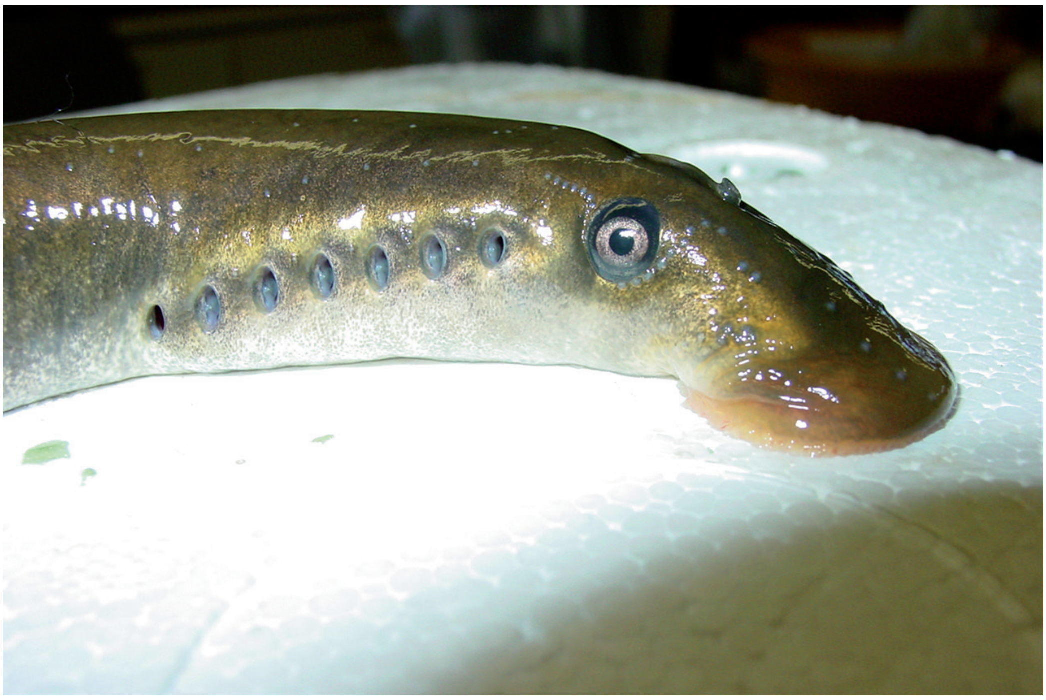
JYVÄSKYLÄ STUDIES IN BIOLOGICAL AND ENVIRONMENTAL SCIENCE
301

**Kimmo Aronsuu**

# Lotic Life Stages of the European River Lamprey (*Lampetra fluviatilis*): Anthropogenic Detriment and Rehabilitation



JYVÄSKYLÄN YLIOPISTO

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UNIVERSITY OF JYVÄSKYLÄ

JYVÄSKYLÄ 2015

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# ABSTRACT

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The goal of this study was to increase knowledge about the migratory behaviour of adult river lampreys and the habitat of riverine life stages of river lamprey. Furthermore, the detrimental effects of various anthropogenic activities on lamprey populations and the efficacy of different rehabilitation measures were evaluated over three decades of monitoring the development of river lamprey populations in two intensively regulated northern rivers. River discharge, illumination by the moon, wind conditions and water temperature all affected the migratory activity of upstream migrating adults, while artificial lighting may create illumination barriers for migration. A natural-like fish ramp was observed to enhance passage over low-head barriers. During the winter holding period, adult lampreys preferred glides, runs and the lowermost parts of riffles with substratum dominated by large boulders (> 256 mm). River lampreys may use a wide variety of gravel sizes for spawning, and flow conditions had an effect on spawning substratum selection. When lamprey larvae reached a total length (TL) of 8 mm they started to select substrata which enabled them to construct a burrow, while the smaller larvae favoured substrata containing holes. Natural gravel with fine material was frequently selected as a burrowing substratum by sub-yearling lampreys with TL > 8 mm. The larvae older than one year rejected clay bottoms. The main results from the monitored field populations suggested that river regulation measures drastically reduced river lamprey habitats and populations. Translocations of adult lampreys did not necessarily compensate for the negative effects of obstructed migration, but insufficient number of translocated adults, habitat degradation or increased predation may lead to reduced population size. Stocking with sub-yearling larvae was an appropriate method for reintroduction of a lamprey population. River restoration may enhance the recovery of river the lamprey population in a short-term regulated river.

Keywords: habitat; *Lampetra fluviatilis*; lamprey; migration; rehabilitation; river regulation.

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# LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following original papers, which will be referred to in the text by their Roman numerals I–V.

The original ideas for article I were formulated by KA, JT and EO. Data were collected by KW, TJ, KA, RV, EO and various field workers and analysed by KA and TM. KA wrote the first draft of the manuscript, which was then finalised by KA, TM, TJ and RV. For II, the original idea was by KA. JT conducted the experiments with the help of KA and K. Wennman. Data were analysed by KA, who also wrote the first draft of the manuscript, which was then completed together. The original idea for III was by KA. PV conducted the experiments with KA. KA analysed the data and wrote the first version of the manuscript, which was then completed together. The original idea for IV was by EO who also collected the data with the field workers. KA wrote the first version of the manuscript, which was then finalised together. For V, the original ideas were by KA, EO, JP and RV. The data were collected jointly, assisted by various field workers. Data analysis was also joint. KA and TM reanalysed part of the data. KA wrote the first version of the manuscript, which was then finalised by KA, TM, RV and JT.

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

II Aronsuu K. & Tertsunen J. 2015. Selection of spawning substratum by European river lampreys (*Lampetra fluviatilis*) in experimental tanks. *Marine and Freshwater Behaviour and Physiology* 48: 41–50.

III Aronsuu K. & Virkkala P. 2014. Substrate selection by subyearling European river lampreys (*Lampetra fluviatilis*) and older larvae (*Lampetra* spp). *Ecology of Freshwater Fish* 23: 644–655.

IV Ojutkangas E., Aronen K. & Laukkanen E. 1995. Distribution and abundance of river lamprey (*Lampetra fluviatilis*) ammocoetes in the regulated River Perhonjoki. *Regulated Rivers: Research & Management* 10: 239–245.

V Aronsuu K., Vikström R., Marjomäki T.J., Wennman K., Pakkala J., Mäenpää E., Tuohino J., Sarell J. & Ojutkangas E. 2015. Rehabilitation of two northern river lamprey (*Lampetra fluviatilis*) populations impacted by various anthropogenic pressures – lessons learnt in the past three decades. Manuscript.

# 1 INTRODUCTION

## 1.1 River lamprey populations and negative human impact on them

The European river lamprey (*Lampetra fluviatilis*) has been caught and used for food in Europe for centuries and has had both cultural and economical value (Sjöberg 1980, Tuunainen *et al.* 1980, Hardisty 1986, Sjöberg 2011). In the twentieth century, lamprey populations and fishing have decreased considerably in many European countries (Hardisty 1986). Yet, river lamprey fisheries still exist in many rivers flowing into the Baltic Sea in Poland, the Baltic States, Sweden and Finland (Sjöberg 2011). Furthermore, in the British Isles and the Netherlands lampreys are exploited for angling baits (Foulds and Lucas 2014). In Finland, river lamprey fisheries are concentrated in the rivers entering the Bothnian Bay. The mean annual catch in Finnish rivers has decreased considerably since the 1970s, when it was about 2.0–2.5 million individuals (Tuunainen *et al.* 1980); in the 2000s, the average annual catch was less than 1 million individuals (Hiltunen *et al.* 2013). Recently, Finnish fisheries associations along the coast of the Bothnian Bay have expressed their concern about decreasing lamprey populations and have requested the development of rehabilitation measures and actions to save the tradition of lamprey fishing (Hiltunen *et al.* 2013).

The decline of river lamprey populations, like that of populations of many other species of lampreys in the northern hemisphere, has been associated with anthropogenic activities (e.g. Tuunainen *et al.* 1980, Valtonen 1980, Renaud 1997, Maitland 2003, Mateus *et al.* 2012) (Fig. 1). Construction of large dams, weirs and other migration barriers prevent access to suitable spawning sites and is therefore considered to be among the main threats to river lamprey populations (e.g. Masters *et al.* 2006, Lucas *et al.* 2009, Mateus *et al.* 2012). Other river regulation measures such as hydropeaking (short-term flow regulation), dredging and embankment have also been associated with lamprey population decline, mainly because they decrease the quantity and quality of suitable habitat for lampreys in their different life stages (Tuunainen *et al.* 1980, Valtonen 1980, Renaud 1997, Maitland 2003). In addition, pollution and poor water quality have occasionally been linked to population declines (Tuunainen *et al.* 1980, Myllynen *et al.* 1997, Mäenpää *et al.* 2001). Fishing mortality has exceeded 50 % in some rivers entering the Bothnian Bay (Valtonen 1980, Sjöberg 2011), but in most of the rivers it is unknown, and the overall impact of exploitation on river lamprey populations is poorly understood (Sjöberg 2011, Foulds and Lucas 2014).

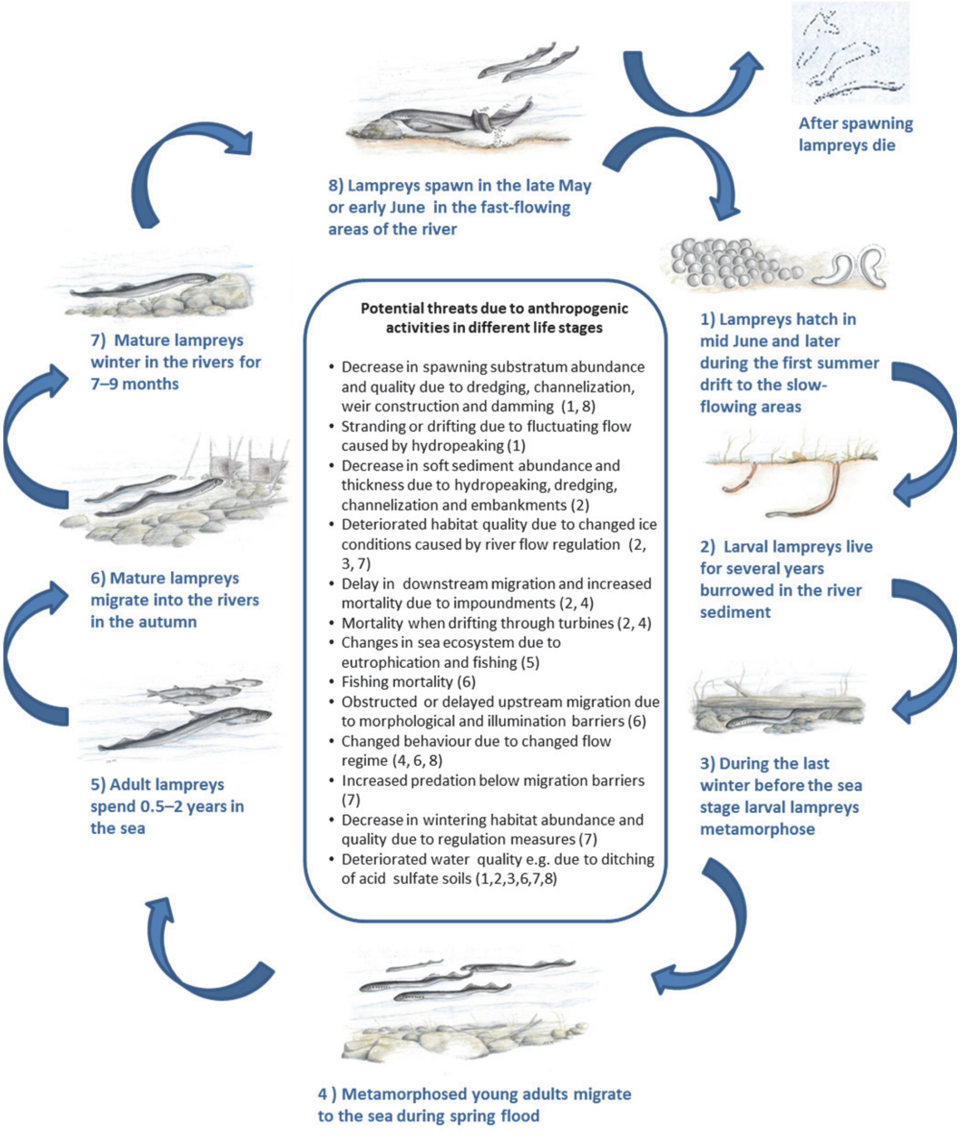
## 1.2 The life cycle of the river lamprey in boreal regions

Adult river lampreys migrate into the rivers entering the Bothnian Bay mainly in the autumn (Wikgren 1954, Sjöberg 1980) (Fig. 1 and 2). The number of enterers varies considerably from night to night even during the peak migration season. This variation has been associated with lunar phase (Tesch 1967, Asplund and Södergren 1975, Abou-Seedo and Potter 1979) and river flow (Asplund and Södergren 1975, Masters *et al.* 2006). Sea water level (Sjöberg 1980), wind conditions (Applegate 1950, Malmqvist 1980a) and photoperiod (Asplund and Södergren 1975) have also been associated with the timing of upstream migration of river lampreys. After entering the river, *L. fluviatilis* has been observed to migrate up to 102 km (Lucas *et al.* 2009). Increase in water flow has been shown to be an important factor increasing lamprey migratory activity in the river (Masters *et al.* 2006).

In boreal rivers, adult river lampreys typically stay in the river from 7 to 9 months before spawning. They have been shown to be in an energy saving hypometabolic state during the winter months (Gamber and Savina 2000), but otherwise knowledge about the wintering stage is sparse.

In the rivers entering the Bothnian Bay, river lampreys spawn in late May or early June (Sjöberg 1977, Tuunainen *et al.* 1980). River lampreys have been observed to spawn in swift-running water with substrata consisting of gravel that is often mixed with sand and cobbles (Jang and Lucas 2005, Nika and Virbickas 2010), but in aquaria they have also used sand as a spawning substratum (Hagelin and Steffner 1958). River lampreys excavate distinct depressions (Nika and Virbickas 2010) or complex areas of excavation (Jang and Lucas 2005) for courtship and spawning, and communal spawning is typical (Jang and Lucas 2005). The average fecundity of river lampreys in Finnish rivers entering the Bothnian Bay is 17 000 eggs (Törmälä 1981). The sticky eggs laid in the nest adhere to sand and some proportion infiltrates to the interstices of the nest (Hardisty 2006), but a marked proportion may be washed out of nests and deposited in areas downstream from the nest (Silva *et al.* 2014). Eggs hatch after 11–12 days at a temperature of 12–15 °C (Hardisty 2006). Adult lampreys die after spawning (Hagelin and Steffner 1958).

After hatching, lampreys undergo a free embryonic phase and are termed prolarvae or proammocoetes. During this stage, lasting a few weeks, first the ability to swim and then the ability to burrow develop (Piavis 1971). After the yolk sac is depleted and the formation of the digestive tract is completed, they are termed larvae or ammocoetes and they are ready to use external food. In this thesis, the exact time when the lampreys achieve the larval stage was not studied. Therefore the lampreys in both prolarval and larval stages will be referred to as larvae throughout the thesis.



8) Lampreys spawn in the late May or early June in the fast-flowing areas of the river

After spawning lampreys die

1) Lampreys hatch in mid June and later during the first summer drift to the slow-flowing areas

2) Larval lampreys live for several years burrowed in the river sediment

3) During the last winter before the sea stage larval lampreys metamorphose

4 ) Metamorphosed young adults migrate to the sea during spring flood

5) Adult lampreys spend 0.5–2 years in the sea

6) Mature lampreys migrate into the rivers in the autumn

7) Mature lampreys winter in the rivers for 7–9 months

**Potential threats due to anthropogenic activities in different life stages**

- Decrease in spawning substratum abundance and quality due to dredging, channelization, weir construction and damming (1, 8)
- Stranding or drifting due to fluctuating flow caused by hydropeaking (1)
- Decrease in soft sediment abundance and thickness due to hydropeaking, dredging, channelization and embankments (2)
- Deteriorated habitat quality due to changed ice conditions caused by river flow regulation (2, 3, 7)
- Delay in downstream migration and increased mortality due to impoundments (2, 4)
- Mortality when drifting through turbines (2, 4)
- Changes in sea ecosystem due to eutrophication and fishing (5)
- Fishing mortality (6)
- Obstructed or delayed upstream migration due to morphological and illumination barriers (6)
- Changed behaviour due to changed flow regime (4, 6, 8)
- Increased predation below migration barriers (7)
- Decrease in wintering habitat abundance and quality due to regulation measures (7)
- Deteriorated water quality e.g. due to ditching of acid sulfate soils (1,2,3,6,7,8)

FIGURE 1 Life cycle of the river lamprey in boreal regions and potential threats due to anthropogenic activities in different life stages. Numbers in parenthesis indicate different life stages. The habitats in the drawings reflect the view of the artist Salla Korkiakangas and do not necessarily match precisely with natural habitats.

During the first summer, larvae disperse downstream to slow-flowing river sections where they burrow in suitable substratum (Potter 1980, but see Silva *et al.* 2014). The larvae burrow by inserting their head into the substratum with vigorous contractions of the tail (Hardisty and Potter 1971). By secreting mucus from the endostyle line, they form a fragile tube at the entrance of the burrow (Sterba 1962). The substratum protects larvae against predators (Smith *et al.* 2012), and it must be suitable for burrow construction and water exchange. While in the burrow, larvae are dependent on unidirectional flow of water through their branchial chamber for the provision of food and exchange of respiratory gases and metabolic wastes (Hardisty and Potter 1971). Many studies have shown that their preferred substratum type changes (Beamish and Jebbink 1994, Almeida and Quintella 2002, Sugiyama and Goto 2002, Smith *et al.* 2011) and burrowing depth increases (Hardisty and Potter 1971) as larvae grow, with larger larvae preferring coarser and deeper soft substratum than smaller larvae (Almeida and Quintella 2002, Sugiyama and Goto 2002). Lamprey larvae have been shown to reject clay bottoms and coarse inorganic substrata (Lee 1989, Smith *et al.* 2011). During their 3 to 6 year larval stage, the larvae move gradually downstream while their total length increases from less than 10 mm to 90–150 mm (Potter 1980).

After the larval stage, lampreys metamorphose to young adults (transformers). Transformers in northern rivers have been suggested to emigrate during a relatively short period in spring (Fogelin 1972, Sjöberg 1980). The sea phase is believed to last typically from one to two years (Maitland 2003), but it may also last only one summer (own unpublished data). After the sea phase, mature lampreys migrate to rivers for spawning.

## 1.3 Conservation and rehabilitation of river lamprey populations

In Europe, the river lamprey is categorised as a “least concern” species (Freyhof and Brooks 2011). However, its current Red List category varies a lot among European countries and it is widely considered threatened (see Mateus *et al.* 2012). In the 2010 Red List of Finnish Species (Urho *et al.* 2010), it was noted that catches of river lamprey have recently decreased and the numbers of larvae have fluctuated, but it was still retained in the category “near threatened”.

The river lamprey is listed under Annex II of the European Commission Habitats Directive (92/43/EEC), which stipulates that member states must maintain or restore habitats and species to a condition that ensures their favourable conservation status in the community. Finnish and Swedish river lamprey populations are excluded from the Annex II, but not from the Annex V, which lists animal and plant species of community interest, for which capture and exploitation may be controlled by management measures. The river lamprey also receives conservation protection through the Bern Convention (82/72/EEC), which places a particular importance on protection of endangered natural habitats and endangered vulnerable species.

Understanding the basic life history characteristics, including migratory behaviour and habitat requirements of different life stages, is one of the most important preconditions for effective conservation and rehabilitation of the river lamprey. Information regarding its life history has increased recently (e.g. Fine *et al.* 2004, Jang and Lucas 2005, Gaudron and Lucas 2006, Masters *et al.* 2006, Goodwin *et al.* 2008, Taverny *et al.* 2012, Nika and Virbickas 2010, Silva *et al.* 2014), and numerous studies have been conducted of the passage of adult lampreys over anthropogenic barriers (e.g. Lucas *et al.* 2009, Kemp *et al.* 2011, Russon *et al.* 2011, Foulds and Lucas 2013). However, understanding of successful rehabilitation methods for river lamprey populations in modified rivers is still limited and there are still uncertainties regarding the basic life history of the river lamprey as well as the impacts of different anthropogenic pressures on its different life stages. Furthermore, in boreal regions the marked seasonal conditions (e.g. freezing water temperatures with various ice phenomena) may intensify the effects of anthropogenic pressures and even lead to adaptive changes in behaviour and habitat use (see Huusko *et al.* 2013). Therefore, drawing inferences from studies of more southern river lamprey populations must be done with caution. For the above-mentioned reasons, decisions on lamprey conservation and mitigation measures have to be made in the face of considerable uncertainty about their effectiveness.

## 1.4 Objectives of the study

The goal of this study was to increase knowledge about the migratory behaviour of adult river lampreys and their habitat selection in different riverine life stages (I, II, III). Furthermore, the detrimental effects of various anthropogenic activities on lamprey habitats and populations and the efficacy of different rehabilitation measures were evaluated over three decades of monitoring the development of lamprey populations in two intensively regulated northern rivers (IV, V).

The increased information on the lotic stages of river lamprey helps to determine the factors that most likely threaten the viability of the populations and enhances the efficacy of actions aimed at conservation and rehabilitation of the populations. The enhanced knowledge can be utilized in mitigation operations such as river restoration, translocation of adult lampreys over migration barriers, outplantation of sub-yearling larvae and improvement of passage and water flow regulation.

# 2 MATERIAL AND METHODS

## 2.1 The study rivers and their regulation and rehabilitation measures

Three field studies (I, IV, V) were conducted in the Rivers Kalajoki and Perhonjoki, which flow into the Bothnian Bay, the northernmost part of the Baltic Sea (Fig. 2). Their water quality is typical of rivers entering the east coast of the Bothnian Bay, being humic and, especially during high flows, having high content of suspended solids. The pH is occasionally low and simultaneously the concentrations of metals (e.g. Al, Fe, Cd) are high.

The total length of the River Kalajoki is 100 km, the total drop 100 m and the mean discharge 29 $m^3 s^{-1}$. Its main tributary, the River Vääräjoki flows into the main channel at the river kilometre (rkm) 9. Above rkm 45, the River Kalajoki is heavily modified. The lowermost 45 km is less modified, but has been partly embanked and dredged and the flow is short-term regulated (Fig. 6 in V). The methods aiming at rehabilitation of the lamprey population include construction of fish-ways at the weir (rkm 22), restoration of all the fast-flowing river sections below rkm 43 and mitigation of hydropeaking (Appendix 2 in V).

