 1000 lbs (approx. 360 - 450 kg) per season, although the fisher has now retired (P. Bird comm.). Masters *et al.* (2006) estimated that Fisher A was operating at a minimum relative exploitation level of 9.9% (12.0% after accounting for mark loss), although it is evident that the exploitation level in the tidal Ouse (accounting for all three fishers), was likely to be double this figure up until 2010 (closed season for eel fishing) and 2011 (catch restrictions imposed). Interestingly, this suggests that recent river lamprey fisheries in the tidal Ouse have indeed been operating at a similar level to those that existed before the First World War, although lamprey were caught in a channel bypassing Naburn weir at that time (Masters *et al.,* 2006). Today, the 522 kg river lamprey catch limit per fishing season per fisher on the tidal Ouse represents 28.3% and 39.1% of Fisher A's and Fisher B's mean seasonal catches during the unrestricted fishing seasons before 2011, respectively. It is evident that today, river lamprey catches in the Humber River basin (by extention, Britain) are only a fraction of the size of current catches in Latvia, Finland, Sweden and Lithuania, although catches there come from a greater number of rivers (FAO, 2011; Kesminas and Švagždys, 2010; Sjöberg, 2011).

There was no evidence to suggest that there has been a decline in mean seasonal river lamprey CPUE in the tidal Ouse over the past 12 years, although this does not necessarily equate to stability in lamprey relative abundance. Firstly, detecting a meaningful decline in mean seasonal CPUE is difficult over such a relatively short time period, particularly when mean seasonal CPUE varies dramatically between fishing seasons. In this case, mean seasonal CPUE varied up to 11-fold over the 12 year period (2000 vs. 2003). Other studies have been able to collate and analyse extensive datasets of lamprey catches, spanning a century in one particular case (Thiel *et al.,*2009), and although catches or CPUE also differed significantly between seasons (years) in these studies, the authors were able to distinguish long term trends in the data (Beaulaton *et al.,* 2008; Birzaks and Abersons, 2011).

Changes in fishing gear type used may also preclude an accurate assessment from being made about the trend of seasonal CPUE, given that gear type often exerts a strong influence on CPUE (Beaulaton *et al.,* 2008, Morris and Maitland, 1987). From 2000 season Fisher A used a combination of uncovered netted traps and netlon covered netted traps, whilst from 2011 Fisher A was only using netlon covered netted traps. Netlon covered netted traps are likely to yield significantly higher catches as they have a robust structure, are less likely to accumulate debris and offer a refuge for lamprey seeking dark resting areas, although there is evidence to suggest that Great Lakes sea lamprey may be attracted to traps with lit entrances (Stamplecoskie *et al.,* 2012). Furthermore, Morris and Maitland (1987) found that solid trap constructions were superior to more open cage constructions as the latter offers the best shelter for overwintering lamprey, although the design and location of these traps differed from the netlon covered traps used in the tidal Ouse. In addition, Masters *et al.* (2006) showed that the efficiency of fishing gear can differ significantly with river flow, thus CPUE is unlikely to be a true reflection of relative lamprey abundance for a particular season given the considerable variation in flow patterns between seasons. Therefore, whilst seasonal CPUE has generally remained stable since 2000, concluding that lamprey fisheries in the tidal Ouse have been operated in a sustainable manner is discouraged. The new regulations implemented in the tidal Ouse in 2011 to limit lamprey catches are encouraging, although strict enforcement and the collection of accurate data is a necessity to promote and detect an increase in the lamprey stock.

High fluctuations in seasonal (yearly) catch and CPUE are typical in other European lamprey fisheries (Beaulaton *et al.,* 2008; Birzaks and Abersons, 2011; Sjöberg, 1980; Thiel *et al.,* 2009). For example, seasonal sea lamprey catches in the tidal part of the Garonne Basin, France, have greatly varied from one year to the next; 120 000 lamprey were caught in 1993 followed by just 27 500 lamprey being caught in 1994 (Beaulaton *et al.,* 2008). Variations in seasonal (yearly) CPUE and total catches are often attributed to year class strength, which may be influenced by numerous biotic and abiotic factors (Birzaks and Aberson, 2011; Masters *et al.,* 2006). For instance, mismatches in the main spawning runs of lamprey and high river flows may restrict access to key spawning habitat above barriers (Lucas *et al.,* 2009; Nunn *et al.,* 2008) and the limited availability of food at sea may also reduce the numbers of adult lamprey returning to rivers to spawn (Birzaks and Aberson, 2011; Murauskas *et al.,* 2013). Both of these factors can therefore contribute to poor recruitment, which may ultimately lead to a reduction in seasonal CPUE and total catch when the cohort returns to the river as adults to spawn. Furthermore, some authors have noted a cyclic pattern in river lamprey catches, with peaks in catches occurring at regular yearly intervals - that may suggest a relationship between the numbers of spawners and number of offspring (Murauskas *et al.,* 2013; Sjöberg, 1980) - although others have found no such pattern (Ryapolova, 1962). In this chapter, there is very little evidence to suggest a cyclic pattern in seasonal catches, although substantially more data points (years) would be necessary to detect a relationship between spawning stock generations.

Compiling data from 2000 to 2012 seasons from Fisher A, and compiling all of Fisher B's available data, it is clear that CPUE reaches a peak in early–mid December, with 6 days separating the expected days of maximum CPUE for the fishers (8^{th} and 14^{th} December). In contrast, river lamprey fisheries in the Baltic region, in general, have caught most of their lamprey between September and November, although fishing has sometimes ceased in November due to ice (Sjöberg, 1980; Valtonen, 1980). This study predicts that CPUE is low before mid-October and after late-January in the tidal Ouse, although only in the 2000 season did a fisher (A) fish for lamprey beyond January. However, Fisher B continued to fish his traps in the tidal Ouse through until June-July (year of 2005) to catch smelt, and from early February no more river lamprey were caught (Anon. unpublished data). Therefore, whilst some rivers in Britain, for instance the River Dee in Wales (Jenkins and Bell, 1985), and Europe (Witkowski and Koszewski, 1995; Thiel *et al.,* 2009) experience a spring-run of river lamprey, there is no evidence to suggest this occurs in the tidal Ouse.

The revision of SAFFA through the Marine and Coastal Access Act to legislate for lamprey exploitation has been a promising step towards protecting lamprey in the Humber. Authorising the trapping of lamprey allows the EA to closely monitor exploitation levels through the obligatory provision of catch returns. The quality of catch returns has now improved, as the lamprey catch return forms ask for the number of instruments fished and the number/weight of lamprey caught for each date the traps are lifted to be stipulated, information which was not always recorded in the past. The attachment of conditions to authorisations, such as temporal and total catch restrictions imposed on lamprey fisheries in the Humber from 2011, has ensured that authorities can now regulate the level of exploitation and help protect lamprey stocks. Hence, although this study has highlighted that exploitation levels in the tidal Ouse have been underestimated in the past, since 2011 the threat of exploitation on river lamprey in the Ouse, and more broadly the Humber, has been significantly reduced. Furthermore, although the Marine and Coastal Access Act could also allow the exploitation of adult sea lamprey, it is extremely unlikely to be allowed in the Humber (both the rivers Ouse and Trent) at this time as sea lamprey remain very rare in these rivers, and indeed in rivers throughout the UK.

Although river lamprey can now only be legally fished between 1st November and 15th December since 2011 season, the peak in CPUE estimated in this study falls within these dates, therefore the catch limit imposed in the tidal Ouse is a crucial component in regulating the lamprey stock. Consequently, whilst it is important to ensure there is no illegal lamprey trapping outside these dates, it is advisable that catch limits are also enforced during this period when the threat of overexploitation is highest, although due to limited resources this is likely to be difficult in practice. Furthermore, it is important to collect data outside of the legal ~6 week fishing period, that will no longer be 'collected' by fishers, to accurately compare and monitor annual CPUE between seasons before and after regulations were imposed. Active management of this type, along with continued dialogue with lamprey fishers, is necessary to ensure the sustainability of lamprey in the Humber.

3.5.2. SCALE AND STRUCTURE OF THE RIVER LAMPREY ANGLING BAIT MARKET IN BRITAIN

This study reveals that there are at least five main wholesale suppliers of river lamprey in Britain, marketing them predominantly as pike bait and selling them to other suppliers, tackle shops or directly to anglers. However, one of these suppliers has now stopped stocking lamprey due to a lack of customer interest. From summer 2011 to summer 2012 these wholesale suppliers supplied an estimated total of 9.01 tonnes of lamprey to these customers in Britain, with no lamprey being exported. This "top-down" estimate falls within the independently calculated "bottom-up" estimate of 7.79 – 9.25 tonnes of lamprey having been stocked by tackle shops in the Supplier A and *Yellow Pages* sampling frames. Although there are undoubtedly other tackle shops in Britain not found in either sampling frame, the similarity between both estimations suggests that this study achieved an adequate coverage of tackle shops in Britain. Hence, it can be deduced that approximately 9 tonnes of lamprey were supplied in Britain between summer 2011 and summer 2012.

It is evident that the lamprey angling bait market in Britain is now mainly reliant upon river lamprey stocks in continental Europe, with only ~14% of lamprey being sourced from Britain (Humber River Basin) in 2011-2012; the Environment Agency confirmed that just two fishers (those in this study) were issued authorisations to trap lamprey in 2011 in Britain, both of whom operated in the tidal Ouse only. It is important to note, however, that since 2011 there has been a substantial decrease in the proportion of river lamprey sold to tackle shop managers and anglers in Britain having originated from the Humber River Basin. For example, in 2004 approximately 4 147 kg of river lamprey were caught from the tidal Ouse and sold, by Suppliers A and B, to tackle shops in Britain, although since 2011 the total amount of lamprey able to be sourced from the tidal Ouse is limited to 1 044 kg. From 1987, lamprey have also been trapped in the tidal Trent (Humber River basin) by a fisher targeting eel, although lamprey catches have been a few percent of those in the tidal Ouse (Masters *et al.,* 2006) and CPUE was estimated to be one fifth of the CPUE in the tidal Ouse (Greaves *et al.,* 2007). Authorisations for trapping lamprey in the tidal Trent were issued to two fishers in 2012, although only one fisher operated during this season and caught 102 kg of lamprey (restricted to 103 kg per fisher for the season). One lamprey fisher also operated in the Great Ouse, East Anglia, in 2012, although just 10 kg of lamprey were caught, despite their being no temporal or catch licence restrictions in the Great Ouse. Of the tackle shop managers interviewed, none stated that their company fishes, or have fished, for lamprey in the past. Therefore, it appears that in Britain, at present, lamprey are trapped in the tidal Ouse, to a lesser extent in the tidal Trent, and very little are trapped in the Great Ouse.