The length of the River Perhonjoki is 140 km, the overall drop 180 m and the mean discharge 21 $m^3 s^{-1}$. Many large-scale water regulation measures have been carried out there and, additionally, the flow of the lowermost 30 km leg is short-term regulated (Appendix 1 in V). In the 1990s and 2000s, the river was restored and a fish-way complex was constructed to improve the lamprey population. Furthermore, in the late 2000s hydropeaking was mitigated. Rehabilitation of the river lamprey population has also been attempted by releasing adult lampreys and sub-yearling larvae above migration barriers (Appendix 1 in V).

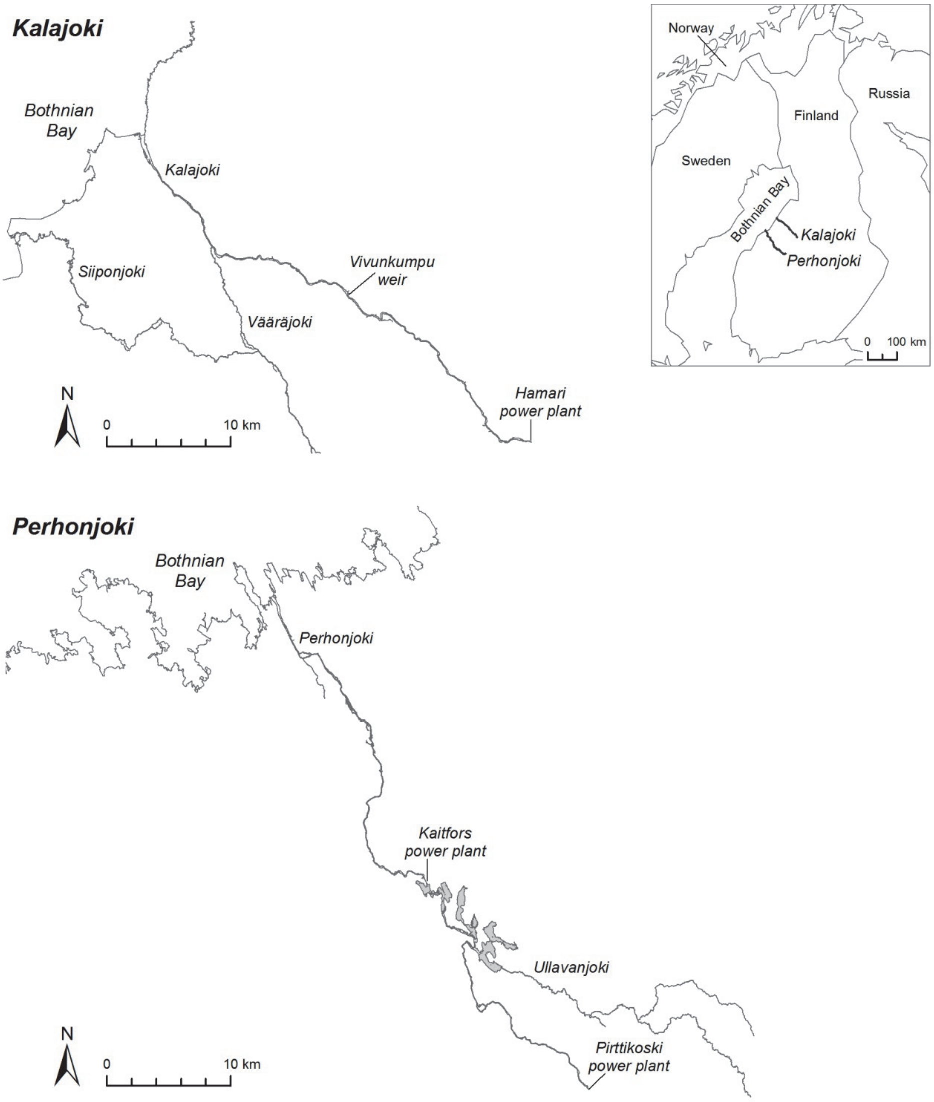


FIGURE 2 Map of study area showing the locations of the Rivers Kalajoki and Perhonjoki and their main tributaries in the lower end of the rivers. The locations of three hydroelectric power plants and one weir are also shown.

## 2.2 Migratory behaviour and holding habitats of adult lampreys

### 2.2.1 Environmental factors affecting the timing of upstream migration (I)

The effect of several environmental factors on between-night variability in migration activity during the most active migration period was analysed using a multivariable linear regression model. The logarithm of daily catch per unit effort (CPUE) from commercial basket trap fishing in the lowest rapid of the River Perhonjoki was used as a dependent variable indicating migratory activity.

To assess the role of discharge and river temperature as cues affecting the relative number of lampreys entering estuaries in early season, fyke net CPUE data from the Rivers Perhonjoki and Kalajoki were utilized to create a dependent variable. The ratio between the early season CPUE and the whole season CPUE was used as an index of migratory activity in the early season. Correlation, partial correlation and regression analysis were applied to study the association between the discharge- and temperature-based variables and migration activity index.

### 2.2.2 Migratory behaviour and holding habitats in the river (I)

To study the migratory behaviour and holding habitats of adult lampreys in the Rivers Perhonjoki and Kalajoki, movements and holding sites of 60 radio-tagged lampreys were tracked. They were released at two locations in the River Perhonjoki and at three locations in the River Kalajoki on various release occasions during the migration season.

The mesohabitat (fast- or slow-flowing river section) of the final (temperature < 1 °C) holding sites of 39 lampreys was determined and regarded as a selected wintering mesohabitat. The total length of the river sections in both the above-mentioned categories within the migration route of each lamprey was measured, and used as a measure of availability of that mesohabitat. Manly’s selection ratio ($w$) with Bonferroni 95 % confidence intervals for both resource categories was calculated (Manly *et al.* 2002).

The locations of wintering sites of 12 lampreys were determined with an accuracy of 0.5 $m^2$. At these locations, the dominant substratum size and the mesohabitat type were determined along with water depth, distance to the nearest river bank and current speed. The availability of different habitat resources was estimated for 10 lampreys. Habitat characterisation was made along transects perpendicular to stream flow. Each environmental factor was first divided into 3–5 resource categories (see Manly *et al.* 2002). Availability of each category for each lamprey was assigned based on the measurements from all transects the lamprey had crossed before selecting the final holding site. The selection ratios and confidence intervals for each resource category were then estimated.

### 2.2.3 Efficacy of fish-ways (I, V)

The radio-tagged lampreys released at the uppermost release location in the River Kalajoki (see 2.2.2) were used to estimate success of passage through the fish passages in the Vivunkumpu weir (Fig. 2).

Migratory behaviour in the Kaitfors fish-way complex (4 fish ramps, restored flood channel and a fish-way with natural-like and vertical slot fish-way sections) was studied by releasing 9 radio-tagged lampreys in the lower end of the flood channel and by loacating their positions with a receiver twice per week. Furthermore, a continuous monitoring telemetry receiver was attached at the uppermost end of the fish-way complex. The passage success was also assessed by tagging 200 lampreys with anchor tags and catching all the lampreys that had passed the fish-way. One hundred anchor-tagged lampreys were released to the lower end of the flood channel 2.5 km downstream from the regulation dam and 100 lampreys just below the 320 m long fish-way.

## 2.3 Spawning substratum selection (II)

Four gravel types with different particle size compositions (2–8 mm, 4–20 mm, 2–40 mm and 8–40 mm) mixed with 15 % of fine material were used in a laboratory arena experiment to test the selection of spawning substratum. Two 3.8 $m^2$ tanks, with low current speed (LCS) and high current speed (HCS), were used in the experiment. The bottom of each tank was divided into 4 equal-sized sectors, to which a 15 cm thick layer of gravel was added. The current speed and direction in the tanks were monitored. The average current speeds in the LCS tank 10 cm below the surface were 26 cm $s^{-1}$ next to the wall, 21 cm $s^{-1}$ 10 cm from the wall and 9 cm $s^{-1}$ 20 cm from the wall. In the HCS tank the values were 30, 25 and 21 cm $s^{-1}$, respectively.

When lampreys were ready to spawn, a female and a male lamprey were released simultaneously into the experimental tank and their behaviour was monitored continuously. Selection of the spawning substratum was considered to have occurred when the male lamprey had constructed a nest and the pair had started to copulate in it or the male had spent over an hour in the immediate proximity of the constructed nest. After trials, the lampreys were weighed. The current speed for every nest location was estimated using the current speed grid.

Differences in substratum selection ratios ($w$) were analysed using $X^2$ tests and pairwise comparisons. Multinomial logistic regression was used to study the effect of the mass of lamprey on substratum selection and covariance analysis was applied to assess the importance of different factors on current speed selection.

In a field survey, an attempt was made to locate natural nests in the River Perhonjoki. In the 4 nests found, the water depth and current speed in multiple locations were measured and the substratum composition determined.

## 2.4 Substratum selection by larval lampreys (III)

Substratum selection by sub-yearling lampreys was studied using 4 gravel (0–11 mm, 1–11 mm, 2–11 mm and 4–11 mm) and 4 soft (very fine sand, organic very fine sand, fine sand, and coarse sand) sediments. The bottom of each round test aquarium was divided into 4 equal sized sectors. Substratum selection was studied in three series of experiments. In series A the selection between 4 soft sediments and in series B the selection between 4 gravel types with different grain size were studied. In series C the selection between gravel sediment and soft sediment was compared. Depending on their average TL, 60–100 larvae were released into each aquarium, and allowed to select the substratum for 40 h. The first experiments were started 8 days after hatching and continued for 10 weeks.

In the first experiment, the substratum selection by 3 size groups of larvae older than one year was studied. The sediments used were 15 cm of find sand, 4 cm of find sand on top of 11 cm of clay, coarse particle organic matter and clay. The bottom of each of the 3 test aquaria was divided into 4 equally sized sectors. In separate aquaria, 50, 30 and 20 individuals of the total length classes 23–55 mm, 70–98 mm and 110–146 mm, respectively, were allowed to select burrowing substratum for 64 h. The trial was replicated. In the second experiment, the selection between 4 very find sand sediment depths (1, 3, 6 and 10 cm) by larvae with TL of 80–110 mm was studied. The experiment was conducted as described above for different size groups.

## 2.5 Monitoring of lamprey populations and their habitats in the field

### 2.5.1 Larval densities (IV, V)

To evaluate the impact of regulation and rehabilitation measures on larval populations, larval densities were monitored by collecting sediment samples and counting larvae. In the River Kalajoki, sampling was carried out 6 times in 1984–1995 with the protocol of taking 20 samples per site from a depth of 10–100 cm. From 52 to 73 sites between river kilometre (rkm) 1 and 45 were sampled in different years. In 1999–2010, a nested sampling protocol was used: 4 slow-flowing river sections in the main channel and one section in the River Vääräjoki tributary were monitored. On each section, 10 sites were selected and 14 samples from a depth zone 10–70 cm were taken from each site.

Sampling in the River Perhonjoki in 1982, 1985, 1993 1999 and 2004 was carried out as in the River Kalajoki in 1984–1995, except that in 1982 and 1985 some samples were taken with an Ekman–Birge grab. The number of sampling sites between rkm 0 and 60.5 was 191. In 2007 and 2010, a nested sampling was used similar to that in the River Kalajoki: In the main channel, 7 slow-flowing sections were selected for monitoring and one study section was situated in the River Ullavanjoki tributary.

The success of rehabilitation measures was also assessed by monitoring the abundance of sub-yearling larvae below 3 restored riffles in the River Kalajoki. In addition, 3 sites from other rivers were selected as control sites. Monitoring was performed in early August 50–300 m below the riffles. From each site in the main channel, 250 samples (area ≈ 350 $cm^2$) were taken from a soft-bottomed area with water depth less than 50 cm. From the control sites, 50 samples were taken per site. Each sample was sifted and the number of sub-yearling larvae was counted. The monitoring was performed annually during 2000–2010.

### 2.5.2 The number of downstream migrating lampreys (V)

To evaluate the success of the rehabilitation measures in the River Ullavanjoki and in the River Perhonjoki above the Kaitfors hydroelectric power plant (HPP), the number of migrating transformers was monitored using 6–10 drift nets in the spring. Nets were placed in the river in the evening. These were emptied the next morning and the number of transformers was counted. The study was carried out during 2002–2005 in the River Ullavanjoki and during 2000–2010 in the River Perhonjoki. Netting in the River Ullavanjoki could be commenced during the migration season once drifting ice floats had disappeared and was halted when discharge had decreased and no, or only occasional, transformers were caught. In the outlet channel of the HPP, trapping was started already before the migration season. The average fishing mortality of the drift nets was estimated by mark-recapture and the number of migrating transformers with the Petersen method.

When estimating the total number of transformers migrating in a particular night, the trapping efficiency was assumed to be directly proportional to the number of traps and inversely proportional to discharge. When estimating the total number of transformers migrating through the non-monitored flood channel, it was assumed that the number of migrating lampreys was proportional to the ratio of discharges of this and the outlet channel.

### 2.5.3 Quantity and quality of larval habitats (IV, V)

In 1982, 1985 and 1993, the total larval production area in the different sections of the River Perhonjoki below rkm 60.5 was roughly estimated using cross-sections and field observations (IV).

The quantity and quality of habitats were studied more accurately in 1995–1998 (V). In each slow-flowing river section, habitat characterisation was made along study lines perpendicular to stream flow with 100 m increments. In the River Kalajoki, characterisation was carried out at 1–2 m horizontal intervals down to the point where water depth was 1 m. Based on type and depth of the substratum, the sample points were categorized as unsuitable, weak, moderate or good for larval lampreys. Furthermore, a rough larval habitat suitability index for each slow-flowing section was calculated. In the River Perhonjoki, the sample points close to river bank were with shorter intervals than in the River Kalajoki. Otherwise methods were similar to those used in the River Kalajoki.

### 2.5.4 The number of upstream migrating adults, fishing mortality and escapement (V)

The number of adult lampreys entering the rivers and their proportional fishing mortality during the catching season was monitored in the Rivers Perhonjoki and Kalajoki since the early 1980s using the catch records of local fishermen and the Petersen mark-recapture method. The majority of lamprey fishermen recorded their daily catch and effort and the number of tagged lampreys in the catch. The yearly catch of other fishermen was estimated on the basis of postal surveys or personal interviews. Lampreys were tagged with group-coded anchor tags and were released downstream from the first traps. The yearly number of release groups of about 500 tagged lampreys in each was from 2 to 5. The escapement (ie. the number of lampreys escaping fishing and continuing their migration towards the wintering and spawning sites) was estimated simply by subtracting the seasonal total catch estimate from the estimate of the number entering the river. The reliability (= accuracy and precision) of the estimates was also qualitatively assessed.

# 3 RESULTS AND DISCUSSION

## 3.1 Upstream migration of adults

The timing of migration into the rivers depends on the physiological state of the animal, which is affected by hormone balance and external triggering factors, such as water flow, temperature and light conditions (Northcote 1984). Environmental factors may also guide the direction of migration and affect migratory activity. The results of the regression analysis indicated that discharge, moonlight and wind speed coupled with wind direction controlled the migration of river lampreys (I). The results also suggested that river water temperature had an effect on migratory activity.

The river discharge in early season into the estuaries of the Kalajoki and Perhonjoki, and during the peak migration season into the lowermost part of the River Perhonjoki, was an important predictor of the dynamics of the number of migrating river lampreys (I). Consistent with the results of earlier studies (e.g. Asplund and Södergren 1975, Masters *et al.* 2006), an increase in discharge stimulated river lamprey migration.

Pheromones released by larval lampreys are an important migratory cue for adult sea lampreys (*Petromyzon marinus*) entering the river (e.g. Wagner *et al.* 2009, Vrieze *et al.* 2010, 2011). As larval river lampreys also release common migratory pheromones (Fine *et al.* 2004) and adult river lampreys are sensitive to them (Gaudron and Lucas 2006), it is probable that pheromones spread by river water are also a cue for river lampreys seeking a spawning river and may partly explain the positive association between discharge and number of river lampreys entering estuaries. On the other hand, in high flows the concentration of larval pheromones is diluted and other factors like fresh water or environmental odours may also direct migration from sea into the rivers. Given that home river fidelity of lampreys is suggested to be weak (Tuunainen *et al.* 1980, Bergstedt and Seeley 1995), the extent of the plume, in addition to its pheromone concentration, is potentially a key factor controlling the number of lampreys entering different rivers during the migration season (see also Keefer *et al.* 2009, Vrieze *et al.* 2010, 2011).

Many previous studies have revealed that migratory activity of river lampreys which have already entered a river is positively associated with river flow (Masters *et al.* 2006, Lucas *et al.* 2009, Foulds and Lucas 2013). Thus, once lampreys have entered a river or are close to the river mouth, non-odour driven rheotaxis also promotes upstream migration.

As discharge is an important factor controlling migration of lampreys, the patterns of regulation of river flow may considerably affect migration of lampreys. It is typical of flow-regulated rivers that reservoirs or regulated lakes are filled during autumn. This reduces discharge during the migration season and may consequently decrease the number of lampreys entering regulated rivers compared to unregulated rivers. Short-term regulation may also reduce the number of migrating lampreys and their migration distances if discharge is reduced during the night, when lampreys are migrating (see also Andrade *et al.* 2007). Flow-regulation of severely modified rivers may even be beneficial for lampreys if it makes them prefer the unregulated rivers where wintering, spawning and larval habitats are more suitable. Unfortunately, human-induced changes in flow regime may also attract lampreys to migrate into regulated rivers (Birzaks and Abersons 2011).

The regression analysis indicated that the migration activity was negatively associated with the night-time light intensity of the moon (I). These results support the observations of the local fishermen and earlier studies that low migratory activity occurs at or near the time of full moon (Asplund and Södergren 1975), and that high river lamprey catches are obtained during moonless, dark nights (e.g. Abakumov 1956, Asplund and Södergren 1975). Intense migration of *Geotria australis* has also been associated with extensive cloud cover or the dark phase of the moon (Potter *et al.* 1983). In most studies the effect of the lunar cycle has been linked to illumination (e.g. Abou-Seedo and Potter 1979, Binder *et al.* 2010) as the anti-predatory behaviour of light avoidance is an obvious explanation for nocturnal animals (see Keefer *et al.* 2013a). According to regression analysis, cloud cover was positively associated with activity at or near the period of full moon (I) which indicated that the moon affects the migratory activity of river lampreys primarily by regulating the night-time light level. It is also possible that increased migratory activity during high flows is in part associated with illumination, as increased water depth and turbidity reduce light intensity on the river bed, where adult lampreys tend to swim during the spawning migration (Lucas *et al.* 2009, Kemp *et al.* 2011).

Interestingly, most radio-tagged lampreys which met an illuminated bridge on their migration route halted there (I). Typically, they did not continue migration, and if they did migration was delayed. As moonlight with low illumination intensity depresses lamprey migratory activity, it is understandable that much more intensive illumination of bridges will markedly obstruct upstream movements of lampreys (I). Cumulative effects of migration delays due to illuminated bridges may have as severe consequences on lamprey populations as low-head morphological barriers (see Jackson and Moser 2012, Foulds and Lucas 2013).To my knowledge, there have been no other studies revealing that light pollution may affect migratory behaviour of river lampreys. However, fishermen have observed that brightly illuminated bridges may delay migration of river lampreys (Tuunainen *et al.* 1980), and some other aquatic migratory animals have been found sensitive to artificial illumination (e.g. Moser and Russon 2009, Riley *et al.* 2012). However, as the sites near the bridges offered good holding habitats, it cannot be completely ruled out the possibility that halting by the bridges was, at least to some extent, normal behaviour rather than light avoidance. Therefore, more studies on the effect of artificial illumination on migratory behaviour are needed. If further studies support the observation on light avoidance, some solutions to bridge lighting will be required, for example covers to prevent the river being illuminated or switching off the lights for some period if it is safe for traffic.

Actual river water temperature did not significantly affect migratory activity in the early or peak migration season (I). This result was consistent with earlier observations that discharge is more important than river temperature in controlling migratory activity of river lampreys (e.g. Abou-Seedo and Potter 1979, Masters *et al.* 2006, Foulds and Lucas 2013). This study demonstrated that significant number of lampreys may already enter the estuary at the beginning of the catching season after mid-August, despite the high river water temperature (> 18 °C), provided discharge is high (I). Furthermore, according to the regression analysis river temperatures between 12 and 16 °C did not significantly depress migratory activity. Radio-tagged lampreys released at a temperature of 16.5 °C showed low migratory activity, which may be linked to too high river water temperature and/or to the fact that river temperature did not decrease during the two weeks after release (I). Abou-Seedo and Potter (1979) reported that the first conspicuous influx of river lampreys into an estuary generally occurred when the temperature was 12–16 °C, and Lucas *et al.* (2009) estimated that the upper temperature limit at which migration into rivers normally occurs is probably 8–12 °C. This study (I) thus suggested that the upper temperature limit for active migration may be higher than reported earlier. It is possible, however, that northern populations have adapted to the local environment and start their migration at higher temperatures due to the relatively short migratory period before the river water temperature becomes too cold. According to the results, it also seems possible that river lampreys like sea lampreys (Applegate 1950) aggregate in the estuary in the early season if the river discharge is high, but start intensive migration into the river only when the temperature of the river is low enough.

Although actual river water temperature did not affect migratory activity in the peak migration season, speed (in peak migration season) and magnitude (in early migration season) of cooling of river water were positively correlated with migratory activity (I). Earlier studies did not include the effect of temperature change among the factors which could affect the migratory activity of river lampreys, but the migratory activity of sea lampreys has been shown to increase with increase in temperature and decline with its decrease (Binder *et al.*

2010). It seems that fast and/or large changes in water temperature may act as a trigger for lampreys to start their migration.

In the telemetry experiments, upriver migration ceased after the temperature had dropped near to or below 1 °C (I). If lampreys moved at low temperatures, they typically only migrated to the lower end of the nearest fast-flowing section. The depressed activity is likely connected to the reduced swimming endurance at low temperatures (e.g. Beamish 1974, Huusko *et al.* 2007). The catch data demonstrated that, at least in early winter, increase in discharge and/or temperature may re-activate lampreys to migrate (I). Starcevich *et al.* (2014) observed a similar tendency among Pacific lampreys. In the River Derwent, England, elevated discharge episodes tended to stimulate upriver movement of river lampreys until the end of January, but after that river lampreys that had migrated a substantial distance upriver were not stimulated to continue upriver migration despite discharge elevations (Dr M.C. Lucas, University of Durham, pers. comm.).

As their migratory activity diminishes at low temperatures, river lampreys transplanted in water temperatures < 2 °C should be released near potential wintering/spawning sites, because they are likely to migrate only to the nearest fast-flowing river section. According to telemetry experiments, lampreys do not migrate long distances in the spring after winter holding, but mainly stay to spawn in the nearest fast-flowing area (Senior inspector J. Tuohino, ELY-centre for North Ostrobothnia, pers. comm.). This further emphasizes the importance of the selection of transplantation sites at low temperatures.

Onshore wind was also found to affect migration positively (I), as for *L. planeri* by Malmqvist (1980). Onshore winds give rise to surface currents parallel to the wind direction, and may speed up the migration towards the shore or towards the river mouth when a lamprey has already detected the plume. Counter to that, offshore winds may slow down the migration. It is possible that wind also influences migratory activity via sea level changes (Lisitzin 1967) and the dispersal of the river plume (Choi and Wilkin 2007).

In the long run, climate change may markedly alter migration patterns of adult lampreys. It is likely that due to warming, migration to the rivers will start later and, especially in boreal areas, the potential migration period will be prolonged. River flow and wind conditions are also predicted to change (Gregov *et al.* 2008, Jylhä *et al.* 2009), which will affect the timing of migration and may also affect dispersion of adult lampreys to different rivers.

Constructing hydroelectric power plants (HPP), dams and weirs obstructed migration of adult lampreys to the potential spawning sites in both studied rivers (I, IV, V). In the River Perhonjoki, translocation of totally 571 000 adult lampreys above the Kaitfors HPP in 1981–2010 was the main measure to overcome the problem caused by migration barriers (IV, V). The outcome was poorer than expected and, despite the translocations, the larval densities above the Kaitfors HPP decreased dramatically after natural migration to area was obstructed (IV, V).

In the mid 2000s, the first measures to enhance passage over the Kaitfors dam were introduced and a fish-way complex was constructed (V). The tagging experiments suggested that the whole complex was passable by river lampreys (V). However, the proportion of lampreys passing it was so low that the fish-way complex does not much benefit the rehabilitation of the river lamprey population above the Kaitfors. Elevated freshwater flows activate river lampreys to migrate and enter fish-ways (e.g. Masters *et al.* 2006, Foulds and Lucas 2013); thus the uniform discharge of less than 1 $m^3 s^{-1}$ in a rather long flood channel may have inactivated lampreys in the Kaitfors fish-way complex and caused the observed low passage efficiency (V). The technical fish-ways are challenging for river lampreys (Laine *et al.* 1998, Foulds and Lucas 2013), but bristles at the bottom of the slots are known to slightly enhance migration through vertical slot fish-ways (Laine *et al.* 1998). The results imply that the vertical slot fish-way section of the Kaitfors fish-way may be difficult to pass by river lampreys despite the boulder bed and bristles at the bottom of the slots (V).

The majority of adult lampreys entering the Vivunkumpu weir, constructed in the early 1990s at rkm 22 in the River Kalajoki, could not pass it (Aronen 1995). This likely accelerated the decrease in larval densities above rkm 22 (V). Therefore, in the mid 2000s, the passage of lampreys over the Vivunkumpu weir was improved by covering the concrete weir with boulders and constructing a super-active baffle (Larinier) fish-way and a natural-like fish ramp side-by-side at one end of the weir. All radio-tagged lampreys selected the fish ramp instead of the technical fish-way and passed the weir via it (I, V). It is likely that the high flow through the fish-ramp directed lampreys to select it and, therefore, the suitability of the super-active baffle fish-way for river lampreys remains unknown. However, the result suggests that a natural-like fish ramp is an appropriate solution to enhance passage of river lampreys over low-head barriers (I, V).

In both the studied rivers, efficient trapping in the estuaries or in the lowermost riffles has terminated the upstream migration of a large proportion of adult lampreys (V). In both rivers, the average fishing mortality during the fishing season in the 1980s and the 1990s was about 50 %, but has been declining recently, and more so in the River Perhonjoki. Also the number of adult lampreys entering the rivers has decreased significantly during the study period, but the decline in the escapement (index of spawning stock) has not been as prominent due to the compensatory effect of the decline in fishing mortality (V). Nevertheless, according to the precautionary approach of responsible fisheries management (Anon. 1995), it must be taken as a starting point that the data best supported the conclusion of a declining trend in escapement in both rivers, and thus measures to prevent any further decline must be adopted soon. It must also be stressed that the typical mortality and its variability of the escapees before spawning is poorly understood. So far, the larval densities have varied independently of the escapement, suggesting that the dynamics of reproduction output has been driven mostly by other factors than the abundance of spawning stock. However, in the 2000s the environmental circumstances for lamprey reproduction, especially in the River Kalajoki, have improved due to mitigation measures (V). Therefore, the spawning stock size can be expected to increasingly regulate the reproduction potential. Thus, regulation of fishing mortality should be included in the tool box for rehabilitation of lamprey populations. Fisheries associations of the River Kalajoki and of many other rivers have already far-sightedly adopted a precautionary policy of voluntarily restricting their lamprey fishing (Hiltunen *et al.* 2013).

## 3.2 Habitats of wintering adults

According to the telemetry experiments, lampreys may already become sedentary and start a prolonged holding phase during the early migration season, and migration of all lampreys ceases at the latest when the temperature drops below 1 °C (I). However, during the formation of ice cover some lampreys were still observed to move short distances from the shoreline to the deeper part of the river, and in early winter increased discharge or/and temperature still induced lampreys to change location.

Given that in boreal rivers water temperatures near 0 °C persist typically 6–7 months and that river lampreys are in an energy saving hypometabolic state during the winter months (Gamber and Savina 2000), the wintering site should offer a safe, energy saving and stable position in a harsh environment with various ice phenomena. The mesohabitat observations (I) revealed that the temporary resting sites and the more permanent locations at low temperatures, considered as wintering sites, resembled each other. River lampreys were typically holding in a run at the lower end of a riffle or in the glide above a riffle, but they were only occasionally observed to hold in slow-flowing river sections or in the middle or upper part of riffle sections. Results are consistent with observations on wintering habitats of Pacific lampreys (Starcevich *et al.* 2014, Biologist R. Lampman, Yakama Nation FRMP, pers. comm.).

River lampreys preferred holding sites dominated by large boulders (diameter > 256 mm) and they were observed to hold under and between the crevices of boulders and not on them (I). It is likely that these sites were preferred because they offered sufficiently large crevices to hide in. This suggestion is supported by Binder and McDonald (2007, 2008) who showed that sea lampreys use tactile and/or hydraulic cues to search for refuges before dawn, but after dawn the dermal photoreceptors ensure that the animal's tail remains fully concealed from the light. Pacific lampreys (Robinson and Bayer 2005, Starcevich *et al.* 2014) and *Geotria australis* (Kelso and Glova 1993) also use boulders as a cover while holding. The amount of possible refuge types other than boulders is limited in the Rivers Perhonjoki and Kalajoki, so in this study their suitability for river lampreys remained unknown (I). However, in the River Derwent, England, river lampreys hold in areas associated with riparian willows with large underwater root masses (Dr M.C. Lucas, University of Durham, pers. comm.), and sea lampreys may also use overhanging banks and fallen branches (Binder and McDonald 2007) and *Geotria australis* logs (Jellyman *et al.* 2002) as refugia.

River lampreys rejected slow-flowing river sections as wintering sites (I). The potential reason for this behaviour is that these sections are dominated by substrata like silt, clay and sand, which do not provide any refuge. Lampreys halting in slow-flowing river sections usually selected sites where boulders were dominant, although the availability of boulder substratum was low. The tendency of river lampreys to favour fast-flowing areas may also be connected to water quality, water temperature, ice conditions, anti-predatory behaviour or proximity of potential spawning sites. Thus, more detailed studies of the reasons for mesohabitat selection are needed.

River lampreys also seemed to avoid steep riffles and high current speed for holding sites (I). Holding under very high current speed may be too energy consuming, although refuge from high current speed could probably be found inside boulder piles. Avoidance of shallow, steep and fast-flowing river sections for holding could also have evolved in response to harsh and unstable conditions during the winter. These sites develop permanent ice cover last if at all and consequently formation of anchor ice may frequently fill the potential holding sites (see Huusko *et al.* 2013). Neither water depth nor closeness of the river margin significantly affected the selection of wintering habitat, suggesting that refuge availability and current speed are more important factors in directing the selection.

Dredging, channelization of fast flowing areas and replacing riffles with weirs decreased potential wintering habitats suitable for river lamprey (V). In dredged or channelized rivers, the availability of refugia was reduced (V). Block stone weirs offered lots of crevices for wintering adults to hide in, but the current velocity in them was mostly much higher than known to be selected by wintering river lampreys (I).

The negative effects of hydropeaking on larval river lampreys are evident (IV, V), but its effects on adult life stages are not well known. In boreal rivers, the wintering stage of adult river lampreys lasts for 7–9 months (I). Fluctuating water flow and multiple changes in ice processes due to hydropeaking are known to be harmful for wintering fish (e.g. Huusko *et al.* 2007, Huusko *et al.* 2013, Weber *et al.* 2013). For example, formation of anchor ice may cause habitat exclusion and energy-intensive migrations. Given that river lampreys do not eat after entering fresh water and they are in an energy saving hypometabolic state, the disturbances during wintering are potentially even more detrimental for them than for other fishes and may increase their energetic costs, stress and exposure to predation and consequently increase mortality and reduce their reproductive success.

Following the restoration of fast-flowing sections, larval densities in the River Kalajoki have increased (V), which may partly be associated with improved wintering survival of adults due to the increase in potential wintering sites like boulder piles and other instream structures (I) and with the reduction in the negative effects of hydropeaking. Restored riffles may get permanent ice cover earlier (Lind and Nilsson 2014) than dredged ones and consequently offer more stable habitat with less formation of anchor ice. On the other hand, the effect of restoration is site-specific and it may also increase anchor ice formation (Lind and Nilsson 2014). However, the direct evidence of negative impacts of human-induced hydro-morphological changes or positive impacts of mitigation measures on wintering survival of river lampreys in boreal rivers is scarce. Nevertheless, telemetry experiments indicated that predation risk to wintering lampreys increased when they aggregated below migration obstruction (I).

## 3.3 Habitats for spawning and embryonic development

Jang and Lucas (2005) observed gravel and cobbles to be dominant substrata in the spawning habitat of river lampreys in the River Derwent, England, but substratum composition between different spawning sites varied considerably. In a small stream in Lithuania, dominant particle sizes in river lamprey nests were coarse (16–32 mm) or very coarse (32–64 mm) gravel (Nika and Virbickas 2010). In the few nests found in the River Perhonjoki, particle sizes > 16 mm were also prevailing (II).

Tank experiments (II) suggested that lampreys may use a wide variety of gravel sizes as spawning substratum as long as they are able to excavate a nest depression by waggling their tails and/or by carrying gravel particles out of the nest with their oral disks and/or with the aid of the current. Lampreys also actively selected their spawning substratum and water flow conditions affected the selection.

Observations on river lamprey nesting behaviour (II) were in line with the results of Hagelin and Steffner (1958) and Hagelin (1959). Lampreys removed smaller particles from the nest by swiping the posterior part of the body vigorously and medium-sized and large gravel particles individually with their oral disk. Hagelin and Steffner (1958) and Hagelin (1959) did not, however, report the use of current in nest construction. It was observed (II) that especially the smaller male river lampreys, like sea lampreys (Applegate 1950), used the current to aid removal of larger gravel particles from the nest.

In the tank with lower current speed (LCS tank) and a narrower high current velocity zone, the lampreys did not seem able to use the current as efficiently as in the tank with higher current speed (HCS tank). This may explain the tendency of lampreys in the LCS tank to select the finest gravel (2–8 mm), in which they were able to construct a nest just by waggling their tails, and only rarely to select the coarsest gravel (8–40 mm) which required excavation mostly by moving gravel particles one by one with the oral disk. As lampreys in both tanks rejected medium grain size (4–20 mm) gravel as a spawning substratum, it seems that neither way of nest building was well suited for that size of gravel. Most of the particles in the medium grain size gravel were too small to be picked up individually with the oral disk but they might be too big or too compact to be removed by swiping the posterior part of the body alone.

Even the smallest lamprey species have not been reported to use as fine a spawning substratum as was found to be the most preferred in the LCS tank for river lampreys (II) (e.g. Sokolov *et al.* 1992, Takayama 2002, Mundahl and Sagan 2005, Nika and Virbickas 2010), although Hagelin and Scheffer (1958) reported that river lampreys in an experimental aquarium preferred sand to coarser material for spawning. It is possible that in natural environments current speed directs the selection of the spawning site, and lampreys select spawning sites with such a high current speed that fine gravel or sand are not available. Jang and Lucas (2005) observed river lampreys to spawn in sites where the average surface velocity varied between 47 and 82 cm $s^{-1}$. The nests in the River Perhonjoki were situated in locations with a surface velocity around 40 cm $s^{-1}$ and a bottom velocity around 20 cm $s^{-1}$ (II). As knowledge of river lamprey spawning biology is so limited the possibility cannot be denied that in their natural environment river lampreys may spawn in areas with even lower water velocity and may use fine gravel or even sand substrata (see also Tuunainen *et al.* 1980).

The behaviour of animals evolves to maximize fitness and it is therefore obvious that behavioural traits that affect the survival of eggs and larvae by selection of spawning habitat have evolved in river lampreys. In II, the survival of eggs or proammocoetes in different substrata was not examined. However, I postulate from the results that the gravel size composition may not have a prominent effect on egg or proammocoete survival, or at least it may not have been the driving force in the evolution of spawning site selection of river lamprey as long as there is gravel suitable for constructing a depression. The depressions which river lampreys excavate are sites for courtship and spawning (Hagelin 1959) and they have been considered to be shelters for eggs (Maitland 2003) and for larvae before they leave the nest (III). However, Silva *et al.* (2014) have proposed that the nests may function more as egg dispersal structures than as egg shelters, and most of the eggs may disperse and be deposited downstream from the spawning site. This might partly explain why river lampreys may use a wide variety of gravel sizes for spawning.

Silva *et al.* (2014) concluded that requirements for embryonic development and hatching of river lamprey eggs are less stringent and less dependent on the quality of spawning habitat than for salmonid fishes. Study II supports the previous conclusion when it comes to gravel size. Yet, it is possible that some other factor, such as the proportion and composition of fine material in the spawning substratum, may affect hatching success. Applegate (1950) suggested that in the spawning gravels of sea lampreys a small amount of sand must be available to which eggs will adhere and which will imbed them in the interstices of the gravel. Furthermore, sand separates eggs from one another, helping to prevent fungal attack (Smith and Marsten 2009). Nika and Virbickas (2010) reported that, even if coarse or very coarse gravel were dominant in the nests of river lamprey, in undisturbed conditions nests were usually embedded with fine gravel and sand. When these findings are coupled with the fact that proammocoetes prefer gravel with fine material to sieved gravels (III) soon after hatching, when they start constructing a burrow, it seems possible that the amount of fine material may be an important factor in defining the suitability of spawning substratum for lampreys. As 15 % of fine material (0–2 mm) was added in all the substrata used in the tank experiments (II) it is not possible to say whether the lack of fine material in gravel would have made lampreys reject the substratum for spawning.

Due to damming, dredging, and substituting natural riffles with weirs and siltation, gravel beds suitable for spawning of fishes and lampreys have decreased dramatically (e.g. Pauwels and Haines 1994; Yrjänä 1998; Laine *et al.* 2001, IV, V). Silva *et al.* (2014) have suggested that ensuring the availability of high quality salmonid spawning habitat will undoubtedly benefit river lampreys. This may be partly true, although the widely used method of adding sieved/washed gravels when restoring spawning grounds of salmonid fishes (e.g. Rubin *et al.* 2004, Eloranta 2010, McManamay 2010, V) may not optimally restore river lamprey spawning habitats. As discussed above, the removal of fine material from the spawning gravel may decrease its suitability for river lamprey spawning. This may be a particular concern when restoring a severely dredged riffle or constructing an artificial one, where no fine material is available naturally (V). In restorations, the coarseness of the added gravel depends on the target fish species and its size. For example, in Finland the recommended grain sizes for salmon (*Salmo salar*), trout (*Salmo trutta*) and grayling (*Thymallus thymallus*) are 60–100, 15–65, and 6–15 mm, respectively (Eloranta 2010). When comparing these grain sizes intended for salmonid fishes to the results from the tank experiments (II), they seem suboptimal for river lampreys, despite the fact that river lampreys will use a wide variety of gravel sizes for nest construction. The gravel composition recommended for grayling resembles the substratum type 4–20 mm, which lampreys rejected (II). River lampreys might use gravel beds constructed for trout, but, especially in the sites where water velocity is low, it may be too coarse to be optimal for river lampreys. Gravel recommended for salmon is far too coarse for river lampreys.

In the Rivers Kalajoki and Perhonjoki, 8–40 mm sieved gravel was actively added into nearly all restored riffle sections (V). In the River Kalajoki, gravel beds for lamprey spawning were also restored with two other methods (V): natural gravel (≈ 1–50 mm) was dumped down the stream bank and into the channel just above newly restored, long riffle sections, and spawning sites were constructed out of natural gravel found under boulder piles while restoring riffles. The increase in the density of sub-yearling larvae in the River Kalajoki after restoration may at least partly be explained by the improved reproduction success due to marked increase in gravel habitats suitable for lamprey spawning and embryonic development (II, III, V). In the River Perhonjoki, the restoration did not positively affect larval densities. Spawning gravels suboptimal for river lampreys may, among many other limiting factors, have been causing the low success (V). However, there is no direct evidence that sieved/washed spawning gravels intended for salmonid fish are poorly suited for river lampreys, and further study is needed of whether the restoration practices targeted at improving spawning habitats of salmonids are adequate to restore river lamprey spawning grounds collaterally, or if more tailored species-specific methods are needed.

The main results of II come from the laboratory experiments with only a few field observations. The results must therefore be extrapolated to field conditions with caution. In the natural environment the heterogeneity of flow conditions and substratum structure may have an effect on spawning habitat selection. Furthermore, communal spawning is typical for river lampreys (Jang and Lucas 2005) which in the natural situation may influence nesting behaviour and habitat selection.

Spawning behaviour and survival of the early life stages of the river lamprey may also be impaired by hydropeaking. The spawning substratum selection and nesting behaviour of river lampreys are affected by flow conditions (II) and, furthermore, fluctuating water level may increase the mortality of eggs and sub-yearling larvae as gravel beds are exposed to scouring risk at peak flow and to dewatering at off-peak flow (McMichael *et al.* 2005), while elevated discharge increases downstream dispersion of river lamprey eggs from spawning areas (Silva *et al.* 2014). In the River Perhonjoki, hydropeaking was prohibited during the period of spawning and embryonic development (V). However, various other factors continuously limited lamprey reproduction success, so that possibly the mitigation of hydropeaking did not lead to increased larval densities (V).

## 3.4 Habitats for larvae

### 3.4.1 Sub-yearling larvae

Substratum selection by sub-yearling larvae approximately 8–10 days after hatching (1st experiment week) differed clearly from that of older sub-yearling larvae (III). During the first experiment week, larvae with an average TL of 6.9 mm were not able to construct a burrow, but actively selected a substratum which offered existing holes to hide in (gravel) in or shelters to hide under (large detritus). Before developing the ability to construct a burrow, larval lampreys just swim and occasionally settle down to lie on the sediment (Piavis 1971) and it is possible that they continue this behaviour until they find a suitable substratum. A tendency to search actively for existing holes may have evolved because it increases the survival of those individuals which leave the nest before burrowing ability has developed (see Hardisty 1979, Kirillova *et al.* 2011, Silva *et al.* 2014).

Substratum selection changed significantly after the first week (III), likely due to the development of the ability to construct a burrow. Larvae started favouring the gravel type with the finest material enabling burrow construction, and they also started to select fine sediments, indicating that they were now able to construct a burrow and no longer dependent on existing holes in a gravel substratum.

After larvae have gained the ability to burrow, the substratum has to provide the characteristics that allow burrowing into sediment and constructing a tube and also allow vital water flow for gas exchange and feeding once external feeding begins. The distribution of lamprey larvae has been suggested to be mostly a function of sediment grain size (Young *et al.* 1990, Almeida and Quintella 2002). Fine (0.125–0.25 mm) or/and medium-fine sand (0.25–0.5 mm) has been the most preferred substratum for larvae older than one year (Potter *et al.* 1986, Lee 1989, Beamish and Lowartz 1996, Yamasaki 2007, Smith *et al.* 2011) and its properties have been suggested to best meet the needs of larvae (Beamish and Lowartz 1996). In some studies the highest densities of larval river and/or brook lampreys have been associated with even coarser sediment (Malmqvist 1980b, Goodwin *et al.* 2008, Taverny *et al.* 2012). In III, sub-yearling larvae preferred finer soft sediment (very find sand) than larger larvae in earlier studies and clearly selected against coarse sand which was associated with the highest *Lampetra* spp. abundance (Goodwin *et al.* 2008, Taverny *et al.* 2012). Results agree with the findings of Beamish and Jebbink (1994), Almeida and Quintella (2002) and Sugiyama and Goto (2002) that smaller larvae selected finer sediment than larger ones. However, in those studies the larvae were older than one year, and to my knowledge there are no earlier quantitative studies on habitat requirements of sub-yearling lampreys. The selection of very fine sand by sub-yearling larvae may be linked to their weak burrowing capacity (see Quintella *et al.* 2007) or/and small diameter of tube, which may lead to a need for small particles in order to construct a stable burrow.

Lamprey larvae (Lee 1989, Smith *et al.* 2011), and especially smaller larvae (Almeida and Quintella 2002, Sugiyama and Goto 2002), reject gravel and coarse sand substrata. In III, coarse sand was rejected by sub-yearling larvae. This may be due to the fact that large particles are too heavy to dislodge for larvae (Beamish and Jebbink 1994, Beamish and Lowartz 1996) and small larvae had more difficulty than larger larvae in burrowing into coarse sediments (Quintella *et al.* 2007).

However, after the first experiment week (III), natural gravel seemed to be at least as desirable a substratum for sub-yearling larvae as soft sediments. Most of the particles in gravel substrata might be too heavy for sub-yearling larvae to dislodge, but small larvae were probably able to use the interstitial spaces between big particles. The result suggests that, under natural conditions, beside soft sediments gravel beds may also offer an important habitat for sub-yearling lampreys. In rivers and streams gravel beds are usually subjected to a higher current speed than gravel substrata in the experimental aquaria, and therefore the results do not allow interpretation of the suitability of gravel substratum in the natural environment. Nevertheless, some field observations do support the importance of gravel beds for sub-yearling larvae (Tuikkala 1971). As larvae grow, the space between gravel grains may become a limiting factor, and it is probable that larvae have to move to soft sediment areas during the first summer.