The majority of lamprey appear to have been sourced from The Netherlands (~68%). Although suppliers were unaware of which river system their river lamprey were sourced, one supplier explained that their river lamprey are caught as by-catch in an eel fishery operating in The Netherlands. River lamprey are listed as vulnerable in the Dutch Red List and are a designated feature in the Voordelta and Noordezeekustzone SACs under the EC Habitats Directive (de Nie, 2003; Dotinga and Trouwborst, 2009). Historical evidence suggests that at least until the late 1950s lamprey catches in The Netherlands were substantial. Lanzing (1959) described that at Lith weir, River Meuse, a single fisherman had captured between 19 and 40 lbs of river lamprey per year between 1953 and 1957, and suggested that annual catches could have easily been increased but catches were mostly dependent upon the gastronomic demands of the German markets. Lanzing (1959) also noted that there were other fishermen operating at the weir and that catches varied from 100 to 150kg per night during the season. However, evidence of modern, sizeable river lamprey fisheries operating in The Netherlands is relative absent in published literature, which mostly considers river lamprey fisheries in either Britain (Masters *et al.,* 2006) or countries in the Baltic region (Thiel *et al.,* 2009; Birzaks and Abersons, 2011; Sjöberg. 2011). However, Jansen *et al.* (2007) state that river lamprey are currently common in The Netherlands and found in all major flowing waters, particularly the rivers Meuse and Rhine. Typically, a few thousand lamprey are caught per year in total in all river sections, and the population in all rivers is considered to be in the 100 000s (Jansen *et al.,* 2007). However, given that possibly up to 6.1 tonnes of lamprey were sourced from waters in The Netherlands in 2011-2012, this represents a substantial exploitation rate based upon the population estimates by Jansen *et al.* (2007).

The remaining 18% of lamprey supplied in Britain in 2011-2012 originated from Estonia, although again the exact source was not known. It is probable they originated from the Narva river, which flows into the Gulf of Finland, as this river currently contributes the highest catches of river lamprey in Estonia (Anon, 2007; Oras, 2007; Estonian Fisheries Strategy 2007–2013 (2007)). Here, lamprey are mostly caught using small fyke nets during autumn and spring (Oras, 2007). It is also possible that lamprey were sourced from the River Pärnu, which flows into the Pärnu Bay, as this is also recognised as an important river for catching river lamprey (Sjöberg, 2011). According to OECD (2009), river lamprey are caught in small lakes as well as rivers in Estonia:

"*Commercial catches from other inland waters (smaller lakes and rivers) are small and the most important species in terms of volume and value is the river lamprey*"

FAO (2011) statistics suggests that 59 tonnes of river lamprey were captured in Estonia in 2009, and the highest catch in recent times was 67 tonnes in 2008. Records from 1994 suggest that river lamprey have also been caught in Estonian coastal waters of the Baltic Sea, with all river lamprey being caught in coastal waters in 1996 (18.6 tonnes; Estonian Fisheries Strategy 2007–2013 (2007)). However, the contribution of coastal waters towards total lamprey catches in Estonia has decreased since 1996, and just 0.75 tonnes were captured in coastal waters in 2005 (Estonian Fisheries Strategy 2007–2013 (2007)). Although river lamprey catches have declined in Estonia over the last 60-70 years, probably due to loss of spawning grounds according to Saat *et al.* (2002), the river lamprey stock is "generally stable in the rivers of Estonia" (Estonian Fisheries Strategy 2007–2013 (2007)). There are certain conservation measures established in Estonia to protect river lamprey populations. Firstly, commercial targeting of river lamprey is allowed in Estonia as long as there are special protective measures in operation (Oras, 2007), and there is a closed season for lamprey fishing between 1st April and 30th June (Sjöberg, 2011). Furthermore, lamprey larvae have been artificially bred and distributed in Estonian rivers since the 1950s (Saat *et al.,* 2002), although the effectiveness of restocking lamprey larvae, which also occurs in Latvia and Finland, remains largely unknown (Sjöberg, 2011; Birzaks and Abersons, 2011) After consideration, it appears that the relatively small provision of river lamprey from Estonia for angling bait in Britain (~1.6 tonnes, 2011-2012) poses relatively little risk to river lamprey populations in Estonia in the short-medium term.

This study suggests that, of the tackle shop managers interviewed, the sales of river lamprey in Britain as pike bait mostly began 16 to 20 years ago (early 1990s), coinciding with the period when lamprey had begun to be caught commercially in the Trent and Ouse for angling bait. One tackle shop owner and one wholesale supplier believed they had been selling lamprey for 60 years (early 1950s) and from 1980, respectively, and whilst it appears that lamprey had not become widely popularised as effective pike bait at these times, Fickling (2012) claimed that:

"we were catching pike with them [lamprey] *down their throats in 1973".*

Furthermore, lamprey ammocoetes, or "prides", have been used historically to catch eel in Britain, and as early as the mid-17th century, Izaak Walton (1906) wrote:

"…but the Eel may be caught, especially, with a little, a very little lamprey, which some call a Pride".

Indeed, according to Buller and Falkus (1994), brook lamprey have also been used as recreational bait for eel, chub, perch and pike. Nowadays, river lamprey appear to be sold in the majority of fishing tackle shops in Britain, with 53 ± 6.9% and 86.9 ± 3.9% of tackle shops registered in the *Yellow Pages* and Supplier A sampling frame selling river lamprey, respectively. However, shops <5km from the coast were less likely to sell lamprey than tackle shops further inland as lamprey are sold predominantly for pike bait, and coastal tackle shops, not surprisingly, specialise in catering for sea angling for which lamprey are rarely used. All tackle shops obtained lamprey from wholesale suppliers operating in Britain and, although it has been postulated that indiscriminate catching of lamprey may occur (Masters *et al.,* 2006; Maitland, 2003), there was no evidence to suggest tackle shops fished for lamprey themselves. The vast majority of tackle shop managers (80.0%) said the ease to which customer demands for lamprey could be met over the past five years has remaining the same. This suggests that, in general, the supply of lamprey has not wavered in recent years. However, 11 tackle shop managers supplied by Supplier A, which source their lamprey from the Humber and Estonia, stated it had become harder to meet the demands of their customers as there had been a shortage of lamprey in recent years. This was perhaps a direct result of regulations in the Humber limiting the catch of lamprey, and such regulations may continue to affect the supply of lamprey to some tackle shops in Britain in the future.

3.5.3. KNOWLEDGE AND ATTITUDES OF STAKEHOLDERS

Studies have often highlighted differences within and between stakeholder groups in terms of their knowledge and attitudes and stress how these differences need to be recognised by conservationists when designing and implementing management policies (Dorow *et al.,* 2010; Worthington *et al,.* 2010; Aas *et al.,* 2000; Jacobson and Marynowski, 1997). This study reveals the similarities and differences that exist within and between key stakeholder groups in the lamprey bait market (tackle shop managers and wholesale supplier managers) and defines the factors that likely influence stakeholders' attitudes.

The knowledge of these two stakeholders in relation to the lamprey that they sold varied greatly. There was a general lack of awareness amongst tackle shop managers about which species of lamprey they sold and where they originated from; just 1.5% of managers knew they sold river lamprey and only 14.7% of managers "knew" the country from which they were sourced, although countries were named in which European river lamprey are absent, such as Spain, Canada and Iceland. Furthermore, 69.3% of tackle shop managers did not know whether they were from a threatened or non-threatened population. It should, however, be noted that a small proportion of tackle shops (5.1%) sold lamprey despite believing that they were from a threatened population. In comparison, the main wholesale supplier managers were relatively knowledgeable about the lamprey that they sold, with all suppliers knowing the country from which their lamprey were sourced and all but one knowing which species they sold.

Despite the tackle shop managers' relative lack of knowledge towards the lamprey they sold, the vast majority were positive towards the regulation of their sales. For instance, 83.8% of managers said they would either reduce or stop all together their selling of lamprey if they were reliably informed they were threatened, although slightly fewer managers (77.0%) were prepared to support a ban on the capture and selling of lamprey in Britain if they were considered to be threatened. Whilst the general support for a ban likely reflects genuine conservation concern, for some respondents their support might have been a result of acquiescence bias; there was evidence to suggest that significantly fewer managers disagreed that there *should not* be a ban than agreed that there *should* be a ban.

The tackle shop managers who would not personally alter their sales were those who felt it was just slightly, or not at all important knowing if the lamprey they sell are threatened. This apparent lack of conservation concern was also associated with indecisiveness over a ban (not enough respondents disagreed with a ban for this response to be incorporated into analysis), although managers whose businesses would be most impacted by lamprey unavailability were also those who were indecisive over a ban. This suggests that, regardless of whether managers' businesses would be impacted by lamprey unavailability, most would personally alter their selling behaviour, although when it came to strict state regulation (i.e. ban) the impact of lamprey unavailability became a determining factor when deciding whether to agree to a ban. Other studies have detailed scenarios in which stakeholders wish to support conservation objectives up until regulatory measures become highly restrictive and impact upon their livelihood. For example, Dorow *et al.* (2009) detailed how eel anglers were willing to accept tight regulations on harvestings, although were strongly against any form of temporal closures to the fisheries. They suggested that eel anglers were against temporal closures because it would be difficult for them to find another acceptable fish species or recreational activity to substitute for eel fishing (Dorow *et al.* 2010). Interesting parallels can be drawn between Dorow *et al.* (2010) and this study, as those tackle shops impacted the most by lamprey unavailability were those that considered lamprey to be an irreplaceable product. Many tackle shop managers considered that the high blood content and the scent trail that lamprey leave in the water makes it very effective as pike bait. From their perspective, it is also a tough, durable bait that can be cast a long distance and can be fished for a relatively extended period of time. However, most managers (77.9%) felt that there are other products available which could sufficiently replace lamprey. Several tackle shop managers felt that European eel and smelt make suitable alternatives to lamprey.

However, given that both species are widely recognised as threatened species themselves (Maitland and Lyle, 1997; Lassalle *et al.,* 2009; Freyhof and Kottelat, 2010), they do not constitute a sustainable substitute to lamprey. Conservationists should, therefore, be wary about strictly regulating lamprey fishing which may drive the exploitation of other threatened species.

Similar to tackle shop managers, most suppliers stated they would discontinue lamprey sales if they were reliably informed they were threatened. However, wholesale supplier managers were mostly indecisive towards a ban, as three of the five suppliers said they would either be moderately or strongly impacted by lamprey unavailability and all but one supplier felt that lamprey are an irreplaceable product. It was apparent that most suppliers would need to be convinced that the lamprey they supply are under threat before they would support a ban. This underscores how essential it is to communicate with key stakeholders during the development of management policies to anticipate any negative impacts on their businesses (Granek *et al.,* 2008; Arlinghaus *et al.,* 2002; Dorow *et al.,* 2010). Wholesale supplier managers in this case represent the stakeholders who would, in general, be most affected by regulations in lamprey fisheries either in Britain or elsewhere in Europe.