Natural gravel was clearly preferred over sieved gravels by sub-yearling larvae after the first experiment week (III). The main reason for rejecting sieved gravels was probably its very low portion of fine material, which made it difficult or impossible to construct a stable burrow (Beamish and Jebbink 1994, Beamish and Lowartz 1996).

During 1997–2010, a total of 247 million sub-yearling river lamprey larvae were artificially propagated for stocking aimed at compensating for the depletion of the population in the River Perhonjoki (V). The propagation methods were adequate to produce an ample number of prolarval stage lampreys , but the risk of high mortality emerged after individuals had reached a mean size of 7 mm. Methods for rearing lampreys beyond the larval stage have not been developed, and thus larvae have to be stocked before they begin to external feeding.

Site suitability may play an important role in the survival of stocked individuals. River lamprey < 7 mm should be stocked in areas where the substratum provides existing holes for larvae (III). Gravel areas with low or moderate current speed may offer the best sites. Individuals averaging 7–8 mm should probably also be stocked in similar areas as smaller larvae, because it is likely that a certain proportion of them is still unable to construct a burrow. Once the mean TL of lampreys exceeds 8 mm, the vast majority of individuals is probably capable of constructing a burrow; hence stocking could then be done also in soft sediments. Substratum with a high proportion of the fine fraction (< 0.125 mm) is the best type of soft sediment (III).

In the River Perhonjoki, sub-yearling larvae were stocked to soft-bottomed areas during the first years, but later fast-flowing sections were also used as release sites (V). After 2004, all sub-yearlings were released at the fast-flowing sections. However, it is not known what proportion of stocked sub-yearlings in different release sites or in different flow conditions drifted immediately after release to the soft-bottomed areas and whether the mortality of larvae was higher there. The outcome of stocking sub-yearling larvae in the unregulated River Ullavanjoki tributary was only a few thousand migrating transformers per one million stocked sub-yearling larvae (V). If lamprey populations are to be rehabilitated by stocking sub-yearling larvae in the future, it will be important to know the effect of different release procedures and the size of stocked larvae on the mortality, and based on that knowledge to further develop the release procedures and, if deemed necessary, also methods for rearing larger larvae.

### 3.4.2 Larvae older than one year

The size of the larvae affected their substratum selection: the two largest size groups preferred coarse organic sediments to fine sand, whilst the smallest larvae did not have that preference (III). Many earlier studies have also demonstrated that habitat selection by larval lampreys changes as they grow (Beamish and Jebbink 1994, Sugiyama and Goto 2002, Almeida and Quintella 2002, Smith *et al.* 2011).

Medium or fine sand is regarded as the most suitable habitat for larvae older than one year (Potter *et al.* 1986, Lee 1989, Beamish and Lowartz 1996, Yamasaki 2007, Smith *et al.* 2011). In contrast to III, most earlier studies did not find coarse organic matter to be preferable to fine sand as a burrowing substratum (e.g. Smith *et al.* 2011). However, the importance of organic material as a part of the substratum has been widely emphasised (Enequist 1937, Applegate 1950, Sterba 1962, Potter *et al.* 1986, Beamish and Lowartz 1996). The benefit of organic sediment is connected to food availability (Hardisty and Potter 1971, Shirakawa *et al.* 2009), although it has also been suggested that the dietary significance of organic matter is limited (Malmqvist 1980b, Beamish and Lowartz 1996, Sugiyama and Goto 2002). Furthermore, coarse organic sediment is very porous, enabling ample water flow through the sediment, and thus gas exchange and food intake are probably easier than in fine or medium-sized sand (see Lee 1989, Beamish and Lowartz 1996).

However, it is not appropriate to infer from the results of the aquarium experiments (III) that coarse organic matter is always the best burrowing substratum for large larvae. The source of particulate organic matter may affect its suitability for lamprey larvae (Beamish and Jebbink 1994) and the proportion of fine particles mixed with coarse organic particles may play an important role (Smith *et al.* 2011). Furthermore, under natural conditions decomposing coarse organic material may lead to depletion of oxygen in the sediment, especially when the water flow through the sediment is low, making the sediment unsuitable for larvae (own field observation).

In the laboratory experiments (III), clay was not selected as a substratum by larvae of any size. This is consistent with other aquarium experiments performed with different lamprey species (Lee 1989, Smith *et al.* 2011). Clay as a burrowing substratum is challenging for larval lamprey in many ways: it prevents or slows down the movement of larvae into the sediment (Young *et al.* 1990, Smith *et al.* 2012) and slows down the water flow through the sediment (Lee 1989) and furthermore, very fine particles may clog the gill lamellae and dermal pores and hinder the gas exchange of larvae (Beamish and Lowartz 1996).

Large larvae preferred the deepest sediment available (10 cm) (III). This is consistent with results for large larvae of the Far Eastern brook lamprey (*Lethenteron reissneri*) (Sugiyama and Goto 2002) and *Geotria australis* larvae (Kelso 1993). Sediment depth is an important factor for predicting larval abundance (Potter *et al.* 1986, Kelso and Todd 1993, Goodwin *et al.* 2008). Large lampreys need deeper substratum than smaller ones (Sugiyama and Goto 2002) and consequently, the burrowing depth increases as a larva grows (Hardisty and Potter 1971). The experiments in III and previous results cannot rule out the possibility that larvae would have selected even deeper sediment if available. More detailed knowledge is needed on substratum depth selection of different sized larval lampreys in order to understand better their habitat requirements.

River regulation measures, including dredging, channelization, embankment and water flow regulation, have impaired larval habitats by decreasing the area of soft bottomed habitats which may lead to a decrease in lamprey populations (Renaud 1997, Maitland 2003, IV, V). In the River Perhonjoki, channelization of the lowermost section of the river created a morphologically and hydrologically monotonous environment resulting in loss of flow refugia and backwaters and elevated flow velocity, so that, consequently, depositional bottoms suitable for larval habitat became scarce (IV, V; see also Negishi *et al.* 2002, Garcia *et al.* 2012, Elosegi & Sabater 2013). Furthermore, embankments markedly reduced important larval habitats, as they increased the current speed during flood peaks which flushed away most of the soft material suitable for larval habitat (IV).

Hydropeaking in the Rivers Perhonjoki and Kalajoki caused severe problems by thickening the ice cover and inducing erosion and consequently deterioration of larval habitats (IV, V). This was most likely the main reason for the collapse of larval densities in the areas below the HPPs in the mid and late 1980s (IV, V). Due to fluctuating flow, ice cover thickened, especially next to the river bank, and moved up and down, which increased erosion (Sarkki 2005). Continuously changing flow and water level also induced erosion, but to a lesser extent than the altered ice conditions (Sarkki 2005). Hydropeaking has also been suggested to induce formation of ice jams in both rivers (Ruhanen 1987, Savolainen and Leiviskä 2008). Hydraulic force during ice jams and break-up, along with the mechanical effects of moving ice blocks, can severely erode the channel bed (Prowse and Culp 2003) and consequently deteriorate larval habitats. Hydropeaking increases ice thickness, especially close to the river bank, and thus freezing and ice compression may reduce the suitability of shallow areas for lamprey larvae despite availability of soft sediment (IV, V). This suggestion is supported by observations from many northern regulated lakes, where in soft-bottomed shallow shores the richness and biomass of benthic fauna have markedly decreased due to freezing and/or ice compression (Palomäki and Koskenniemi 1993, Aroviita and Hämäläinen 2008).

As river regulation has reduced the quantity and quality of larval habitats, mitigation measures should aim at increasing their area. One possible method is to modify the straightened shore lines and embankments enabling the accumulation of fine sediments and organic matter, and, especially in channelized rivers, to restore the pool-riffle structure. This kind of restoration experiment was carried out in the River Perhonjoki (V). Unfortunately, the habitat surveys a decade after the restoration showed that new larval habitats had not been formed (V). More radical measures are thus needed to create larval habitats in channelized river sections affected by hydropeaking. The harmful effects of hydropeaking can be mitigated by constructing morphological structures, yet the mitigation of hydropeaking itself is likely to be one of the key measures in rehabilitating lamprey populations in short-term regulated rivers. No morphological improvements can be successful if the flow regime is not within the acceptable range (e.g. Weber *et al.* 2007).

# 4 CONCLUSIONS

This study has increased knowledge of the behaviour and habitat requirements of the river lamprey in its lotic life stages and has provided insight into the effects of various anthropogenic stressors and the efficacy of different measures to mitigate them. Based on the results some notes and recommendations for conserving and rehabilitating lamprey populations can be offered:

- Discharge is an important factor controlling upstream migration of adult lampreys, which should be taken into account in regulation patterns of flow-regulated rivers.
- Further studies are needed to verify the finding that illumination of bridges, especially at shallow areas, reduces the migratory activity of river lampreys, and if confirmed, some solutions to prevent the disturbance by bridge lighting will be required.
- As adult lampreys need refugia for holding, lampreys transplanted during daylight should be released at sites offering refuge from predation pressure and stress.
- Predation risk to adult lampreys is high when they aggregate below migration obstructions. Thus, transplanting lampreys below migration barriers in the autumn should be avoided.
- The efficacy of transplantations must be monitored, especially if lampreys are released in areas markedly affected by anthropogenic stressors.
- As the migratory activity of adult lampreys diminishes at low temperatures and migration distances in spring time are probably low, river lampreys should not be transplanted in low water temperatures (< 2 °C) or they should be released near potential wintering/spawning sites.
- A natural-like fish ramp is an appropriate solution to enhance passage of adult river lampreys over low-head barriers.
- In projects aiming at restoring previously dredged fast-flowing areas, it is important to place boulders in run/glide sections to offer wintering

habitats for adult lampreys. It is likely that piles of boulders provide a better refuge for lampreys than individual stones.

- Adding washed/sieved gravel intended for salmonids may not optimally restore the habitats for spawning and embryological development of river lampreys or habitats for sub-yearling larvae.
- River lamprey larvae seem to achieve the ability to construct a burrow only at a length of 7–8 mm; therefore larvae less than 8 mm long should be stocked in areas where the substratum provides existing holes for them.
- When restoring habitats for larval lampreys in channelized, short-term regulated boreal rivers, measures should be rather radical to ensure accumulation of fine material and avoid erosion due to hydropeaking, high flow or ice.
- As river regulation is detrimental for river lamprey populations, it should be avoided, or if that is not possible at least mitigated.

In the future, more detailed knowledge of basic life history, impact of anthropogenic pressures on different life stages and efficacy of rehabilitation measures would help in developing the best policies for conserving and rehabilitating lamprey populations and restoring their environment. Important topics for future research include:

- Lamprey mortality and the main factors affecting it in different life stages, e.g. adult mortality during wintering, effects of fishing mortality on lamprey population dynamics, mortality and migration delay of migrating transformers in impoundments
- Efficacy of different mitigation measures and their combinations in rivers affected by different kinds of anthropogenic pressures, e.g. suitability of different fish-way types for river lamprey, suitability of sieved, washed gravels for river lamprey spawning and embryonic development
- Migratory behaviour, e.g. migratory patterns of adult lampreys in the sea and factors affecting their spawning river selection, effects of artificial illumination on migratory behaviour

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# YHTEENVETO (RÉSUMÉ IN FINNISH)

## Nahkiaisen (*Lampetra fluviatilis*) jokivaiheet: ihmistoiminnannasta aiheutuvat haitat ja niiden vähentäminen

Nahkiaista (*Lampetra fluviatilis*) on pyydetty Euroopassa ravinnoksi vuosisatojen ajan, ja sillä on ollut sekä kulttuurista että taloudellista merkitystä. Nahkiaispopulaatioiden koko ja saaliit ovat pienentyneet huomattavasti 1900-luvulla. Joissakin Euroopan maissa nahkiainen on jo hävinnyt alueellisesti kokonaan tai populaatiot ovat taantuneet niin paljon, että nahkiaisen pyynti on kielletty. Kuitenkin nahkiaisia pyydetään vielä monissa Itämereen laskevissa joissa mm. Puolassa, Baltian maissa, Ruotsissa ja Suomessa. Suomessa nahkiaisten pyynti on painottunut Perämereen laskeviin jokiin, joista saadaan 80–90 % kokonaissaaliista. Suomessakin nahkiaissaaliit ja hyvin todennäköisesti myös nahkiaispopulaatiot ovat pienentyneet huomattavasti viime vuosikymmenten aikana. Suomen vuotuisen nahkiaissaaliin arvioitiin 1970-luvulla olleen 2,0–2,5 miljoona yksilöä, kun se 2000-luvulla oli enää alle miljoona yksilöä.

Nahkaispopulaatiot ovat taantuneet pääasiassa ihmistoiminnan vuoksi. Jokien patoaminen on paikoin kokonaan estänyt nahkiaisen pääsyn kutu- ja poikastuotantoalueille. Lisäksi vesistörakentaminen sekä virtaamien säännöstely ovat vähentäneet ja muuttaneet nahkiaisen elinkierron kannalta välttämättömiä elinympäristöjä, minkä on arveltu osaltaan johtaneen nahkiaispopulaatioiden heikentymiseen. Kuitenkin elinympäristöjen muuttumisen vaikutukset nahkiaisen eri elämänvaiheisiin tunnetaan melko huonosti. Nahkiaisten pyynti voi verottaa merkittävän osan jokiin nousevasta nahkiaiskannasta, ja joissakin joissa pyyntikuolevuus voi ylittää jopa 50 %, mutta pyynnin vaikutusta nahkiaispopulaatioihin ei ole tutkittu. Paikoin myös ihmistoiminnan vuoksi heikentynyt vedenlaatu, mm. alhainen pH ja korkeat metallipitoisuudet, voi rajoittaa nahkiaisen esiintymistä.

Viimeisimmässä Suomessa tehdyssä uhanalaisluokituksessa nahkiaisen arvioitiin kuuluvan edelleen luokkaan silmällä pidettävä, vaikka saaliiden todettiinkin laskeneen. Euroopan komission habitaattidirektiivissä (92/43/EEC) nahkiainen on kirjattu liitteeseen II, jonka perusteella jäsenmaiden on osoitettava nahkiaisen suojelemiseksi erityisiä suojelutoimenpiteiden alueita lajin suotuisan suojelutason takaamiseksi. Tämä velvoite ei kuitenkaan koske Suomen ja Ruotsin nahkiaispopulaatioita. Kuitenkin myös ne kuuluvat habitaattidirektiivin liitteen V piiriin, jonka perusteella lajin hyödyntämistä tulee tarvittaessa rajoittaa siten, ettei hyödyntäminen ole ristiriidassa sen suotuisan suojelutason säilyttämisen kanssa. Myös Bernin yleissopimus (82/72/EEC) Euroopan luonnonvaraisen kasviston ja eläimistön sekä niiden elinympäristön suojelusta velvoittaa nahkiaispopulaatioiden ja niiden elinalueiden suojeluun.

Nahkiaisen ekologian, mukaan lukien elinympäristövaatimukset ja käyttäytyminen, tunteminen on lajin suojelun ja populaatioiden elvyttämisen perusedellytys. Tieto nahkiaisen ekologiasta on lisääntynyt 2000-luvulla, ja lisäksi on selvitetty erilaisten kalatieratkaisuiden soveltuvuutta nahkiaiselle. Nahkiaisen ekologiassa on kuitenkin vielä melko paljon huonosti tunnettuja seikkoja. Esimerkiksi aikuisten nahkiaisten merivaelluksesta ja sen jälkeisestä talvehtimisesta joessa tiedetään hyvin vähän, mutta myös kaikkien muiden elämänvaiheiden ekologian tuntemuksessa on puutteita. Muualla kuin Suomessa nahkiaispopulaatioiden elvytystoimenpiteet ovat rajoittuneet pääasiassa aikuisten nahkiaisten vaelluksen edistämiseen nousuesteiden yli, joten kokemukset erilaisten elvytystoimenpiteiden tuloksellisuudesta ovat erittäin vähäisiä. Suomessa nahkiaispopulaatioita on jo 1980-luvun alusta lähtien pyritty elvyttämään ja ylläpitämään siirtämällä jokeen kudulle nousevia nahkiaisia vaellusesteiden yli. Näidenkin kompensaatiotoimenpiteiden tuloksellisuus on melko huonosti tunnettu.

Perämereen laskevissa Kalajoessa ja Perhonjoessa, joissa Suomen valtio on vastannut vesistörakentamishankkeista ja virtaaman säännöstelystä, nahkiaispopulaatioita on pyritty hoitamaan monin menetelmin: aikuisten nahkiaisten ylisiirto, toukkien istutus, elinalueiden kunnostus, kalateiden rakentaminen sekä lyhytaikaissäännöstelyn lieventäminen. Sekä vesistörakentamisen ja virtaaman säännöstelyn että elvytystoimenpiteiden vaikutuksia on arvioitu seuraamalla nahkiaisen toukkatiheyden ja jokeen nousevan nahkiaiskannan kehitystä 1980-luvun alkupuolelta saakka noin 30 vuoden ajan. Lisäksi hoitotoimenpiteiden tuloksellisuutta on arvioitu seuraamalla mereen laskeutuvien nahkiaisten määrää. Kalateiden toimivuutta on tutkittu radiotelemetrian ja merkintätutkimusten avulla. Kaksi tämän väitöskirjan osajulkaisuista (IV, V) käsittelee kyseisiin aineistoihin pohjautuen vesistörakentamisen ja säännöstelyn sekä elvytystoimenpiteiden vaikutuksia nahkiaispopulaatioihin.

E.m. tapaustutkimusten lisäksi nahkiaisen elinympäristövaatimuksia ja käyttäytymistä on selvitetty tarkemmin kokeellisin tutkimuksin. Kaksi osajulkaisuista (II, III) käsittelee pääasiassa laboratorio-olosuhteissa tehtyjä valintakokeita. Tutkimuksessa II selvitettiin kahdessa eri virtausnopeudessa, millaista soraraekokoa nahkiainen suosii kutualustanaan. Tutkimuksessa III selvitettiin, millaista soraa tai pehmeää pohjamateriaalia ensimmäistä kesää elävät nahkiaisen toukat valitsevat kaivautumisalustakseen. Siinä selvitettiin myös vanhempien toukkien kaivautumisalustan valintaa sekä sitä, miten pehmeän sedimentin paksuus vaikuttaa kaivautumisalustan valintaan.

Julkaisussa I tutkittiin aikuisten nahkiaisten vaelluskäyttäytymistä sekä talvehtimiselinympäristön valintaa Perhonjoessa ja Kalajoessa. Ympäristötekijöiden vaikutusta jokeen nousevien nahkiaisten vaellusaktiivisuuteen tutkittiin regressio- ja korrelaationalyyseillä, joissa vaellusaktiivisuutta kuvaava muuttuja perustui kirjanpitopyytäjien pyyntiyökohtaiseen yksikkösaaliiseen. Nahkiaisten vaelluskäyttäytymistä joessa tutkittiin merkitsemällä 60 jokeen noussutta yksilöä radiolähettimillä ja seuraamalla niiden liikkumista joessa. Lisäksi tutkittiin näiden yksilöiden talvehtimiselinympäristön valintaa.

Kokeellisten tutkimusten (I–III) tärkeimmät tulokset olivat:

- Jokeen nousevien nahkiaisten vaellusaktiivisuus kasvaa joen virtaaman ja jokisuuta kohti puhaltavan tuulen voimakkuuden kasvaessa sekä veden lämpötilan laskiessa nopeasti. Kuun valaistuksen määrän kasvu vähentää vaellusaktiivisuutta.
- Valtaosa radiolähettimellä merkityistä nahkiaisista lopetti vaelluksen joko pysyvästi tai ainakin hetkellisesti kohdatessaan vaellusreitillään valaistun sillan.
- Kaikki kymmenen nahkiaista, jotka vapautettiin 350 m Vivunkummun pohjapadon alapuolelle, ohittivat padon käyttäen nousuväylänään luonnonmukaista kalaluiskaa.
- Aikuiset nahkiaiset suosivat talvehtimisalueinaan nivoja ja koskien alaosia, joissa oli isoja lohkareita (> 256 mm). Vaelluskaudellaan nahkiaiset pysähtyivät vuorokauden valoisaksi ajaksi talvehtimisalueita muistuttaville alueille.
- Hitaamman virtaaman koealtaassa nahkiaiset suosivat kutualustanaan hienorakeisinta tarjolla olevaa soraa (2–8 mm) ja hylkivät raekooltaan 4-20 mm ja 8–40 mm soraa. Myös nopeamman virtaaman altaassa ne hylkivät raekooltaan 4–20 mm:n soraa, mutta valitsivat yhtä usein muita raekokoja (2–8, 2–40 ja 8–40 mm).
- Runsas viikko kuoriutumisen jälkeen nahkiaisen toukat (keskipituus 6,9 mm) valitsivat kaivautumisalustakseen pohjan, joka tarjosi niillä valmiita suojapaikkoja. Ilmeisesti ne eivät vielä tuolloin kyenneet rakentamaan suojaputkea.
- 8–11 mm pituiset toukat valitsivat pohjan, johon ne pystyivät rakentamaan suojaputken. Suosittuja kaivautumisalustoja olivat hienojakoiset pehmeät sedimentit ja hienoainesta sisältävä sora. Toukat hylkivät karkeaa hiekkaa ja soraa, josta hienoaines oli poistettu.
- Yksikään yli yksivuotias toukka ei valinnut kaivautumisalustakseen savea.
- Suuret toukat (80–110 mm) suosivat paksuinta pehmeää sedimenttiä (10 cm), jota oli tarjolla.

Perhojoen ja Kalajoen tapaustutkimusten (IV ja V) perusteella:

- Perkauksilla, pengerryksillä, lyhytaikaissäännöstelyllä ja joen patoamisella on merkittäviä haittavaikutuksia nahkiaiskantoihin ja nahkiaisten elinympäristöön.
- Aikuisten nahkiaisten ylisiirrot nousuesteen yläpuolelle eivät välttämättä kompensoi patoamisen aiheuttamaa haittaa. Pieni ylisiirrettyjen yksilöiden määrä, mm. vesistörakentamisesta johtuva elinympäristön heikentyminen nousuesteen yläpuolella tai nahkiaisiin kohdistuvasta saalistuksesta johtuva talvikuolleisuus seuraavan nousuesteen alla voivat johtaa tavoiteltua heikompaan lopputulokseen.