In the near future, it would be prudent to evaluate the knowledge and attitudes of pike anglers in Britain. It would, first and foremost, be interesting to establish whether pike anglers feel there are adequate substitutes to river lamprey (e.g. other natural baits or artificial lures) when fishing for pike, as this study suggests there are. For example, the Pike Anglers Club (PAC) of Great Britain claim on their website that *"today, the use of coarse and sea deadbaits…and artificial lures and even flies are enormously popular"* (PAC, 2012a). A study evaluating the effectiveness of different "baits" for northern pike (including natural baits and artificial lures – spinners, spoons, plugs and soft plastic baits) demonstrated that the size of pike caught was mostly related to bait size rather than bait type (Arlinghaus *et al.,* 2008). However, substantial variations in the size of artificial lures did not yield significantly different sized pike, suggesting that the individual action and associated variation in size of the lure influences the size of pike caught. Furthermore, Arlinghaus *et al*. (2008) showed that natural baits were swallowed more deeply than artificial baits that may lead to hooking mortality. It appears, therefore, that there are alternatives to using lamprey when fishing for pike, although the effectiveness of baits likely vary between waters and some anglers may exhibit strong preferences for bait types. Indeed, although northern pike are widely distributed in Europe and North America (Crossman, 1996), only in Britain is the method of using dead fish baits for catching pike widespread and common. In many countries where pike are a target species for recreational angling, non-natural bait methods are favoured.

Whether pike anglers in Britain would choose to switch bait type (from lamprey to other natural baits or artificial lures) is currently unclear. However, the PAC have produced a document online in association with the National Anguilla Club (NAC) which discourages members from using European eel as pike bait (PAC, 2012b). European eel recruitment has declined by 90% across most of Europe since the 1980s (Dekker, 2003), and as a result they are listed as a ‘critically endangered’ species in the IUCN Red List (Freyhof and Kottelat, 2010). Although European river lamprey populations have not, in general, exhibited declines on this scale, the European eel remains far more widespread than the river lamprey (Freyhof and Kottelat, 2010; Kottelat and Freyhof, 2008). Furthermore, whilst river lamprey remain rare in rivers in Britain, it has been suggested that eel stocks in some, perhaps many, rivers along the west coast of England and Wales, and possibly some rivers in north-east England, are still at or near to carrying capacity (Bark *et al.,* 2007). However, the study remarked that eel stocks are likely to continue to decline in rivers in the south-east of England. The PAC do not currently recommend against the use of river lamprey as bait, and whether they will do so in the future is uncertain, although their demonstrable support for eel conservation is encouraging.

Chapter 4: General Discussion

The research presented in this thesis addressed two major anthropogenic factors which are likely impacting upon the river lamprey population in the Humber River Basin; poor longitudinal connectivity due to man-made barriers and commercial exploitation. This chapter provides a summary of the key findings in this thesis and offers recommendations for future work.

Using PIT telemetry, chapter 2 evaluated the attraction and passage efficiencies of two technical, conventional fishways, located at barriers on the lower Derwent SAC, for upstream migrating river lamprey. The pool and weir fishway at Elvington Sluices, constructed in 1937, was demonstrably inefficient for upstream migrating river lamprey, with attraction and passage efficiencies of 42.6% and 5.0%, respectively, during their migration and spawning period. Although this fishway has a relatively distinct geometry (Fig. 2.4), it is probable that other types of pool passes in the Humber, Britain and Europe that offer poor attraction flow, high water velocities and streaming flows at notches (in this case ramps) are inefficient for river lamprey and other non-climbing lamprey species. For instance, Cromwell weir is significantly limiting the distribution of river lamprey in the River Trent and it is extremely unlikely that the small pool and weir fishway installed at the weir is improving connectivity for this species in this river (Greaves *et al.,* 2007). This chapter also revealed that the more recently constructed plain Denil baffled fishway (built in 1996) at Stamford Bridge weir, lower Derwent, is extremely inefficient for river lamprey, with 91.8% of upstream migrants entering the fishway, on up to 12 separate days, but none of them successfully passing.

Consequently, Chapter 2 indicates how fishways currently located within SACs can be ineffective for species which are a primary feature of these sites, such as the river lamprey in the lower Derwent SAC. Although old style fishways principally designed for salmonids, such as the pool and weir fishway at Elvington, are no longer selected for installation at barriers in Britain, they are still abundant within the distributional range of river lamprey. Indeed, pool and weir and Denil type designs were historically the chief candidates for installation at low-head barriers in England and Wales (Beach, 1984). As this chapter has revealed the extreme inefficiencies of these fishways (granted that individual fishways vary in their geometry, slope etc.), it is recommended that there is a reappraisal of *in situ* fishways, particularly those with old design features, in order to inform decisions on whether to upgrade, remove or replace them. The monetary costs of these actions can be considerable, therefore action should first be taken at sites which will derive the most benefit e.g. where the target species are afforded protection, such as SACs. Nunn and Cowx (2012) ranked barriers at Naburn (River Ouse), Sprotbrough (River Don) and Cromwell (River Trent) as the highest priority for passage improvements for river lamprey in the Humber, although prioritisation was subjective and rankings were sometimes based upon 'expert judgement'. The authors suggested that before passage improvements are undertaken, further quantitative studies to assess passage efficiencies at barriers are needed to reduce the subjectivity of this prioritisation tool. This chapter therefore makes an important contribution towards future passage improvement decisions and warns against assuming free passage is being provided for river lamprey, and indeed other fish species, at barriers with technical fishway installations.

To complement this study, there is an urgent need to quantitatively evaluate other technical fishways for river lamprey and other species of various swimming modes and capabilities. Whilst experimental flume studies are developing passage criteria for a range of fish species (Kemp *et al.,* 2011; Russon *et al.,* 2011; Russon and Kemp, 2011a, 2011b), *in situ* quantitative evaluations of fishways (i.e. assessing delay time, attraction anad passage efficiencies) remain the best way of determining their efficacy. A current priority is to determine the efficacy of the Larinier super-active baffled fishway which is being widely installed in rivers in Britain, on the assumption it is an effective multi-species fishway. Whilst this may be the case, there has been no assessment of delay times, attraction and passage efficiencies of this fishway for any fish species to date. A Larinier super-active baffled fishway has recently been installed at Buttercrambe weir, lower Derwent (Fig. 2.11), and a PIT telemetry study is being conducted in the near future to evaluate its efficacy for upstream migrating river lamprey and other species in the lower Derwent fish community. This study will supplement the findings in this thesis and advance our understanding of which conventional fishways offer the best solutions for river lamprey passage. However, it is recommended that, where vertical slot and nature-like fishways are installed in UK rivers with lamprey populations, the efficacy of these fishways for river lamprey are evaluated, as it appears these fishways may offer the best solution for lamprey passage at man-made barriers.

Chapter 3 consisted of two main investigations: to reassess the level of commercial exploitation of river lamprey in the tidal Ouse and to investigate the river lamprey angling bait market in Britain. This chapter confirmed that Masters *et al.* (2006) were correct in suggesting that the actual exploitation of river lamprey in the tidal Ouse may have been twice the level they had originally calculated (9.9%, or 12.0% after accounting for mark loss). This chapter revealed that a second fisher has operated at a similar level to the original fisher accounted for by Masters *et al.* (2006), for at least four fishing seasons; data was only available for four fishing seasons from the second fisher, although the fisher has been operating a commercial river lamprey fishery for a similar number of years as the original fisher. Furthermore, a third fisher had, in the recent past, been operating in the tidal Ouse, taking 800-1000 lbs of river lamprey per season, but has now retired. Hence, up until 2010 when there was a close season on the fishery, a more realistic exploitation level in the tidal Ouse was >20%. This fishing mortality level is substantial since river lamprey are a fully semelparous species which, by their life history, are susceptible to impacts of large-scale exploitation (Masters *et al*., 2006). Despite this, analysis of CPUE effort data gave no indication that the lamprey stock in the Ouse has declined between 2000 and 2012.

The UK Marine and Coastal Access Act 2009 has been an important step towards the careful regulation of lamprey exploitation. Since 2011 a maximum of 2 301 lbs (1 044 kg) of river lamprey can be taken from the tidal Ouse per fishing season (per year) between 1st November and 10th December. This restriction represents a 5% exploitation impact on the Ouse river lamprey population, above the River Wharfe confluence, agreed by Natural England and the Environment Agency. Similarly, a 5% exploitation level is permitted in the Trent which is estimated at a total of 456 lbs (206 kg), given that river lamprey abundance in the Trent is estimated to be one fifth of that in the Ouse (Greaves *et al.,* 2007). It is imperative that the total catch and temporal restrictions in lamprey fisheries, in both the Ouse and Trent, are enforced to ensure this legislative change succeeds in promoting the river lamprey population in the Humber. The population estimate used to calculate the 5% limit is, however, fraught with uncertainty. A mark-recapture study by Masters *et al.,* (2006) suggests the upstream migrating river lamprey population in the Ouse, above the Wharfe confluence, is in the region of 300 000 individuals, whilst APEM (2007) reported estimates of between 62 403 and 275 687 (Hopkins, 2008). Furthermore, the population estimate for the Trent was calculated by comparing CPUE values between the Trent and the Ouse for a single season (Greaves *et al.,* 2007). Unlike for salmon, whereby survival rate analyses can be used to determine a sustainable level of exploitation, this is exceptionally difficult for lamprey and requires a stock-recruitment relationship to be ascertained. This is inherently complex given that there is variability in larval life spans, time spent at feeding grounds and that the survivorship of larvae and transformers is currently unknown (Kelly and King, 2001). Therefore, the 5% limit currently set must be flexible and the fisheries must be actively monitored in the future to detect and respond to changes in the lamprey stock.

Where fishery restrictions do not exist in Britain, for instance on the Great Ouse, it is recommended that a precautionary principle is adopted and a catch limit imposed to prevent the acute escalation of river lamprey exploitation in rivers where little information exists regarding the size of their population. Furthermore, this chapter revealed that smelt are the most popular product in 11.4% of tackle shops surveyed (Supplier A sampling frame). Given that the Marine and Coastal Access Act amends SAFFA to legislate for smelt as well as lamprey, this chapter suggests that there should be careful monitoring of smelt exploitation in Britain which may rise as a result of lamprey fishery restrictions; smelt were commonly cited by tackle shop managers as a suitable substitute bait for river lamprey.

Moves towards the regulation of lamprey exploitation in Britain have proved vital given the market force demonstrated in this country for this resource to be utilised as bait; *c.*9 tonnes of lamprey were supplied to tackle shops and anglers in Britain in 2011-2012. Whilst the exploitation pressure on the Humber population has eased since restrictions were enforced in 2011, pressure has shifted to river lamprey stocks elsewhere in Europe; this chapter estimated that a maximum of 6.1 tonnes of lamprey were sourced from The Netherlands between 2011-2012, of which three tonnes were sourced as by-catch in eel fisheries in The Netherlands, and 1.6 tonnes were sourced from Estonia over the same period. Although it appears that the demand for lamprey in Britain for angling bait is probably not impacting upon lamprey stocks in Estonia, the exploitation of river lamprey from The Netherlands is likely to be having an effect on their populations, given that the population for all rivers is suggested to be in the 100 000s only (Jansen *et al.,* 2007). However, although the vast majority of tackle shops (from Supplier A's sampling frame) were in favour of a ban on the capture and selling of lamprey in Britain if threatened (77%), possible future restrictions adopted in Estonia or Holland that limit the availability of lamprey for British angling businesses are likely to have at least a slight impact on a significant number of tackle shop businesses, and a very strong impact on at least one supplier in Britain, and will mostly affect businesses that feel lamprey are an irreplaceable bait. It is recommended that a study is conducted in the future to understand the attitudes of pike anglers towards lamprey, and indeed smelt, restrictions, given that they may exhibit strong preferences for bait type and may also be strongly affected by regulations of lamprey catches on the continent.