- Muutaman viikon ikäisten toukkien istutuksilla on mahdollista elvyttää taantunutta nahkiaispopulaatiota. Kuitenkin mereen arvioitiin vaeltavan vain muutama tuhat muodonmuutoksen läpikäynyttä yksilöä miljoonaa toukkaistukasta kohden, joten 15 miljoonan toukan vuotuinen istutus yhdessä ylisiirtojen kanssa kompensoi vain pienen osan vesistörakentamisen aiheuttamasta haitasta.
- Perattujen koski- ja niva-alueiden kunnostamisella saattaa olla myönteinen vaikutus nahkiaispopulaatioon. Kalajoessa sekä yksikesäisten että vanhempien toukkien tiheys kasvoi kunnostusta seuraavan vuosikymmenen aikana.
- Nahkiaisen ekologia, ihmistoiminnan vaikutukset nahkiaispopulaatioihin sekä erilaisten elvytystoimien tehokkuus ja soveltuvuus tunnetaan edelleen melko puutteellisesti. Päätökset nahkiaiskantojen suojeluun ja ylläpitämiseen tähtäävistä toimenpiteistä joudutaan siis jatkossakin tekemään sangen suuren epävarmuuden vallitessa.

Tutkimusten perusteella voidaan tehdä seuraavia nahkiaiskantojen suojeluun ja elvyttämiseen liittyviä huomioita ja suosituksia:

- Jokien rakenteen muokkaamista yksipuolisemmaksi samoin kuin intensiivistä lyhytaikaissäännöstelyä tulisi välttää sekä tarvittaessa kunnostaa jokiuomaa ja lieventää säännöstelyä.
- Joen virtaama vaikuttaa merkittävästi nahkiaisen vaelluskäyttäytymiseen, mikä tulisi mahdollisuuksien mukaan huomioida jokien säännöstelykäytännöissä.
- Jos jatkotutkimukset tukevat havaintoa, että valaistut sillat hidastavat merkittävästi nahkiaisen vaellusta, siltojen valaistukseen tulee tehdä sellaisia muutoksia, jotka vähentävät jokeen johtuvan valon määrää.
- Koska aikuiset nahkiaiset hakeutuvat valoisana aikana suojaa tarjoaviin paikkoihin, päiväaikana ylisiirrettävät nahkiaiset tulisi vapauttaa mieluiten alueelle, jossa on suojaa tarjolla vapautuspaikan välittömässä läheisyydessä. Tämä todennäköisesti pienentäisi petojen aiheuttamaa kuolevuutta ja stressiä.
- Telemetriatutkimusten perusteella nahkiaisiin kohdistuva saalistus kasvaa, kun nahkiaiset pakkautuvat nousuesteen alapuolelle. Tästä syystä tulisi välttää ylisiirtoja alueelle, jolla tällainen vaara on olemassa, tai vaihtoehtoisesti vapauttaa ylisiirrettävät nahkiaiset vasta talvisäilytyksen jälkeen keväällä.
- Nahkiaisten ylisiirtojen tuloksellisuus tulisi selvittää seurantatutkimuksin etenkin, jos nahkiaisia siirretään ihmistoiminnan muuttamille alueelle.
- Koska vaellusaktiivuus vähenee kylmässä vedessä ja keväällä ennen kutua tapahtuvat vaellukset ovat todennäköisesti lyhyitä, syksyllä kylmän veden aikana (< 2 °C) ylisiirrettävät nahkiaiset tulisi vapauttaa lähelle potentiaalisia talvehtimis- ja kutualueita.

- Koska toukille näyttää kehittyvän kaivautumiskyky vasta 7–8 mm pituisena, alle 8 mm pituiset toukat on syytä istuttaa sellaisille alueille, joiden pohjamateriaali tarjoaa valmiita koloja, ja pyrkiä välttämään niiden ajautumista pohjille, joilla niille ei ole suojaa tarjolla.
- Luonnonmukainen kalaramppi mahdollistaa nahkiaisen vaelluksen matalien patojen yli.
- Virtavesiä kunnostettaessa tulisi tarvittaessa huomioida myös nahkiaisen elinympäristövaatimukset:
    - lohkarekasojen sijoittaminen kosken alaosaan ja välittömästi kosken ylä- ja alapuolelle talviaikaiseksi suojapaikaksi
    - sora-alueiden kunnostaminen kutu- ja mätimunien hautoutumisalueiksi sekä yksikesäisten toukkien elinalueiksi. Todennäköisesti soran tulee sisältää hienoainetta
    - kanavoiduilla/suoristetuilla hidasvirtaisilla alueilla toukka-alueiden lisääminen uomaa leventämällä, virtausnopeutta hidastamalla, rantaviivaa muotoilemalla ja mutkittelua lisäämällä

Lisää tietoa nahkiaiskantojen ylläpitämiseksi ja suojelemiseksi tarvitaan niin nahkiaisen ekologiasta, ihmistoiminnan vaikutuksista kuin erilaisten suojelu- ja elvyttämistoimenpiteiden tuloksellisuudestakin. Tärkeitä tutkimusaiheita ovat mm.

- Nahkiaisen kuolevuus ja tärkeimmät siihen vaikuttavat seikat eri elämänvaiheissa, mm. aikuisen nahkiaisen kuolevuus talvehtimiskaudella ja siihen vaikuttavat tekijät, kalastuksen vaikutus nahkiaispopulaatioihin, alaslaskeutuvien, muodonmuutoksen läpikäyneiden nahkiaisten kuolleisuus ja vaelluksen viivästyminen patoaltaissa
- Erilaisten suojelu- ja elvyttämistoimenpiteiden tuloksellisuus erilaisissa jokivesistöissä, mm. seulotun/pestyn soran soveltuvuus nahkiaisen kutuun ja mätimunien hautoutumisalustaksi, nahkiaisille soveltuvat kalatietyypit korkeissa patorakennelmissa
- Vaelluskäyttäytyminen, mm. aikuisten nahkiaisten vaellukset merialueella ja kutujoen valintaan vaikuttavat tekijät, keinotekoisen valaistuksen vaikutukset nahkiaisen vaelluskäyttäytymiseen

Suomessa valtaosa nahkiaistutkimuksesta on tehty ELY-keskuksissa liittyen valtion luonnontaloudellisiin velvoitteisiin. Tutkimustyö ELY-keskuksissa on loppunut ja valtionkin säännöstelemissä vesistöissä nahkiaisseurannoista vastaavat jatkossa ajoittain vaihtuvat konsulttiyhtiöt. Tulevaisuudessa luonteva taho Suomen nahkiaiskantojen suojeluun ja elvyttämiseen liittyvän tutkimus- ja kehitystyön jatkajaksi on Luonnonvarakeskus.

# REFERENCES

Abakumov V.A. [Абакумов В.А.] 1956. [The mode of life of the Baltic River Lamprey.] *J. Vopr. Ikhtiol.* 6: 122–128. [In Russian].

Abou-Seedo F.S. & Potter I.C. 1979. The estuarine phase of the spawning run of the river lamprey *Lampetra fluviatilis*. *J. Zool.* 188: 5–25.

Almeida P.R. & Quintella B.R. 2002. Larval habitat of the sea lamprey (*Petromyzon marinus* L.) in the River Mondego (Portugal). In: Collares-Pereira M.J., Coelho M.M. & Cowx I.G. (eds.), *Freshwater fish conservation: options for the future*, Fishing News Books, Blackwell Science, Oxford, pp. 121–130.

Andrade N.O., Quintella B.R., Ferreira J., Pinela S., Póvoa I., Pedro P. & Almeida P.R. 2007. Sea lamprey (*Petromyzon marinus L.*) spawning migration in the Vouga river basin (Portugal): poaching impact, preferential resting sites and spawning grounds. *Hydrobiologia* 582: 121–132.

Anon. 1995. *Code of conduct for responsible fisheries*. FAO, Rome.

Applegate V.C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. *Spec. Sci. Rept. U.S. Fish and Wildlife Serv.* 55: 1–237.

Aronen K. 1995. Kalajoen kalataloudellinen tarkkailututkimus 1990–1992 – Alavieskan tulvasuojelutöiden vaikutukset kala-, nahkiais- ja rapukantoihin. *Vesi- ja ympäristöhallituksen monistesarja* 456: 1–91.

Aroviita J & Hämäläinen H. 2008. The impact of water-level regulation on littoral macroinvertebrate assemblages in boreal lakes. *Hydrobiologia* 613: 45–56.

Asplund C. & Södergren S. 1975. Flodnejonögats (*Lampetra fluviatilis* L.) lekvandring i Rickleån. *Zool. Revy* 36: 111–119.

Beamish F.W.H. 1974. Swimming performance of adult sea lamprey, *Petromyzon marinus*, in relation to weight and temperature. *T. Am. Fish. Soc.* 103: 355–358.

Beamish F.W.H. & Jebbink J. 1994. Abundance of lamprey larvae and physical habitat. *Environ. Biol. Fish.* 39: 209–214.

Beamish F.W.H. & Lowartz S. 1996. Larval habitat of American brook lamprey. *Can. J. Fish. Aquat. Sci.* 53: 693–700.

Bergstedt R.A. & Seelye J.G. 1995. Evidence for lack of homing by sea lampreys. *T. Am. Fish. Soc.* 124: 235–239.

Binder T.R. & McDonald D.G. 2007. Is there role for vision in the behaviour of sea lampreys (*Petromyzon marinus*) during their upstream spawning migration? *Can. J. Fish. Aquat. Sci.* 64: 1403–1412.

Binder T.R. & McDonald D.G. 2008. The role of dermal photoreceptors during the sea lamprey (*Petromyzon marinus*) spawning migration. *J. Comp. Physiol. A* 194: 921–928.

Binder T.R., McLaughlin R.L. & McDonald D.G. 2010. Relative importance of water temperature, water level, and lunar cycle to migratory activity in spawning-phase sea lampreys in Lake Ontario. *T. Am. Fish. Soc.* 139: 700–712.

Birzaks J. & Abersons K. 2011. Anthtropogenic influence on the dynamics of the river lamprey *Lampetra fluviatilis* landinds in the River Daugava basin. *Scientific Journal of Riga technical University* 7: 32–38.

Choi B.-J. & Wilkin J.L. 2007. The effect of wind on the dispersal of the Hudson River plume. *J. Phys. Oceanogr.* 37: 1878–1897.

Eloranta A. 2010. Virtavesien kunnostus. *Kalatalouden keskusliiton julkaisu nro* 165: 1–278.

Elosegi A. & Sabater S. 2013. Effects of hydromorphological impacts on river ecosystem functioning: a review and suggestions for assessing ecological impacts. *Hydrobiologia* 712: 129–143.

Enequist P. 1937. Das Bachneunauge als ökologische Modification des Flussneunauges. Über die Fluss- und Bachneunaugen Schwedens. *Arkiv für Zoology* 29 A: 1–22.

Fine J.M., Vrieze L.A. & Sorensen P.W. 2004. Evidence that Petromyzontid Lampreys employ a common migratory pheromone that is partially comprised of bile acids. *J. Chem. Ecol.* 30: 2091–2110.

Fogelin P. 1972. Studier över drift av larver och nymetamorfoserade ungar av flodnejonöga (*Lampetra fluviatilis* L.) i Indalsälven och Rickleån. *Report from Rickleå Field Station No.* 20: 1–11.

Foulds W.L. & Lucas M.C. 2013. Extreme inefficiency of two conventional, technical fishways used by European river lamprey (*Lameptra fluviatilis*). *Ecol. Eng.* 58: 423–433.

Foulds W.L. & Lucas M.C. 2014 Paradoxical exploitation of protected fishes as bait for anglers: evaluating the lamprey bait market in Europe and developing sustainable and ethical solutions. *Plos One* 9 (6): 1–10.

Freyhof J. & Brooks E. 2011. *European Red List of freshwater fishes*. Publications Office of the European Union, Luxembourg.

Gamper N. & Savina M.V. 2000. Reversible metabolic depression in hepatocytes of lamprey (*Lampetra fluviatilis*) during pre-spawning: regulation by substrate availability. *Comp. Biochem. Physiol.* 127: 147–154.

Garcia X.F., Schnauder I. & Pusch M.T. 2012. Complex hydromorphology of meanders can support benthic invertebrate diversity in rivers. *Hydrobiologia* 685: 49–68.

Gaudron S.M. & Lucas M.C. 2006. First evidence of attraction of adult river lamprey in the migratory phase to larval odour. *J. Fish Biol.* 68: 640–644.

Goodwin C.E., Dick J.T.A., Rogowski D.L. & Elwood R.W. 2008. Lamprey (*Lampetra fluviatilis* and *Lampetra planeri*) ammocoete habitat associations at regional, catchment and microhabitat scales in Northern Ireland. *Ecol. Freshw. Fish* 17: 542–553.

Gregow H., Venäläinen A., Laine M., Niinimäki N., Seitola T., Tuomenvirta H., Jylhä K., Tuomi T. & Mäkelä A. 2008. Vaaraa aiheuttavista sääilmiöistä Suomen muuttuvassa ilmastossa. Ilmatieteen laitos. *Raportteja* 2008 (3) 1–99.

Hagelin L.-O. 1959. Further aquarium observations on the spawning habits of the river lamprey (*Petromyzon fluviatilis*). *Oikos* 10: 50–64.

Hagelin L.-O. & Steffner N. 1958. Notes on the spawning habits of the river lamprey (*Petromyzon fluviatilis*). *Oikos* 9: 221–238.

Hardisty M.W. 1979. *Biology of the cyclostomes*. Chapman & Hall, London.

Hardisty M.W. 1986. General introduction to lampreys. In: Holcík J. (ed.), *The Freshwater Fishes of Europe. Vol. 1, Part I. Petromyzontiformes*, Aula-Verlag, Wiesbaden, pp. 19–84.

Hardisty M.W. 2006. *Lampreys: life without jaws*. Forrest Text, Ceredigion.

Hardisty M.W. & Potter I.C. 1971. The behaviour, ecology and growth of larval lampreys. In Hardisty M.W. & Potter I.C. (eds.), *The biology of lampreys*, Academic Press, London, pp. 85–125.

Hiltunen E., Tolonen R., Kaski O. & Oikarinen J. 2013. *Nahkiainen –Perämeri, Tornio-Kokkola alue*. Nahkiainen ennen, nyt ja tulevaisuudessa -hanke, Ii.

Huusko A., Vehanen T. & Stickler M. 2013. Salmonid Habitats in Riverine Winter Conditions with Ice. In: Maddock I., Harby A., Kemp P. & Wood P. (eds.), *Ecohydraulics: An Integrated Approach*, Wiley-Blackwell, New Delhi, pp. 177–192.

Huusko A., Greenberg L., Stickler M., Linnansaari T., Nykänen M., Vehanen T., Koljonen S., Louhi P. & Alfredsen K. 2007. Life in the ice line: The winter ecology of stream salmonids. *River Res. Appl.* 23: 469–491.

Jackson A. & Moser M.L. 2012. Low-elevation dams are impediments to adult Pacific lamprey spawning migration in the Umatilla River, Oregon. *N. Am. J. Fish. Manage.* 32: 548–556.

Jang M.H. & Lucas M.C. 2005. Reproductive ecology of the river lamprey. *J. Fish Biol.* 66: 499–512.

Jellyman D.J., Glova G.J. & Sykes J.R.E. 2002. Movements and habitats of adult lamprey (*Geotria australis*) in two New Zealand waterways. *New Zeal. J. Mar. Fresh.* 36: 53–65.

Jylhä K., Ruosteenoja K., Räisänen J., Venäläinen A., Tuomenvirta H., Ruokolainen L., Saku S. & Seitola T. 2009. Arvioita Suomen muuttuvasta ilmastosta sopeutumistutkimuksia varten. ACCLIM-hankkeen raportti 2009. Ilmatieteen laitos. *Raportteja* 2009 (4) 1–102.

Keefer M.L., Boggs C.T., Peery C.A. & Caudill C.C. 2013a. Factors affecting dam passage and upstream distribution of adult Pacific lamprey in the interior Columbia River basin. *Ecol. Freshw. Fish* 22: 1–10.

Keefer M.L., Caudill C.C., Peery C.A. & Moser M.L. 2013b. Context-dependent diel behavior of upstream-migrating anadromous fishes. *Environ. Biol. Fish.* 96: 691–700.

Keefer M.L., Moser M.L., Boggs C.T., Daigle W.R. & Peery C.A. 2009. Variability in migration timing of adult Pacific lamprey (*Lampetra tridentate*) in the Columbia River, U.S.A. *Environ. Biol. Fish.* 85: 253–264.

Kelso J.R.M. 1993. Substrate selection by *Geotria australis* ammocoetes in the laboratory. *Ecol. Freshw. Fish* 2: 116–120.

Kelso J.R.M. & Glova G.J. 1993. Distribution, upstream migration and habitat selection of maturing lampreys, *Geotria australis*, in Pigeon Bay Stream, New Zealand. *Aust. J. Mar. Fresh. Res.* 44: 749–759.

Kelso J.R.M. & Todd P.R. 1993. Instream size segration and density of *Geotria australis* ammocoetes on two New Zealand streams. *Ecol. Freshw. Fish* 2: 108–115.

Kemp P.S., Russon I.J., Vowles A.S. & Lucas M.C. 2011. The influence of discharge and temperature on the ability of upstream migrant adult river lamprey (*Lampetra fluviatilis*) to pass experimental overshot and undershot weirs. *River Res. Appl.* 27: 488–498.

Kirillova E.A., Kirillov P.I., Kucheryavyy A.V. & Pavlov D.S. 2011. Downstream migration in ammocoetes of the Artic lamprey *Lethenteron camtschaticum* in some Kamchatka rivers. *J. Ichtyol.* 51: 1117–1125.

Laine A., Heikkinen K. & Sutela T. 2001. Incubation success of brown trout (*Salmo trutta*) eggs in boreal humic rivers affected by peatland drainage. *Arch. Hydrobiol.* 150: 289–305.

Laine A., Kamula R. & Hooli J. 1998. Fish and lamprey passage in a combined Denil and vertical slot fishway. *Fish. Manage. Ecol.* 5: 31–44.

Lee D.S. 1989. *Qualified laboratory assessment of larval lamprey substrate habitat se*lection. Research Completion Report, Great Lakes Fishery Commission, Michigan.

Lind L. & Nilsson C. 2014. *River ice processes in channelized and restored streams and rivers*. Abstract in 10th International Symposium on Ecohydraulics, Trondheim, Norway.

Lisitzin E. 1967. Day-to-day variation in sea level along the Finnish coast. *Geophysica 9*: 259–275.

Lucas M.C., Bubb D.H., Jang M.-H., Ha K. & Masters J.E.G. 2009. Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lampreys. *Freshwat. Biol.* 54: 621–634.

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

Malmqvist B. 1980a. Habitat Selection of Larval Brook Lampreys (*Lampetra planeri*, Bloch) in a South Swedish Stream. *Oecologia* 45: 35–38.

Malmqvist B. 1980b. The spawning migration of the brook lamprey, *Lampetra planeri* Bloch, in a South Swedish stream. *J. Fish Biol.* 16: 105–114.

Manly B.F.J., McDonald L.L., Thomas D.L., McDonald T.L. & Erickson W.P. 2002. *Resource selection by animals*. Kluwer Academic Publishers, Dordrect.

Masters J.E.G., Jang M.-H., Ha K., Bird P.D., Frear P.A. & Lucas M.C. 2006. The commercial exploitation of a protected anadromous species, the river lamprey (*Lampetra fluviatilis* (L.)), in the tidal River Ouse, north-east England. *Aquat. Conserv.* 16: 77–92.

Mateus C.S., Rodríguez-Muñoz R., Quintella B.R., Alves M.J. & Almeida P. 2012. Lampreys of the Iberian Peninsula: distribution, population status and conservation. *Endang. Species Res.* 16: 183–198.

McManamay R.A, Orth D.J., Dolloff C.A., Mark A. & Cantrell M.A. 2010. Gravel Addition as a Habitat Restoration Technique for Tailwaters. *N. Am. J. Fish. Manage.* 30: 1238–1257.

McMichael G.A., Rakowski C.L., James B.B. & Lukas J.A. 2005. Estimated fall Chinook salmon survival to emergence in dewatered redds in a shallow side channel of the Columbia River. *N. Am. J. Fish. Manage.* 25: 876–884.

Moser M.L. & Russon I.J. 2009. *Development of a separator for juvenile lamprey 2007-2008*. U.S. Army Corps of Engineers, Walla Walla, Washington.

Mundahl N.D. & Sagan R.A. 2005. Spawning ecology of the American book lamprey, *Lampetra appendix*. *Environ. Biol. Fish.* 73: 283–292.

Myllynen K., Ojutkangas E. & Nikinmaa M. 1997. River water with high iron concentration and low pH causes mortality of lamprey roe and newly hatched larvae. *Ecotoxicol. Environ. Safety* 36: 43–48.

Mäenpää E., Myllynen K., Pakkala J., Aronsuu K. & Koskenniemi E. 2001. *Talvehtimisaikaisen veden laadun vaikutus sukukypsien nahkiaisten (Lampetra fluviatilis) fysiologiseen tilaan ja mädin hedelmöittymiseen*. Länsi-Suomen ympäristökeskus, Kokkola.

Nika N. & Virbickas T. 2010. Brown trout *Salmo trutta* redd superimposition by spawning *Lampetra* species in lowland stream. *J. Fish. Biol.* 77: 2358–2372.

Negishi J.N, Inoue M. & Nunokawa M. 2002. Effects of channelisation on stream habitat in relation to a spate and flow refugia for macroinvertebrates in northern Japan. *Freshwat. Biol.* 47: 1515–1529.

Northcote T.G. 1984. Mechanisms of fish migration in rivers. In: McCleave J.D., Arnold G.P., Dodson J.J. & Neil W.H. (eds.), *Mechanisms of migration in fishes*, Plenum Press, New York - London, pp. 317–355.

Palomäki R. & Koskenniemi E. 1993. Effects of bottom freezing on macrozoobenthos in the regulated Lake Pyhäjärvi. *Arch. Hydrobiol.* 128: 73–90.

Pauwels S.J. & Haines T.A. 1994. Survival, hatching, and emergence success of Atlantic salmon eggs planted in three Maine streams. *N. Am. J. Fish. Manage.* 14: 125–130.

Piavis G.W. 1971. Embryology. In: Hardisty M.W. & Potter I.C (eds.), *The biology of lampreys. Vol I,* Academic Press, London, pp. 361–400.

Potter I.C. 1980. Ecology of larval and metamorphosing lampreys. *Can. J. Fish. Aquat. Sci.* 37: 1641–1657.

Potter I.C., Hilliard R.W., Bird D.J. & Macey D.J. 1983. Quantitative data on morphology and organ weights during protracted spawning-run period of the southern hemisphere lamprey *Geotria australis*. *J. Zool.* 200: 1–20.

Potter I.C., Hillard R.W., Bradley J.S. & Mckay R.J. 1986. The influence of environmental variables on the density of larval lampreys in different seasons. *Oecologia* 70: 433–440.

Prowse T.D. & Culp J.M. 2003. Ice breakup: a neglected factor in river ecology. *Can. J. Civil Eng.* 30: 128–144.