In conclusion, whilst exploitation levels in the Humber have decreased due to recent legislation, poor longitudinal connectivity and ineffective fishways continue to impact upon the distribution and migration of river lamprey in rivers in this catchment and may be limiting the Humber river lamprey population as a result.

Appendices

APPENDIX 1: REGIONS AND THEIR ASSOCIATED HISTORICAL COUNTIES FOR STRATIFIED RANDOM SAMPLING (SECTION 3.3.2.2.)

North England	East England	West England/Wales	South England
County Durham	Bedfordshire	Blaenau Gwent	Berkshire
Cumbria	Buckinghamshire	Bridgend	Cornwall
East Riding of Yorkshire	Cambridgeshire	Bristol	Devon
Greater Manchester	Essex	Caerphilly	Dorset
Lancashire	Hertfordshire	Cardiff	East Sussex
Merseyside	Leicestershire	Carmarthenshire	Greater London
North Yorkshire	Lincolnshire	Ceredigion	Hampshire
Northumberland	Norfolk	Cheshire	Isle of Wight
South Yorkshire	Northamptonshire	Conwy	Kent
Tyne and Wear	Nottinghamshire	Denbighshire	Somerset
West Yorkshire	Rutland	Derbyshire	Surrey
	Suffolk	Flintshire	West Sussex
		Gloucestershire	Wiltshire
		Gwynedd	
		Herefordshire	
		Isle of Anglsey	
		Merthyr Tydfil	
		Monmouthshire	
		Neath Port Talbot	
		Newport	
		Oxfordshire	
		Pembrokeshire	
		Powys	
		Rhondda Cynon Taff	
		Shropshire	
		Staffordshire	
		Swansea	
		Torfaen	
		Vale of Glamorgan	
		Warwickshire	
		West Midlands	
		Worcestershire	
		Wrexham	

APPENDIX 2: TACKLE SHOP MANAGER QUESTIONNAIRE (SUPPLIER A SAMPLING FRAME)

1. Hello, I was wondering if your shop sells lamprey at all?

No – Not a problem, thanks anyway.

Yes – Go to 2.

2. Am I speaking with the shop manager?

Yes – Go to 4

No – Go to 3

3. May I speak with the shop manager please

Yes – Go to 4

No – Might I ask why?

Busy – When would be a suitable time to call back?

Why? [*Go to 4*]

4. Hello, [My name is William Foulds calling from the University of Durham. We are conducting a survey of Tackle Shop managers in the UK looking at the extent of lamprey sales in their company and their views on lamprey as bait]. Could I please briefly explain the interview process, after which you can decide whether or not to participate?

Yes – Go to 6

Not interested – Go to 5

Too busy – Go to 5

5. The questionnaire will only last for about 6 minutes and can be rescheduled. Is there another time we could contact you?

   No – Thank you for your time.

   Yes – Arrange a time

6. Thank you. So you've been randomly selected from a list of tackle shops and any information you provide me with will be completely anonymous and confidential. I'm only going to record and cite the county of your store, so there is no chance of you

being identified in any reports about this study. All results will be pooled and written up for a scientific publication and this has had ethical clearance from the Review Committee at Durham. The questionnaire is completely voluntary, so you don't have to answer any question you don't want to, and you can end the interview at any time. The questionnaire will last about 6 minutes. Are you ready to participate?

Yes – Proceed with questionnaire

No – Go to 5

……....

(A) Fantastic. Could I please begin by asking you which age category you fall into? Is it...

1) 20 and under
2) 21-29
3) 30-39
4) 40-49
5) 50-59
6) 60 and over

Great. Now to start with I'd like ask you some general questions about your company and the lamprey that you sell…

(B) How many employees do you have?

(C) How long have you been the company manager for?

(D) How long has your company been selling lamprey for?

Thank you. Are your companies' lamprey currently sold for

1) (E) Angling bait -> No = STOP

    (F) Have you always sold lamprey for angling bait? -> Yes = *Go to H*

        (G) When did you begin selling lamprey for angling bait?

2) (H) Any other purpose -> No = *Go to M*

    (I) What was this purpose?

        (J) Have you always sold lamprey for (*insert other use*)? -> Yes = *Go to M*

            (K) When did you begin selling lamprey for (*insert other use*)?

- If answer "Yes" to 1 and 2, ask: (L) What proportion of your companies' lamprey are sold as angling bait or (*insert other use*)?

(M) Do you know which species of lamprey your company sells? No = *Go to Q*

(N) Please could you specify which species -> Only one species = *Go to Q*

(O) Have you always sold x species?

(P) Have you always sold y species?

(Q) As a follow up question, to the best of your knowledge, do you know how many species of lamprey there are in Britain?

(R) Considering their whole body length, what size of lamprey do you sell?

1) 10-20cm which is 4-8 inches
2) 20-50cm which is 8-20 inches
3) more than 50cm which is above 20 inches

(S) I will now read out a list of possible sources of your companies' lamprey. Please answer yes, no or no but have done in the past to the following options. Does your company currently...

1) (S1) Buy lamprey from a British supplier
2) (S2) Buy lamprey direct from a fisherman in the Britain
3) (S3) Catch your own lamprey
4) (S4) Buy lamprey from a source outside of the Britain
5) (S5) Obtain lamprey through another means. (*Please specify*)

- (T) If "Yes" to 1, ask: Could you please state which suppliers currently supply your lamprey
- (U) If "Have done in the past" to 1, ask: Could you please state which suppliers supplied your lamprey in the past.
- (V) If "Yes" to 2, ask: Is it just the one?

(W) Do you know which country, or countries, the lamprey that you sell originate from? No = *Go to AC*

(X) Could you please specify which country or countries

(Y) Do you know which river or rivers the lamprey they originate from? *Go to AA*

(Z) Could you please specify which river or rivers

(AA) Do you know which region or regions they originate from? No = *Go to AC*

(AB) Could you please specify which region or regions

OK thank you. I would now like to ask you a few questions about the extent of lamprey sales within your company.

(AC) To the best of your knowledge, how many lamprey did you stock in the past 12 months?

(AD) In previous years did you tend to stock

1) More lamprey -> Yes-> (AE) Why is it that your company stocked more?
2) Less lamprey or -> Yes -> (AF) Why is it that your company stocked less?
3) The same amount of lamprey

(AG) On average how often do you get customers buying lamprey

1) More than once a day
2) Once a day
3) More than once a week
4) Once a week
5) More than once a month
6) Once a month
7) Less often

(AH) Are there any months when lamprey sales are highest?

(AI) Hypothetically, if lamprey were no longer available to sell, would this have

1) No impact
2) A slight impact
3) A moderate impact
4) A strong impact

   ...on your company

Thank you, we have got just over 2 minutes left. These next questions are important to determine your thoughts on the lamprey that you sell.

(AJ) Firstly, for the lamprey that your company sells do you believe they have come from a

1) Non-threatened population
2) Threatened population or
3) Unsure

(AK) Hypothetically, if your company was reliably informed that the lamprey that you sell are from a non-threatened population would your company

1) Choose to sell more lamprey
2) Continue to sell the same amount of lamprey
3) Choose to sell less lamprey
4) Stop selling lamprey altogether

(AL) Hypothetically, if your company was reliably informed that the lamprey that you sell are from a threatened population would your company

1) Choose to sell more lamprey
2) Continue to sell the same amount of lamprey
3) Choose to sell less lamprey
4) Stop selling lamprey altogether

(AM) Finally, how important is it for your company to know if the lamprey that you sell come from a threatened or non-threatened population

1) Very important
2) Important
3) Slightly important
4) Not at all important

Great, I will now finish by making a few statements. Could you please state whether you agree, disagree or find it difficult to say to each statement.

(AN) If lamprey were unavailable to sell, there are other available products which could sufficiently replace them. Agree -> (AO) could you please specify which products

(AP) Over the past 5 years, lamprey have become more popular with your customers

- Agree -> (AQ) why do you think this is?
- Disagree/Difficult to say -> (AR) OK, over the past 5 years, lamprey have become less popular with your customers -> Agree -> (AS) why do you think this is?

(AT) In the past 5 years, it has become harder to meet the demands of your customers seeking to buy lamprey.

- Agree -> (AU) why do you think this is?
- Disagree/Difficult to say -> (AV) OK, in the past 5 years, it has become easier to meet the demands of your customers seeking to buy lamprey -> Agree -> (AW) why do you think this is?

(AX) There should/should not be a ban on lamprey fishing in the UK if they are considered to be threatened

APPENDIX 3: WHOLESALE SUPPLIER MANAGER QUESTIONNAIRE

1) How long have you been supplying lamprey for?
2) Which species of lamprey do you sell?
3) Are they sold for:
   a. Angling bait?
   b. Any other purposes? What proportion are sold for this purpose?
4) Are they sold to:
   A. How many tackle shops do you sell to?
   B. Other suppliers – How many?
   C. Directly to fishermen – What proportion are sold directly to fishermen, shops and suppliers?
5) Do you export any of the lamprey that you sell?
   a. Yes -> What proportions are sold in the UK and abroad?
   b. Yes -> Which countries do you export to?
6) How many lamprey did you sell last year, from summer 2011 to summer 2012?
7) Did you sell more or less in previous years?
8) Do you believe lamprey have become a more or less popular bait in recent years?
9) How is it that you obtain your lamprey? For example do you obtain them directly from a fisherman or do you catch the lamprey yourselves?
10) Which countries do the lamprey that you sell originate from?
    a. Numerous -> What proportions of lamprey are obtained from each country?
11) Can you tell me which river systems the lamprey that you sell originate from
    a. In the UK?
    b. Abroad?

Now the final questions are again completely voluntary, and relate to your views on the lamprey that you sell and the importance of lamprey sales in your company.

12) Hypothetically, if lamprey were no longer available to sell, would this have

a. No impact
b. A slight impact
c. A moderate impact
d. A strong impact

13) Firstly, for the lamprey that your company sells do you believe they have come from a

a. Non threatened population
b. Threatened population or
c. Unsure

14) Hypothetically, if your company was reliably informed that the lamprey that you sell are from a threatened population would your company

   a. Choose to sell more lamprey
   b. Continue to sell the same amount of lamprey
   c. Choose to sell less lamprey
   d. Stop selling lamprey altogether

15) Do you agree, disagree or find it difficult to say that If lamprey were unavailable to sell, there are other available products which could sufficiently replace them. Agree -> (AO) could you please specify which products

16) Do you agree, disagree or find it difficult to say that there should be a ban on lamprey fishing in the UK if they are considered to be threatened.

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