Quintella B.R., Andrade N.O., Dias N.M. & Almeida P.R. 2007. Laboratory assessment of sea lamprey larvae burrowing performance. *Ecol. Freshw. Fish 16*: 177–182.

Renaud C.B. 1997. Conservation status of Northern Hemisphere lampreys (Petromyzontidae). *J. Appl. Ichthyol.* 13: 143–148.

Riley W.D., Bendall B., Ives M.J., Edmonds N.J., Maxwell D.L. 2012. Street lightning disrupts the diel migratory pattern of wild Atalantic salmon, *Salmo salar* L., smolts leaving their natal stream. *Aquaculture* 330–333: 74–81.

Robinson T.C. & Bayer J.M. 2005. Upstream migration of Pacific lampreys in the John Day River, Oregon: behavior, timing, and habitat use. *Northwest Science* 79: 106–119.

Rubin J.-F., Glimsäter C. & Järvi T. 2004. Characteristics and rehabilitation of the spawning habitats of the sea trout, *Salmo trutta*, in Gotland (Sweden). *Fish. Manage. Ecol.* 11: 15–22.

Ruhanen T. 1987. *Perhonjoen keskiosan järviryhmän säännöstelyn täydennyshakemus –virtaama- ja vedenkorkeusselvitykset*. Kokkolan vesi- ja ympäristöpiiri, Kokkola.

Russon I.J., Kemp P.S. & Lucas M.C. 2011. Gauging weirs impede the upstream migration of adult river lamprey *Lampetra fluviatilis*. *Fish. Manage. Ecol.* 18: 201–210.

Sarkki H. 2005. *Perhonjoen hydrologiset selvitysvelvoitteet*. Länsi-Suomen ympäristökeskus, Kokkola.

Savolainen M. & Leiviskä P. 2008. Kalajoen vesistön tulvantorjunnan toimintasuunnitelma. *Pohjois-Pohjanmaan ympäristökeskuksen raportteja* 2: 1–94.

Shirakawa H., Yanai S. & Kouchi K. 2009. Habitat selection of fluvial lamprey larvae *Lethenteron japonicum* change with growth stage. *Ecol. Civil Eng.* 12: 87–98.

Silva S., Gooderham A., Forty M., Morland B. & Lucas M.C. 2014 Eggdrift and hatching success in European river lamprey Lampetra fluviatilis: is egg deposition in gravel vital to spawning success? *Aquat Conserv.: Mar. Freshw. Ecosyst.*. doi: 10.1002/aqc.2486.

Sjöberg K. 1977. Locomotor activity of river lamprey *Lampetra fluviatilis* (L.) during the spawning season. *Hydrobiologia* 55: 265–270.

Sjöberg K. 1980. Ecology of the European river lamprey (*Lampetra fluviatilis*) in Northern Sweden. *Can. J. Fish. Aquat. Sci.* 37: 1974–1980.

Sjöberg K. 2011. River lamprey *Lampetra fluviatilis* (L.) fishing in the area around the Baltic Sea. *J. Northern Stud.* 5: 51–86.

Smith D.M., Welsh S.A. & Turk P.J. 2011. Selection and preference of benthic habitat by small and large ammocoetes of the least brook lamprey (*Lampetra aepyptera*). *Environ. Biol. Fish.* 91: 421–428.

Smith D.M., Welsh S.A. & Turk P.J. 2012. Available benthic habitat type may influence predation risk in larval lampreys. *Ecol. Freshw. Fish* 21: 160–163.

Smith S.J. & Marsden J.E. 2009. Factors Affecting Sea Lamprey Egg Survival. *N. Am. J. Fish. Manage.* 29: 859–868.

Sokolov L.I., Tsepkin Y.A. & Barabanova Y.R. 1992 Reproductive ecology of the western brook lamprey, *Lampetra planeri* (Petromyzontidae). *J. Ichthyol.* 32(6): 145–150.

Starcevich S.J., Gunckel S.L. & Jacobs S.E. 2014. Movements, habitat use, and population characteristics of adult Pacific lamprey in a coastal river. *Environ. Biol. Fish.* 97: 939–953.

Sterba G. 1962. Die Neunaugen (Petromyzonidae). In: Demoll R. & Maier H.N (eds.), *Handbuch der Binnenfischerei Mitteleuropas. Vol. 3*, Verlagsbuchhandlung, Stuttgard, pp. 263–352.

Sugiyama H. & Goto A. 2002. Habitat selection by larvae of a fluvial lamprey, *Letheron reissneri* in a small stream and in an experimental aquarium. *Ichthyol. Res.* 49: 62–68.

Takayama M. 2002. Spawning activities and physical characteristics of spawning ground of *Lethenteron reissneri* at headstream of the Himekawa River, central Japan. *Ichthyol. Res.* 49: 165–170.

Taverny G., Lasalle G., Ortusi I., Roqueplo C., Lepage M. & Lambert P. 2012. From shallow to deep waters: habitats used by larval lampreys (genus *Petromyzon* and *Lampetra*) over a western European basin. *Ecol. Freshw. Fish* 21: 87–99.

Tesch F.-W. 1967. Aktivität und Verhalten wandernder *Lampetra fluviatilis*, *Lota lota* und *Anguilla anguilla* im Tidegebiet der Elbe. *Helgol. Wiss. Meeresunters.* 16: 92–111.

Tuikkala A. 1971 Nahkiaisen elintavoista ja sen pyynnistä Pyhäjoella. *Kalataloussäätiön monistettuja julkaisuja n:o* 40: 1–59.

Tuunainen P., Ikonen E. & Auvinen H. 1980. Lampreys and lamprey fisheries in Finland. *Can. J. Fish. Aquat. Sci.* 37: 1953–1959.

Törmälä S. 1981. *Siikajoen nahkiaisen pyynnistä, nahkiaiskannoista ja nahkiaispopulaatiosta*. MSc. Thesis. University of Oulu, Oulu.

Urho L., Pennanen J.T. & Koljonen M.L. 2010. Fish. In: Rassi P., Hyvärinen E., Juslén A. & Mannerkoski I. (eds.), *The 2010 Red List of Finnish Species*, Ympäristöministeriö & Suomen ympäristökeskus, Helsinki, pp. 336–343.

Valtonen T. 1980. European river lamprey (*Lampetra fluviatilis*) fishing and lamprey populations in some rivers running into Bothnian Bay, Finland. *Can. J. Fish. Aquat. Sci.* 37: 1967–1973.

Vrieze L.A., Bjerselius R. & Sorensen P.W. 2010. Importance of the olfactory sense to migratory sea lampreys petromyzon marinus seeking riverine spawning habitat. *J. Fish Biol.* 76: 949–964.

Vrieze L.A., Bergstedt R.A. & Sorensen P.W. 2011. Olfactory-mediated stream-finding behavior of migratory adult sea lamprey (*Petromyzon marinus*). *Can. J. Fish. Aquat. Sci.* 68: 523–533.

Wagner C.M., Twohey M.B. & Fine J.M. 2009. Conspecific cueing in the sea lamprey: do reproductive migrations consistently follow the most intense larval odour? *Anim. Behav.* 78: 593–599.

Weber C., Peter A. & Zanini F. 2007. Spatio-temporal analysis of fish and their habitat: a case study on a highly degraded Swiss river system prior to extensive rehabilitation. *Aquat. Sci.* 69: 162–172.

Weber C., Nilsson C., Lind L., Alfredsen K.T. & Polvi L.E. 2013. Winter Disturbances and Riverine Fish in Temperate and Cold Regions. *BioScience* 63: 199–210.

Wikgren B.-J. 1954. Dygnsrytmen hos nejonögat (*Petromyzon fluviatilis* L.) *Memo. Soc. Fauna Flora Fennica* 29: 24–27.

Yamasaki Y. 2007. Microhabitat use by the larvae of cryptic lamprey species in *Lethenteron reissneri* in a sympatric area. *Ichthyol. Res.* 54: 24–31.

Young R.J., Kelso J.R.M. & Weise J.G. 1990. Occurrence, relative abundance, and size of landlocked sea lamprey (*Petromyzon marinus*) ammocoetes in relation to stream characteristics in the Great lakes. *Can. J. Fish. Aquat. Sci.* 47: 1773–1778.

Yrjänä T. 1998. Efforts for In-stream Fish Habitat Restoration within the River Iijoki, Finland – Goals, Methods and Test Results. In: de Waal L., Large A. Wade M. (eds.), *Rehabilitation of Rivers: Principles and Implementation*, John Wiley & Sons Ltd, Sussex, pp. 239–250.

# ORIGINAL PAPERS

# I

## MIGRATORY BEHAVIOUR AND HOLDING HABITATS OF ADULT RIVER LAMPREYS (*LAMPETRA FLUVIATILIS*) IN TWO FINNISH RIVERS

by

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# Migratory behaviour and holding habitats of adult river lampreys (*Lampetra fluviatilis*) in two Finnish rivers

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The effect of environmental factors on migratory activity of adult river lampreys entering the Kalajoki and Perhonjoki, rivers in Finland, for spawning was studied using correlation and regression analyses. Telemetric tracking of 60 individuals was utilized to study the migratory patterns and holding habitat requirements of adult river lampreys. The increases in the river discharge, wind forcing towards the river mouth and speed and magnitude of river water cooling had positive effects on the numbers of lampreys entering the rivers whereas the increase in the illumination intensity of the moon had a negative effect on their migration activity. Radio-tagged lampreys typically passed slow-flowing river sections as well as steep riffles during one night, and were holding in runs, glides and the lowermost section of riffles. Substratum dominated by large boulders (> 256 mm) was preferred during winter holding behaviour. The migratory activity of lampreys released in low (< 2 °C) and high (> 16 °C) river water temperatures was low. Lampreys tended to halt next to illuminated bridges, and we suggest that this behaviour markedly shortened migration distances. The passage efficiency through a natural-like fish ramp in the low-head barrier was 100%. The results can be utilized in mitigation actions like river restoration, transplanting of adults, and improving passage and water flow regulation.

## Introduction

Populations of the river lamprey (*Lampetra fluviatilis*), like those of many other lamprey species in the northern hemisphere, have declined due to anthropogenic activities (e.g. Ojutkangas *et al*. 1995, Renaud 1997, Maitland 2003, Mateus *et al*. 2012). Consequently, the river lamprey is listed under Annex II of the European Commission Habitats directive (92/43/EEC), and most member states are obligated to create special areas of conservation for them. In Finland, river regulation measures like impoundment, hydropeaking, dredging, and embankments have reduced river lamprey populations during recent decades (Tuunainen *et al*. 1980, Valtonen 1980, Ojutkangas *et al*. 1995). In addition, poor water quality has been linked to population declines (Myllynen *et al*. 1997). In the Red List of Finnish Species 2010, the river lamprey is considered

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near threatened (Urho *et al*. 2010: 336–343), while it is still a species of commercial importance in many rivers in Finland, especially those entering the Bothnian Bay (Sjöberg 2011). In Finland, approximately one million lampreys are caught annually during their migration into the rivers during the catching season beginning on 16 August (Sjöberg 2011). However, the mean annual catch has decreased considerably since the 1970s, when it was estimated to be approximately 2.0–2.5 million individuals (Tuunainen *et al*. 1980). The annual catches have also declined significantly in the Kalajoki and Perhonjoki, rivers in northern Finland (own unpubl. data).

River lampreys migrate into the rivers entering the Bothnian Bay mainly in autumn (Wikgren 1954, Sjöberg 1980). Thus, lampreys typically spend from seven to nine months in the river before they spawn in the fast-flowing river sections in late May or early June (Sjöberg 1977, Tuunainen *et al*. 1980). Lampreys die after spawning. Hatched larvae remain for a few weeks in the nests and later, during summer, disperse downstream to slow-flowing river sections where they burrow in suitable substrata (Potter 1980, but *see* Silva *et al*. 2014). Larvae live burrowed in the sediments of streams and rivers from three to six years before they metamorphose into young adults and migrate to the sea (Potter 1980). After the sea phase, which is believed to last typically from one to two years, they migrate back to rivers for spawning (Maitland 2003).

Habitat requirements of larval river lamprey was recently studied (Goodwin *et al*. 2008, Taverny *et al*. 2012, Aronsuu and Virkkala 2014) and numerous studies were conducted on passage of adult lampreys over anthropogenic barriers (e.g. Lucas *et al*. 2009, Kemp *et al*. 2011, Russon *et al*. 2011, Foulds and Lucas 2013). Moreover, Jang and Lucas (2005) studied the reproductive ecology of the river lamprey in north-eastern England. However, general knowledge of migratory behaviour and holding habitats of adult river lampreys is limited, and is primarily based on observations from recent passage studies conducted in the field and laboratory (e.g. Lucas *et al*. 2009, Foulds and Lucas 2013) and older studies on migratory behaviour of river lampreys entering rivers (e.g. Tesch 1967, Asplund and Södergren 1975, Abou-Seedo and Potter 1979). However, while studying commercial exploitation of the river lamprey in the northeast of England, Masters *et al*. (2006) also studied the effects of some environmental factors on migratory activity.

The number of river lampreys entering rivers varies considerably from night to night even during the peak migration season. This variation has been associated with lunar phase (Tesch 1967, Asplund and Södergren 1975, Abou-Seedo and Potter 1979) and river flow (Asplund and Södergren 1975, Masters *et al*. 2006). Sea water level (Sjöberg 1980), wind conditions (Applegate 1950, Malmqvist 1980), and photoperiod (Asplund and Södergren 1975) have also been associated with the timing of lamprey upstream migration. However, the results of these studies are heterogenous and usually only a small set of variables was evaluated in any one study. After entering the river, *L. fluviatilis* has been observed to migrate up to 102 km (Lucas *et al*. 2009). Increased water flow has been shown to be an important factor increasing lamprey migratory activity (Masters *et al*. 2006) and successful passage of barriers (Lucas *et al*. 2009, Foulds and Lucas 2013), but on the other hand too high flow may slow down upstream migration (Masters *et al*. 2006, Kemp *et al*. 2011). Foulds and Lucas (2013) showed that river water temperature had no effect on visitation of lampreys at fish-way entrances. Recently, migratory behaviour and holding habitats of Pacific lamprey (*Entophenus tridentatus*) (e.g. Robinson and Bayer 2005, Keefer *et al*. 2009, Clements *et al*. 2012, Keefer *et al*. 2013a, 2013b, Starcervich *et al*. 2014) and sea lamprey (*Petromyzon marinus*) (e.g. Almeida *et al*. 2002, Quintella *et al*. 2004, Andrade *et al*. 2007, Binder and McDonald 2008a, 2008b, Binder *et al*. 2010, Vrieze *et al*. 2010, Vrieze *et al*. 2011) have been investigated. However, inferences drawn from studies on other species must be done with caution because migratory behaviour among lamprey species is known to differ, and there are interspecific differences in morphology (*see* Foulds and Lucas 2013). Migratory behaviour of different river lamprey populations is also known to vary (e.g., Abou-Seedo and Potter 1979, Sjöberg 1980, Maitland 2003), and in boreal areas marked seasonal changes, like freezing water temperatures with various ice phenomena, may lead to adaptive changes in behaviour and habitat use (*see* Huusko *et al*. 2013).

The increased information on the freshwater stage of adult lampreys helps to determine possible factors that may limit river lamprey populations and enhances the efficacy of conservation and rehabilitation of lamprey populations. Especially in regulated rivers, the success of migration, winter holding and spawning may be endangered (Ojutkangas *et al*. 1995, Jang and Lucas 2005, Lucas *et al*. 2009). The enhanced knowledge can be utilized in mitigation actions like river restoration, transplanting of adults, and improving passage and water flow regulation.

The main goal of this study was to increase knowledge on migratory behaviour and holding habitats of river lamprey. Historical daily catch data and daily measurements of environmental factors were used to study the effects of environmental factors on migration activity of lampreys entering the Kalajoki and Perhonjoki from the Bothnian Bay. Telemetry was utilized to study migration patterns and holding habitat requirements of adult lampreys in these rivers. In addition to studying general migration patterns and holding habitats, three separate telemetry experiments had more specific objectives relating to migratory behaviour: (1) to compare the suitability of two transplantation times and transplantation sites in the Perhonjoki; (2) to study the success of lampreys in passing a weir, where both natural-like and technical fish-ways were built; and (3) to compare the migration patterns of individuals that entered the Kalajoki in the early, middle and late migration seasons, and to evaluate the effects of illuminated bridges on migratory behaviour.

## Material and methods

### Study area

The study was carried out in the Kalajoki and Perhonjoki which flow into the Bothnian Bay, the northernmost part of the Baltic Sea, at 64°17´22´´N, 23°54´57´´E and 63°54´42´´N, 23°8´13´´E, respectively (Fig. 1). In these rivers, water quality is typical for rivers entering to the east coast of the Bothnian Bay, i.e., the water is humic and, especially during high flows, the content of suspended solids is high.

The drainage area of the Kalajoki is 4260 km$^2$ and the mean discharge (MQ) is 29 m$^3$ s$^{-1}$ (mean maximum discharge [MHQ] 246 m$^3$ s$^{-1}$, mean minimum discharge [MNQ] 4.1 m$^3$ s$^{-1}$). The length of the river is 110 km and the total drop 100 m. The middle and uppermost parts of the river (river kilometer [rkm] 45–110) are heavily modified. In the 1970s and early 1980s, four hydropower plants were built in the river and hydropeaking was started. Furthermore, the river flow is regulated by nine small lakes or reservoirs, which are situated in the upper part of the watershed. The lowermost 45 km of the river has been less modified, although in the early 1990s the Vivunkumpu weir (rkm 22) with a head loss of 1.2 m at MQ was built and about 3 km of river above the weir was heavily dredged. Later, a natural-like fish ramp (with a slope of 1:40) and a technical (Super-active baffle, Larinier) fishway (with a slope of 1:10) were built side by side on the north side of the weir. In the early 2000s, all the fast-flowing river sections (55 ha) below rkm 43, which had previously been dredged to enhance flood control and log floating, were restored to rehabilitate lamprey, crayfish and fish populations.

The drainage area of the Perhonjoki is 2523 km$^2$, and the mean discharge is 21 m$^3$ s$^{-1}$ (MHQ 138 m$^3$ s$^{-1}$, MNQ 3.0 m$^3$ s$^{-1}$). The length of the river is 140 km and the overall drop 180 m. Many large-scale regulation measures have been carried out there. The Pirttikoski power plant (rkm 61.5, Fig. 1) was built in the 1920s and an 80 m long artificial channel was constructed below it. Simultaneously, a 125-m-long natural channel below a regulation dam remained as flood channel. The Kaitfors power plant (rkm 33; Fig. 1) was built in the beginning of the 1980s and at the same time a 9 km section of the river was impounded. In the late 1990s, most of the earlier dredged fast flowing river sections above the reservoir were restored. Besides the reservoir constructed in 1980s, discharge of the Perhonjoki is regulated by three older reservoirs in the upper part of the watershed.

## Timing of migration in autumn

### Effect of environmental factors on the between-night variability in migration activity during the peak migration season

The between-night variability in migration activity during the most active period of spawning migration from 25 August to 25 October was studied using a multiple linear regression model. The dependent variable was the logarithm of catch per unit effort, log($\mathrm{CPUE}_{d,\mathrm{yr}}$), where $d$ = date of the night and yr = year for commercial basket trap fishing in the lowest rapid of the Perhonjoki, 6 km from the sea (Fig. 1). Lamprey basket CPUE can be regarded as a reliable index of migration activity as it is closely proportional to the number of individuals moving upstream on a given night (Binder *et al*. 2010). Baskets were placed side by side against the river bed and attached to stationary wooden constructions (*see* Tuunainen *et al*. 1980, Sjöberg 2011). Commercial fishermen emptied the baskets daily and recorded the numbers of traps in use and lamprey caught. A CPUE value (indiv. basket$^{-1}$ year$^{-1}$) was calculated for every night. Occasionally, when catch was high, they recorded only the total weight of lampreys caught. In those cases the weight was transformed to the number of individuals using the seasonal mean weights reported by Törmälä (1980). For each year (1982–1984), data from 4–5 fishermen were used. The number of basket traps per night ranged from 27 to 72, averaging 52.

During the study years, there were only a few lamprey fyke nets in the river below the baskets and consequently their effect on the catch of the basket traps could be regarded as negligible. However, the number of fyke nets increased markedly later, which is the reason for the use of data from the early 1980s only. The season from 25 August to 25 October was selected for analysis because according to long-term catch data, it is typically the most intensive time period of spawning migration (own unpubl. data).

The previous night log($\mathrm{CPUE}_{d-1,\mathrm{yr}}$) was included in the regression model as a structural independent variable so that the night to night difference could be monitored. This variable also accounted for the serial correlation structure in the CPUE data (*see* e.g. Binder *et al*. 2010). It also moderated the influence of the time-lagged effects of the environmental variables affecting migration.

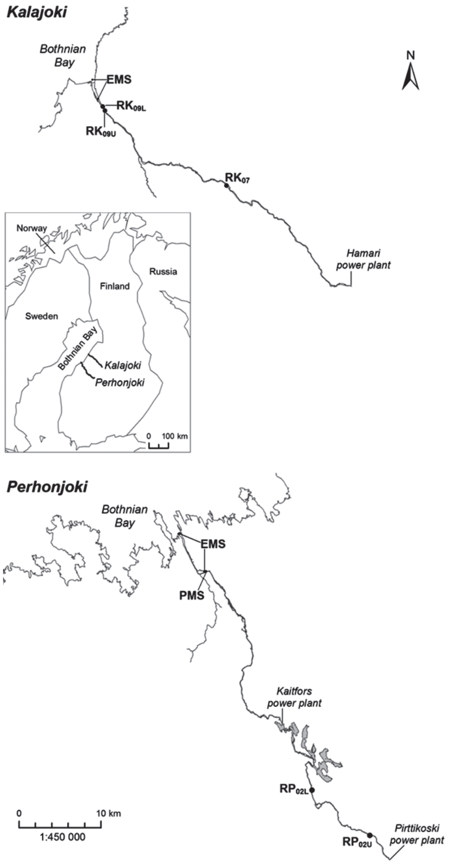

**Fig. 1**. Map of the study area showing the locations of the lamprey catching areas from where the data for the regression analyses were acquired (PMS = peak migration season, EMS = early migration season), and of the release sites in the telemetry experiments $P_{02}$ (release sites $RP_{02L}$ and $RP_{02U}$), $K_{07}$ ($RK_{07}$) and $K_{09}$ ($RK_{09L}$ and $RK_{09U}$).

The level of CPUE varies between years due to variation in migrating spawning population. This variation was accounted for by two dummy variables $D_{1983}$ and $D_{1984}$, having the value 1 for the respective year data and 0 in other years; thus for 1982 they both had the value 0. These variables were also structural, i.e. included in every model irrespective of the $p$ value of their slope estimates.

The selection of independent environmental variables was based on earlier studies and the local experience-based knowledge of the fishermen. The variables were discharge (DIS), river water temperature ($T$), illumination intensity of the moon (MII), percentage of the moon illuminated (MPI), cloud cover (CC), wind vector towards the river mouth (WV), sea water level (SWL), and night length (NL).

The mean discharge of the Perhonjoki was measured daily by the Kokkola Water District with a precision of 0.1 $m^3$ $s^{-1}$. The average of mean discharges for the previous and following days was used as a value of the discharge ($\mathrm{DIS}_{d,\mathrm{yr}}$) for a given night.

Illumination intensity of the moon ($\mathrm{MII}_{d,\mathrm{yr}}$) was estimated using an algorithm by Dr. György Tóth (Gothard Astrophysical Observatory of the R. Eötvös University) adapted for computers by Dr. Miklos Kiss (University of West Hungary Savaria University Centre) (*see* Nowinszky *et al*. 2012). The software calculates the illumination (lux) originating from moonlight for any given geographical locality, date and time, including a correction for cloudiness. The degree of cloud cover (CC) was scored using a scale from 0 to 8 (0 = clear sky, 8 = full cloud cover) in Kruunupyy, 17 km south from the trapping site. For a given night, the illumination intensities at 20:40, 23:40 and 2:40 UTC were estimated, and the average of these was used as an estimate of the illumination intensity of the moon for a given night. For percentages of the moon illuminated (MPI) during each night *see* Appendix on the last page of the online version of the article (at www.borenv.net). The night length ($\mathrm{NL}_{d,\mathrm{yr}}$) was the time in minutes between sunset and sunrise in the city of Kokkola, situated 5 km south from the estuary of the Perhonjoki.

River water temperature ($T_{d,\mathrm{yr}}$) was estimated from the observations of air temperature and solar radiation made by the Finnish Environment Institute. These estimates correlated strongly with the true water temperature measurements in the field (Pearson correlation: $r = 0.98$, $n = 42$, $p < 0.001$). The day-to-day differences between these estimated temperatures were on average less than 0.3 °C. Therefore, the temperature decrease speed $\mathrm{TDS}_{\mathrm{d,yr}}$ was illustrated by the complement of the five previous day slope in temperature. The slope was calculated by linearly regressing the daily temperature estimates for days $d - 1$ to $d - 6$ against day numbers.

Ten-minute mean wind direction (WD) with an accuracy of 10° and wind speed (WS) with an accuracy of 1 m $s^{-1}$ were measured at 3-h intervals in Kruunupyy. The direction was transformed to a direction component towards the river mouth (315°) by

$$\mathrm{WDC} = \cos(\mathrm{WD} - 315°). \qquad (1)$$

Wind direction component and wind speed were combined into a vector component variable (WVC) indicating wind forcing towards the river mouth as follows:

$$\mathrm{WVC} = \mathrm{WDC} \times \mathrm{WS}. \qquad (2)$$

The average of WVC at 17:40, 20:40, 23:40 and 2:40 UTC was used as a value for a given night of wind vector ($\mathrm{WVC}_{d,\mathrm{yr}}$).

Sea water level ($\mathrm{SWL}_{d,\mathrm{yr}}$) was measured with an accuracy of 1 cm twice a day, at 8:00 and 16:00, in Pietarsaari, 26 km south from the estuary of the river Perhonjoki. The value of $\mathrm{SWL}_{d,\mathrm{yr}}$ for a given night was the average of the measurements of previous afternoon and following morning.

Thus, the regression model was

$$\begin{aligned}\log(\mathrm{CPUE}_{d,\mathrm{yr}}) = \beta_0 &+ \beta_1 \log(\mathrm{CPUE}_{d-1,\mathrm{yr}}) \\ &+ \beta_2 D_{1983} + \beta_2 D_{1984} + \beta_i X_{i,d,\mathrm{yr}} \\ &+ \ldots + \beta_j X_{j,d,\mathrm{yr}} + \varepsilon_{d,\mathrm{yr}}, \end{aligned} \qquad (3)$$

where $X$ are the entered environmental variables. These were entered into the model based on the criteria of low $p$ value (< 0.05) for their $\beta$ estimates and avoiding severe multicollinearity of the variables (variance inflation factor, VIF << 5). Several variables, e.g. temperature and night length, were highly correlated and therefore could not be entered simultaneously. Also, if the variables were used in forming other variables [MII = $f$(MPI, CC)], they were not entered simultaneously. Deviation of the distribution of residuals $\varepsilon_{d,\mathrm{yr}}$ from normal was assessed. The linearity of the effects of environmental variables was assessed by visual judgement of the partial regression plots, where $x$ = variable and $y$ = log(CPUE). In case of apparent nonlinearity, transformations were applied to meet the linearity requirement.

To study whether migratory activity was regulated by illumination intensity of the moon or by the lunar cycle itself, possibly affecting internal rhythms of lampreys, the cases when the portion of the moon illuminated (MPI) was > 50% were studied. It was assumed that in those cases the cloud cover may have a marked effect on migratory behaviour by decreasing illumination. The other variables found significant in the previous models for the whole data were kept in the model. MPI and CC were entered into the model instead of MII to determine whether they both significantly affect the migration (slope significantly different from zero) or if only MPI is needed.

### Effect of discharge and river temperature on early season migratory activity

To assess the significance of discharge and river temperature as potential cues controlling the relative number of lampreys entering estuaries in early season, fyke net catch data from years 1995–2010 were utilized to create a dependent variable. Fyke nets are bag-shaped nets which are held open by hoops and equipped with wings (*see* Tuunainen *et al*. 1980, Sjöberg 2011). The data for 1995 from the Perhonjoki, the data for 1997 from the Kalajoki, and the data for 1998 and 2004 from both rivers were excluded due to long-lasting high-flood flows, which affected the catchability of fyke nets and even temporarily prevented fishing. Most of the fishermen catching lampreys from the estuaries of these rivers (Fig. 1) recorded total catch and the number of fyke nets in use every time they emptied their traps, not necessarily daily. In the Kalajoki, the average number of fyke nets in use was 38 and in the Perhonjoki 21. The mean CPUE was calculated annually for the early season (16–31 August) and for the whole season until the end of October (16 August–31 October) in both rivers. The ratio of the early season CPUE and the whole season CPUE was used as an index of relative migratory activity in the early season $\mathrm{reCPUE}_{\mathrm{yr}}$.

The mean discharge of the rivers was measured daily by the Kokkola Water District with an accuracy of 0.1 $\mathrm{m}^3\ \mathrm{s}^{-1}$. The yearly average of mean discharges during early season (16–31 August) was calculated, and the ratio of this average and mean discharge of the river in 1995–2010 was used as a value of the variable relative discharge ($\mathrm{reDIS}_{\mathrm{yr}}$). As the dependence between reCPUE and reDIS was not linear, the discharge was logarithmised.

The daily river water mean temperatures were estimated by the Finnish Environmental Centre, and the annual average ($\mathrm{TA}_{\mathrm{yr}}$), maximum ($\mathrm{TMAX}_{\mathrm{yr}}$) and minimum temperatures ($\mathrm{TMIN}_{\mathrm{yr}}$) of the early season (16–31 August) were calculated. Further, the difference between the highest and the lowest estimated temperatures during the early season, the temperature decrease ($\mathrm{TD}_{\mathrm{yr}}$), were also calculated, for which positive values corresponded with cooling.

Correlation, partial correlation and regression analyses were applied to assess the effects of reDIS and different temperature-based variables on the relative early season migration activity in different years.

## Migratory behaviour and holding habitats of radio-tagged lampreys in the rivers

### Lamprey collection, tagging and radio tracking

Lampreys used in the telemetry experiments were captured by the local fishermen with fyke nets or baskets in the estuaries or the lowermost riffles of the Perhonjoki or Kalajoki one to two days before tagging. Prior to tagging, lampreys were held in livewells in the river near capture sites and then transported to a laboratory in an aerated container.

Transmitters (Advanced Telemetry Systems) were 16 mm long, 8 mm in diameter and equipped with a 20-cm-long whip antenna. The transmitters used in the 2002 and 2009 experiments (model F1420) weighed 1.2 g in air and operated at 150.493–150.872 MHz and 138.201–138.521 MHz, respectively. The transmitter used in the 2007 experiment (model F1555) weighed

1.3 g in air and operated between 151.020 and 151.260 MHz. The expected transmitter battery lives were 25–58 days for the model F1420 and 88–115 days for the model F1555. Lampreys for the experiments were selected so that the weight of a transmitter should not exceed 2% of the total weight of a lamprey; the average percentage was 1.7%. However, for 8 out of the 60 tagged lampreys the weight of the tag did exceed 2% of the total weight; five of these were lampreys from the second release occasion in the experiment conducted in 2009.

Before the implantation of transmitters, lampreys were anesthetized with benzocaine (50 mg $l^{-1}$) and the length (accuracy 1 mm) and mass (accuracy 1 g) of animals were measured. In 2009, the masses of the lampreys for the first release occasion were estimated by length-mass regression based on measurements conducted in 2009. After the measurements, a lamprey was placed on a split tube covered with a moistened tissue, and a 2-cm longitudinal incision was made along the ventral midline of the posterior end of the body cavity. A tag was inserted into the body cavity, and a hypodermic needle was used to pass the antenna through the body wall approximately 3 cm posterior to the incision. The incision was closed with three to four non-absorbable 6/0 monofilament sutures and cleaned with iodine (Betadine®). Lampreys were transferred to an aerated tank and allowed to recover. Before release, lampreys were held for two to seven days in aerated tanks or in livewells in the river near the release site. No mortality occurred during this period.

Altogether 12 release groups of five lampreys were radio-tagged and released. In the first experiment conducted in the Perhonjoki in 2002 ($P_{02}$), lampreys were released at two locations ($RP_{02L}$ and $RP_{02U}$) on two occasions in the middle section of the river to the area, which has been used for transplanting lampreys for decades (Fig. 1 and Table 1). In the experiment conducted in the Kalajoki in 2007 ($K_{07}$), two groups were released on different occasions at rkm 21.6 ($RK_{07}$), approximately 350 m below the Vivunkumpu weir (Fig. 1 and Table 1). In the experiment performed in the Kalajoki in 2009 ($K_{09}$), two release sites ($RK_{09L}$ and $RK_{09U}$) in the lowermost part of the river and three different release occasions (RO) were used (Fig. 1 and Table 1). All the lampreys were released after sunset and 50 to 600 untagged lampreys were released with every release group to decrease their immediate predation probability e.g. by the northern pike (*Esox lucius*). Temperature during release occasions varied between 1.0 and 16.5 °C and discharge between 2.3 and 29 $m^3 s^{-1}$ (Figs. 2–4).

The movements of lampreys were tracked with a telemetry receiver (Advanced Telemetry Systems Inc., model R2100) equipped with a hand held four-element Yagi antenna. In $K_{09}$, another receiver (Lotek wireless Inc., model STR 100) was also used. First, the previous positions of lampreys were checked, and the locations of detected lampreys were documented. Lampreys

**Table 1**. Release dates, weight (minimum-mean-maximum) and the number of observations (minimum-mean-maximum) of lampreys released at different release sites ($RP_{02L}$, $RP_{02U}$,$RK_{07}$, $RK_{09L}$ and $RK_{09U}$) in the telemetry experiments $P_{02}$, $K_{07}$ and $K_{09}$. On every occasion five lampreys were released at each site.

| Experiment | Release site | Release date | Lamprey weight (g) (min-mean-max) | Number of observations (min-mean-max) |
|---|---|---|---|---|
| $P_{02}$ | $RP_{02L}$ | 25 Sep. 2002 | 63-73-82 | 23-27-30 |
| $P_{02}$ | $RP_{02L}$ | 23 Oct. 2002 | 68-87-117 | 15-18-19 |
| $P_{02}$ | $RP_{02U}$ | 25 Sep. 2002 | 66-70-76 | 6-16-24 |
| $P_{02}$ | $RP_{02U}$ | 23 Oct. 2002 | 81-86-95 | 12-17-19 |
| $K_{07}$ | $RK_{07}$ | 17 Sep. 2007 | 60-74-88 | 18-25-29 |
| $K_{07}$ | $RK_{07}$ | 1 Oct. 2007 | 67-75-95 | 11-15-19 |
| $K_{09}$ | $RK_{09L}$ | 27 Aug. 2009 | 60-68-71 | 11-15-20 |
| $K_{09}$ | $RK_{09L}$ | 17 Sep. 2009 | 52-64-76 | 2-14-18 |
| $K_{09}$ | $RK_{09L}$ | 14 Oct. 2009 | 72-78-86 | 1-6-7 |
| $K_{09}$ | $RK_{09U}$ | 27 Aug. 2009 | 58-72-84 | 22-24-27 |
| $K_{09}$ | $RK_{09U}$ | 17 Sep. 2009 | 51-61-71 | 7-13-16 |
| $K_{09}$ | $RK_{09U}$ | 14 Oct. 2009 | 63-69-80 | 5-6-7 |

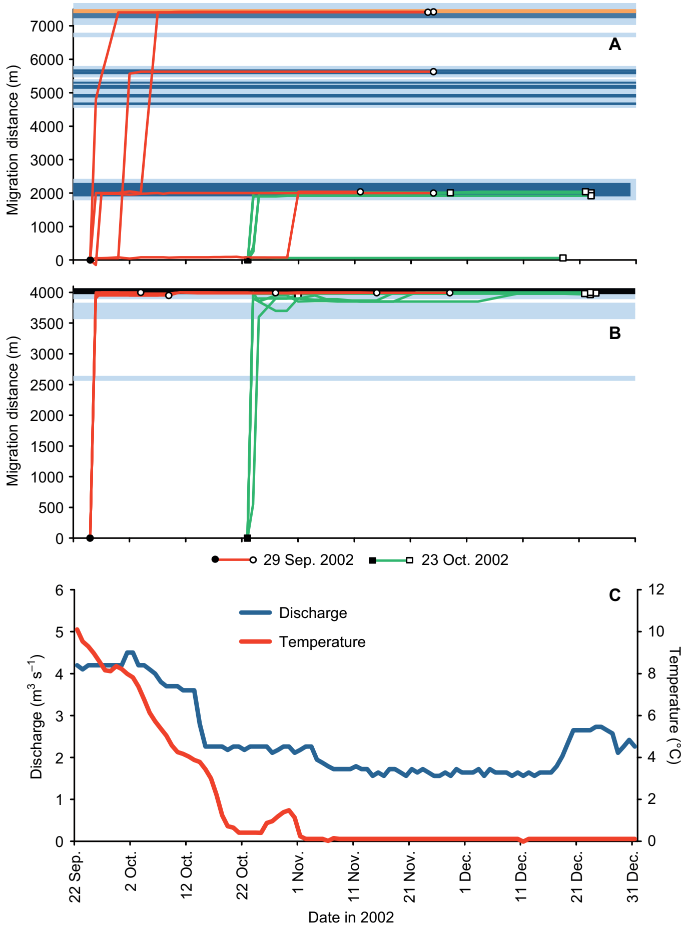

**Fig. 2**. The movements of radio-tagged river lampreys released at sites RP$_{02L}$ (**A**) and RP$_{02U}$ (**B**) on 29 Sep. 2002 (red lines) and 23 Oct. 2002 (green lines). Filled symbols represent release date/site and open symbols the last observation date/site for an individual lamprey. The mesohabitat categories of the river sections are shown as a background colour of the figure: white = pool, light blue = run/glide, dark blue = riffle. The location of an illuminated bridge is shown with a horizontal orange line and the location of the power plant/dam with a black horizontal line. (**C**) The river water temperature (°C) and discharge (m$^3$ s$^{-1}$) during the experiment.

which were not found in the same position as during the previous surveillance were searched for by driving along roads beside the river with a vehicle fitted with a Yagi antenna. While driving, the receiver continuously monitored the assigned channels. Where the roads did not run close to the river, the potential holding sites were checked by tracking lampreys on foot. When a lamprey was found, the new position was located with approximately 5–10 m accuracy by tracking from different directions and adjusting the sensitivity of the receiver and finally recorded by GPS. During the first week after release, the locations of lampreys were monitored almost daily and after that two to three times per week. When river water temperature had cooled to less than 1 °C, due to reduced activity the positions of lampreys were monitored once a week or less frequently. In P$_{02}$ and K$_{07}$, tracking was continued until December when the batteries of most of the transmitters had died. In the K$_{09}$, monitoring was stopped in mid November after water temperature had dropped below 1 °C.

### Habitat characteristics of holding sites

Altogether, 39 lampreys released at RP$_{02L}$, RK$_{07}$,

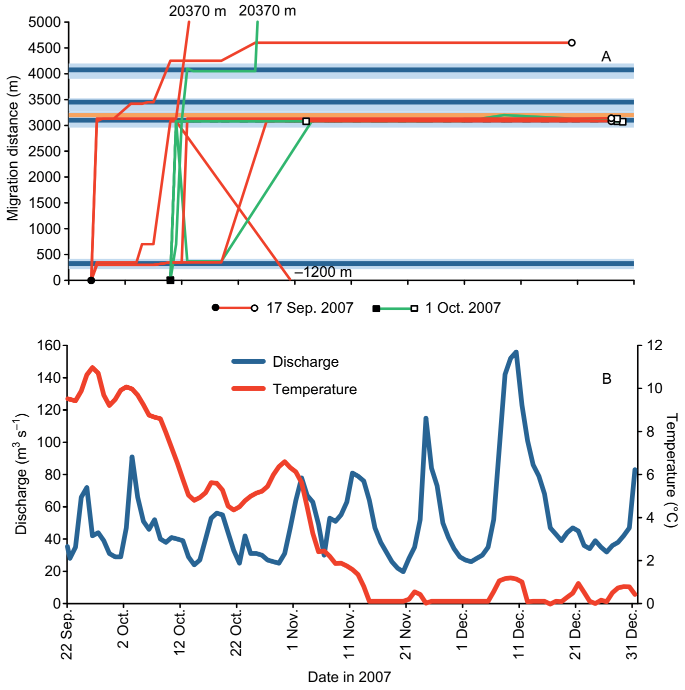

**Fig. 3**. (**A**) The movements of radio-tagged river lampreys released at site RK$_{07}$ on 17 Sep. 2007 (red lines) and 1 Oct. 2007 (green lines). 20 370 m and –1200 m denote the exceptionally long upstream and downstream migrations. Other symbols as in Fig. 2. (**B**) The river water temperature (°C) and discharge (m$^3$ s$^{-1}$) during the experiment.

RK$_{09L}$ and RK$_{09U}$ were being tracked after river temperature had dropped below 1 °C. The mesohabitat of the final holding site of each lamprey was regarded as a selected wintering mesohabitat. Due to rough position accuracy (5–10 m) only two mesohabitat categories, fast-flowing river section (riffles, glides and runs) and slow-flowing river section (pools) were used. In the river sections that lamprey used for migration, the availability and location of fast-flowing and slow-flowing mesohabitats were determined based on earlier mesohabitat surveys conducted during restoration planning. Field surveys and aerial photographs were used to double-check mesohabitat locations and availability. The total length of the river sections in each category within the migration route of each lamprey was measured, and it was used as a measure of available mesohabitats.

In K$_{09}$, the holding locations of 12 lampreys were positioned on 6–13 November with an accuracy of 0.5 m$^2$ and regarded as selected wintering sites. At each location, the dominant substratum size was estimated using the Udden-Wentworth grain size scale (Wentworth 1922) and the mesohabitat type (riffle, run/glide or pool) of the location was determined. In addition, water depth, distance to the nearest river bank and current speed 5 cm above bottom and 5 cm below the surface were measured. The current speed measurements were made with a Schiltknecht Mini Air 2 anemometer. The current speed 5 cm below surface was used for analyses because the water velocity close to bed varied greatly due to bed effect.

Availability of habitat resources was determined for 10 lampreys using wintering sites situated less than 1.6 km from the site they were released (RK$_{09L}$ or RK$_{09U}$). The habitat evaluation was performed between 30 July and 1 August 2013. During the evaluation, the discharge was 7–8 m$^3$ s$^{-1}$, corresponding to that in 2009 when the environmental factors of the winter holding sites were determined. The habitat evaluation

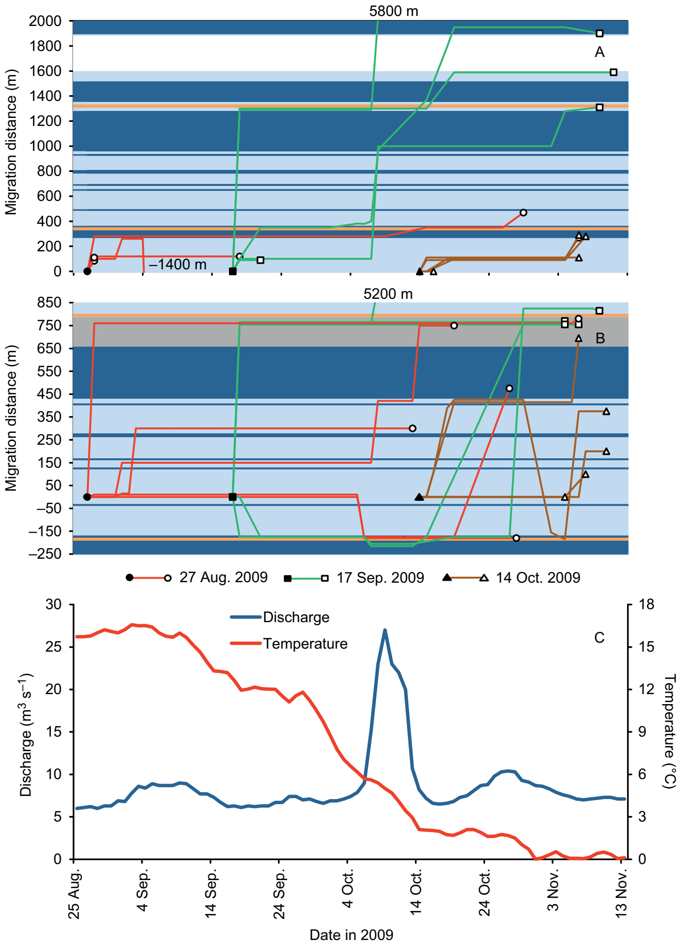

**Fig. 4**. The movements of radio-tagged river lampreys released at sites $RK_{09L}$ (**A**) and $RK_{09U}$ (**B**) on 27 Aug. 2009 (red lines), 17 Sep. 2009 (green lines) and 14 Oct. 2009 (brown lines). 5800 m, 5200 m and –1400 m denote the exceptionally long upstream and downstream migrations. Other symbols as in Fig. 2. (**C**) The river water temperature (°C) and discharge ($m^3$ $s^{-1}$) during the experiment.

was made along transects perpendicular to stream flow with 50 m increments starting 10 m upriver from the lowermost releasing site ($RK_{09L}$). In two locations, three transects were characterised in 50-m-long river sections to get sufficient availability data for lampreys, which migrated only a short distance from the release site. In the final data, these characteristics got a weight of 1/3 as compared with the other ones. The environmental measurements on each transect were made at 10-m intervals. The distance of the first sample point from the bank (0–10 m) was assigned randomly. In total, 214 sampling sites on 36 transects were evaluated.

## Statistical analyses

Only lampreys which were tracked in the river 25 days after release were included in the statistical analysis comparing migration distance between ROs. The significance of differences in migration distances between ROs in $RP_{02L}$ was tested with a Mann-Whitney *U*-test. In $K_{09}$, the results of two release sites ($RK_{09L}$, $RK_{09U}$) were pooled to get sufficient amount of data for statistical analysis, and a Kruskal-Wallis test was used for comparing the difference in migration distance among three ROs. Furthermore, a Mann-Whitney *U*-test with Bonferroni-adjusted

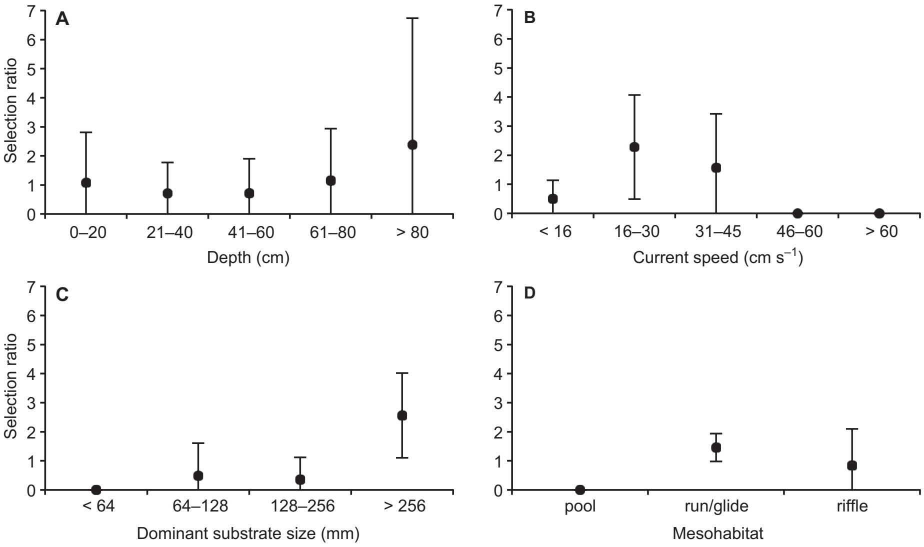

**Fig. 5**. Selection ratios (± 90%CI) for holding sites of 10 river lampreys for different categories of (**A**) water depth, (**B**) surface current speed, (**C**) prevailing substrate type, and (**D**) mesohabitat.

significance levels were used for pairwise comparisons.

To study the wintering mesohabitat selection of the 39 radio-tagged lampreys, Manly's selection ratios (*w*) for the population (lampreys released at $RP_{02L}$, $RK_{09L}$, $RK_{09U}$ and $RK_{07}$, and were still detected when temperature dropped below 1 °C) for both resource categories (fast-flowing and slow-flowing river sections) were calculated according to Manly *et al.* (2002) by using design III, in which availability of different categories of resource units varies between animals. In the calculation, it was assumed that all resources on the lamprey migration route were equally available for wintering habitat selection. Selection ratios close to 1 indicate no selectivity for a given resource category, values > 1 preference and values < 1 avoidance. Bonferroni 95% confidence intervals (95%CI) were also constructed. Habitat preference was considered significant if the lower limit of CI was higher than 1, and similarly avoidance was significant if the upper limit of CI was lower than 1 (Manly *et al.* 2002). Negative lower limits for confidence intervals were replaced by 0 since negative values for selection ratios are impossible.

To calculate selection ratios for wintering microhabitats measured in $K_{09}$, each environmental factor was first divided into 3–5 different resource categories (*see* Manly *et al.* 2002 and Fig. 5 for categories). Availability of each category for each lamprey was assigned based on the evaluation of transects that the lamprey had crossed before selecting the wintering site. The selection ratios and confidence intervals for a population (10 lampreys) for each resource category was calculated as described above, but due to small sample size, a 90% confidence interval (90%CI) was used.

## Results

### Effect of environmental factors on the between-night variability in migration activity during the peak migration season

The environmental variables explaining significantly the variation in migration were river discharge (positive), illumination intensity of the moon (negative), temperature decrease speed (positive) and wind vector, an index of wind forcing towards the river mouth (positive) (Table 2). The detailed analysis of the period when more than 50% of the moon was illuminated (Table 3) indicated that both the proportion of the moon illuminated (negative) and the cloud cover (positive) affected migratory activity (Table 3, model 2). Also, when entered sepa-

**Table 2**. The parameter estimates and $p$ values for a linear regression model explaining the nightly variability in log(CPUE) of river lampreys in basket traps during the period 25 August–25 October in the years 1982–1984. VIF = variance inflation factor, an index of collinearity; CPUE = catch per unit effort; $D$ = dummy variable separating years; DIS = discharge; MII = illumination intensity of the moon; TDS = Temperature decrease speed; WVC = wind vector component; the subscripts $d$ and yr refer to a given night and year, respectively. The residuals do not deviate significantly from normality ($p = 0.200$).

| Variable | Unstandardised | | Standardised $\beta$ | $t$ | $p$ | VIF |
|---|---|---|---|---|---|---|
| | $\beta$ | SE | | | | |
| Adjusted $r^2 = 0.752$ | | | | | | |
| Constant | 0.227 | 0.078 | | 2.917 | 0.004 | |
| $\log(\mathrm{CPUE}_{d-1,\mathrm{yr}})$ | 0.527 | 0.054 | 0.534 | 9.719 | < 0.001 | 2.200 |
| $D_{1983}$ | 0.168 | 0.045 | 0.194 | 3.765 | < 0.001 | 1.934 |
| $D_{1984}$ | –0.050 | 0.040 | –0.058 | –1.246 | 0.214 | 1.599 |
| $\log(\mathrm{DIS}_{d,\mathrm{yr}})$ | 0.185 | 0.068 | 0.118 | 2.716 | 0.007 | 1.377 |
| $\mathrm{MII}_{d,\mathrm{yr}}$ | –2.366 | 0.523 | –0.188 | –4.524 | < 0.001 | 1.260 |
| $\mathrm{TDS}_{d,\mathrm{yr}}$ | 0.143 | 0.068 | 0.089 | 2.089 | 0.038 | 1.320 |
| $\mathrm{WVC}_{d,\mathrm{yr}}$ | 0.023 | 0.006 | 0.149 | 3.672 | < 0.001 | 1.201 |

**Table 3**. The parameter estimates and $p$ values for two alternative linear regression models explaining the variability in log(CPUE) of river lampreys in basket traps during the period 25 August–25 October in the years 1982–1984. Selected data: proportion of the moon illuminated (MPI) > 50%. CC = cloud cover; the other symbols as in Table 2.

| Variable | Unstandardised | | Standardised $\beta$ | $t$ | $p$ | VIF |
|---|---|---|---|---|---|---|
| | $\beta$ | SE | | | | |
| Model 1: Adjusted $r^2 = 0.769$ | | | | | | |
| Constant | 0.134 | 0.113 | | 1.192 | 0.237 | |
| $\log(\mathrm{CPUE}_{d-1,\mathrm{yr}})$ | 0.447 | 0.080 | 0.442 | 5.601 | < 0.001 | 2.517 |
| $D_{1983}$ | 0.300 | 0.076 | 0.328 | 3.931 | < 0.001 | 2.805 |
| $D_{1984}$ | 0.042 | 0.064 | 0.045 | 0.659 | 0.512 | 1.895 |
| $\log(\mathrm{DIS}_{d,\mathrm{yr}})$ | 0.282 | 0.101 | 0.162 | 2.800 | 0.006 | 1.358 |
| $\mathrm{TDS}_{d,\mathrm{yr}}$ | 0.158 | 0.118 | 0.086 | 1.337 | 0.185 | 1.649 |
| $\mathrm{WVC}_{d,\mathrm{yr}}$ | 0.028 | 0.010 | 0.177 | 2.938 | 0.004 | 1.461 |
| $\mathrm{MII}_{d,\mathrm{yr}}$ | –2.633 | 0.649 | –0.219 | –4.058 | < 0.001 | 1.173 |
| Model 2: Adjusted $r^2 = 0.758$ | | | | | | |
| Constant | 0.269 | 0.201 | | 1.341 | 0.183 | |
| $\log(\mathrm{CPUE}_{d-1,\mathrm{yr}})$ | 0.440 | 0.093 | 0.435 | 4.737 | < 0.001 | 3.248 |
| $D_{1983}$ | 0.315 | 0.082 | 0.345 | 3.831 | < 0.001 | 3.119 |
| $D_{1984}$ | 0.057 | 0.066 | 0.062 | 0.861 | 0.392 | 1.971 |
| $\log(\mathrm{DIS}_{d,\mathrm{yr}})$ | 0.274 | 0.104 | 0.158 | 2.637 | 0.010 | 1.377 |
| $\mathrm{TDS}_{d,\mathrm{yr}}$ | 0.177 | 0.121 | 0.096 | 1.465 | 0.147 | 1.654 |
| $\mathrm{WVC}_{d,\mathrm{yr}}$ | 0.032 | 0.010 | 0.205 | 3.237 | 0.002 | 1.548 |
| $\mathrm{MPI}_{d,\mathrm{yr}}$ | –0.005 | 0.002 | –0.158 | –2.511 | 0.014 | 1.519 |
| $\mathrm{CC}_{d,\mathrm{yr}}$ | 0.026 | 0.010 | 0.147 | 2.624 | 0.010 | 1.204 |

rately both MPI ($p = 0.021$) and CC ($p = 0.015$) had a significant effect. Their combination MII, illumination intensity of the moon (Table 3, model 1), was successful in combining these effects but also included the effect of the altitude of the moon and coherent back scattering, which may have accounted for the higher $r^2$ of model 1.

## Effect of discharge and river temperature on early season migratory activity

When comparing different years in the two rivers, a significant positive correlation between the relative early season CPUE and log of relative early season discharge, log(reDIS) ($r = 0.671$, $p < 0.001$) was found. When the effect of log(reDIS) was accounted for, a significant partial correlation (Partial $r = 0.506$, $p = 0.01$) between CPUE and temperature drop (TD) prevailed but not between CPUE and any other temperature-related variable (maximum, minimum, average, all partial $r > 0.13$). Thus, early migration activity is induced by high discharge and prominent cooling of water. In linear regression log(reDIS) and TD explained 56% of interannual variation in the relative early season CPUE (Table 4).

## Migratory behaviour of radio-tagged lampreys

The general migration patterns of radio-tagged river lampreys were similar in every telemetry experiment. Most of the lampreys tended to pass slow-flowing river sections during one night and halt at fast-flowing river sections (Figs. 2–4). The typical mesohabitats for holding were runs just below the riffle or the lowermost section of the riffle and sometimes the glide.

The median migration distance of tagged lampreys, which were still tracked 25 days after release, was only 2.0 km. Only two lampreys migrated more than 20 km (Fig. 3). Migration distances varied between release sites and release occasions (Figs. 2–4).

In telemetry experiments $P_{02}$ and $K_{07}$, there was a long, slow-flowing and in $K_{09}$ a long, fast-flowing river section above the release sites. As lampreys usually did not halt at the slow-flowing river section, the mesohabitats available above the release site had a substantial effect on migratory distances. Consequently, migration distance alone is not an adequate indicator for migratory activity of lampreys released at different sites.

Lampreys released at low river-water temperatures (< 2 °C) were inactive. None of the lampreys from the later release occasion (RO) (temp. 1.0 °C) released at $RP_{02L}$ passed the first riffle section above $RP_{02L}$, whereas three out of five lampreys from the earlier RO (8.5 °C) passed it (Fig. 2). The median migration distance of lampreys from the later RO (2010 m) was significantly lower than that of lampreys from the earlier RO (5630 m) (Mann-Whitney $U$-test: $U = 2.5$, $n_1 = 5$, $n_2 = 5$, $p = 0.032$). In $K_{09}$ migration distances among ROs differed significantly (Kruskal-Wallis test: $H = 16.2$, $n = 24$, $p < 0.001$). The median migration distance of lampreys from the latest RO (1.6 °C) was only 270 m, whereas lampreys released in mid-season (11.2 °C) migrated significantly further (median 1310 m) (Mann-Whitney $U$-test: $U = 0$, $n_1 = 9$, $n_2 = 9$, Bonferroni-adj. $p < 0.001$).

**Table 4**. The parameter estimates and $p$ values for a linear regression models explaining the interannual variability in relatively early season (16–31 August) CPUE of river lamprey in the rivers. $reDIS_{r,yr}$ = relative average discharge; $TD_{r,yr}$ = temperature decrease during the period, subscript r refers to river and yr to year; VIF = variance inflation factor, an index of collinearity.

| Variable | Unstandardised | | Standardised $\beta$ | $t$ | $p$ | VIF |
|---|---|---|---|---|---|---|
| | $\beta$ | SE | | | | |
| Adjusted $R^2 = 0.555$ | | | | | | |
| Constant | 0.551 | 0.143 | | 3.847 | 0.001 | |
| $\log(reDIS_{r,yr})$ | 0.373 | 0.169 | 0.169 | 2.210 | 0.037 | 1.621 |
| $TD_{r,yr}$ | 0.071 | 0.025 | 0.025 | 2.814 | 0.010 | 1.621 |

In $K_{09}$, the lampreys from the earliest RO at high temperature (16.5 °C) showed low upstream migratory activity, the median migration distance (470 m) being significantly lower than that of lampreys released in mid season (Mann-Whitney $U$-test: $U = 3.0$, $n_1 = 6$, $n_2 = 9$, Bonferroni-adj. $p = 0.009$). Only one lamprey released in early season at $RK_{09L}$ was located in the river 22 days after release (Fig. 4).

Both up- and down-stream migrating lampreys tended to halt below or above the illuminated bridges (Figs. 2–4). Furthermore, most of the lampreys which halted next to the illuminated bridges did not continue migration, but held by the bridges until the end of tracking. Two lampreys released at $RP_{02L}$ reached a dimly illuminated bridge after 7.4 km migration and halted permanently 5 and 20 m below it (Fig. 2). In $K_{07}$, all 10 lampreys halted at the short riffle/glide section 30–120 m below an illuminated bridge and only 3 individuals passed the bridge after holding 1 to 15 days below it (Fig. 3).Two out of those three lampreys migrated over 20 km and halted permanently at a block stone weir next to a brightly illuminated bridge, which was the only illuminated bridge on their migration route that crossed the river in a fast flowing river section (i.e. low water depth). In $K_{09}$, all 11 lampreys which reached the upper illuminated bridge halted 10–50 m below or above it and seven of them until the end of the tracking period (Fig. 4). The holding time by the bridge of the four lampreys which later continued migration was on an average 18 days (range 1–30). Furthermore, all five lampreys which were released at $RK_{09U}$ and migrated downstream halted next to the lower illuminated bridge (Fig. 4). The only exceptions from halting by the illuminated bridges were three lampreys released at $RK_{09L}$, which passed the lower illuminated bridge without stopping.

All ten lampreys released at the $RP_{02U}$ eventually halted just below the power plant or regulation dam (Fig. 2). Six of them selected the flood channel as their holding site. Three of these disappeared suddenly 9–12 days after release, and furthermore the tag of one lamprey was located inside the river bank. These four lampreys may have been eaten by minks (*Neovison vison*) or otters (*Lutra lutra*) as many paw prints were observed on the shore and one of the disappeared tags was found on the river bank with teeth marks on it. In $K_{07}$, one lamprey disappeared suddenly 15 or 16 days after release (Fig. 3) and later its tag was found on the river bank in excrement indicating that this lamprey had been eaten.

In $K_{07}$, all the lampreys ($n = 10$) migrated to the natural-like fish way 350 m above the $RK_{07}$ in a few hours. None of the lampreys was detected to approach or enter the technical fishway situating next to fish ramp. Two lampreys from the first RO and all five lampreys from the second RO passed the weir during the first night (Fig. 3). Three of the lampreys spent 8 to 23 days in the fish ramp before they continued migration, but eventually all 10 lampreys passed the weir.

## Holding habitats of radio-tagged lampreys

Several lampreys continued their upstream migration even at river water temperatures around 1 °C, but typically at low temperatures they just moved to the closest fast flowing river section. When the river water temperature decreased close to zero, migration of most lampreys ceased and they started a prolonged holding state (winter holding). As many as 35 out of 39 lampreys with determined wintering mesohabitat selected fast-flowing sections and only four selected slow-flowing sections. The selection ratios of the wintering sites for the fast-flowing section was 2.1 (95%CI = 1.3–2.8) and for the slow-flowing section 0.2 (95%CI = 0–0.4) indicating significant preference for fast-flowing and avoidance of slow-flowing river sections.

Even though lampreys preferred fast-flowing areas for holding, they were rarely observed to halt in the middle or upper part of steep riffle sections. For example, in $K_{09}$, ten out of 13 lampreys which reached the steep riffle section 50–350 m below the upper illuminated bridge passed it without stopping (Fig. 3). Only three lampreys held in this riffle and two of them in the lowermost part (Fig. 3). The only lamprey which halted in the upper part of the riffle selected a deep (> 80 cm) depression for holding. Dominant substratum types for this riffle section were boulders with diameters of > 256 mm and

128–256 mm (67% and 26% of the area, respectively).

The habitat evaluation was carried out for 12 lampreys released at the $RK_{09L}$ and $RK_{09U}$. The availability of habitats was estimated for 10 lampreys only, and hence the confidence intervals of selection ratios were wide.

Big boulders (diameter > 256 mm) was the dominant substratum for 9 of 12 holding sites. In the river section where availability was measured, the selection ratio for the substratum category was 2.6 (90%CI = 1.1–4.0) indicating significant preference for holding sites where big boulders are dominant (Fig. 5). Selection ratios were less than 0.5 for sites with smaller dominant substrates (Fig. 5). None of the lampreys selected a holding site dominated by pebbles (32–64 mm) or finer substrata. In the studied river section their availability was 15% of the area.

The average surface current speed above holding sites was 0.27 m $s^{-1}$ (range 0.10–0.40 m $s^{-1}$). In the lowermost part of the Kalajoki, the selection ratios were 2.3 (90%CI = 0.5–4.1) and 1.6 (90%CI = 0.0–3.4) for the current speed categories 0.16–0.30 and 0.31–0.45 m $s^{-1}$, respectively. Due to wide confidence intervals, the preferences were not significant (Fig. 5). None of the lampreys selected a holding site where surface current speed was higher than 0.45 m $s^{-1}$, although its availability in the measured river section was 24.5%.

The average depth of holding sites was 52 cm (range 20–90 cm). In the river section where availability was determined, two lampreys were detected in every depth category. Selection ratios were mostly close to 1.0 indicating no selection for or against different depth categories (Fig. 5). However, the availability of the deepest category (> 80 cm) was the lowest and therefore the selection ratio for it was higher than for the other depth categories, but without significant preference (Fig. 5). It is noteworthy that two lampreys in the river section where availability was measured were holding in such a deep location that no exact habitat evaluation could be made.

The distances of holding sites to the nearest river margin varied between 2 and 20 m, and averaged 11 m. Two lampreys were holding in the mid-channel (distance to the nearest bank 33.4%–50% of the total width of channel) and five lampreys in two other categories (0%–16.6% or 16.7%–33.3% of the total width of the channel). The selection ratio for mid channel was 0.5 (90%CI = 0.0–1.1) and was 1.3 (90%CI = 0.5–2.0) for the two other categories.

Nine of the lampreys selected run/glide and three riffle mesohabitat for holding. None of the lampreys selected pool habitat. The selection ratio for run/glide habitat was 1.5 (90%CI = 1.0–1.9) and for riffle habit 0.8 (90%CI = 0.0–2.1).

## Discussion

### Migratory behaviour

The timing of migration into the rivers depends on the animal's physiological state, which is affected by hormone balance and external triggering factors, such as water flow, temperature and light conditions (Northcote 1984). Environmental factors may also affect the direction of migration and have an effect on the migratory activity. Our results indicate that discharge, moonlight illumination and wind speed coupled with wind direction control the migration of river lampreys. The results also suggest that river water temperature has an effect on migratory activity. However, collinearity of certain variables in the field data makes exhaustive quantitative analysis of all potential influences impossible. The variable rejected from the final models, night length, correlated strongly ($p < 0.001$) with discharge and temperature, and the other rejected variable, sea water level, correlated with discharge, temperature decrease speed and wind speed.

The river discharge in early season into the estuaries of the Kalajoki and Perhonjoki, and during the peak migration season into the lowermost part of the Perhonjoki, was an important predictor of the number of migrating river lamprey. Consistent with the results of earlier studies (e.g. Asplund and Södergren 1975, Masters *et al.* 2006), increased discharge stimulated migratory activity of *L. fluviatilis*.

Pheromones released by larval lampreys are an important migratory cue for adult lampreys (e.g. Wagner *et al.* 2009, Vrieze *et al.* 2010, Vrieze *et al.* 2011). Before entering a river, sea lampreys seek spawning rivers by swimming actively and, after locating the river plume and the pheromones in it, their behaviour changes leading them eventually to enter the river mouth (*see* Vrieze *et al*. 2011). When the river discharge is high, the plume is broader and thicker (Vrieze *et al*. 2011), which increases the probability that lampreys will find the plume and most likely raises the number of lampreys entering a river. As larval river lampreys also release common migratory pheromones (Fine *et al*. 2004) and adult river lampreys are sensitive to them (Gaudron and Lucas 2006), it is probable that pheromones spread by river water are also a cue for river lampreys seeking a spawning river and may partly explain the positive correlation between discharge and number of river lampreys entering estuaries. On the other hand, in high flows the concentration of larval pheromones is diluted and more general factors like fresh water or environmental odours in river water may also have a role in directing migration from sea into the rivers. Given that homing behaviour of lampreys is suggested to be weak (Tuunainen *et al*. 1980, Bergstedt and Seeley 1995), the extent of the plume, beside its pheromone concentration, is potentially a key factor controlling the number of lampreys entering into different rivers during the migration season (*see* also Keefer *et al*. 2009, Vrieze *et al*. 2010, 2011). Once lampreys have entered a river or are close to the river mouth, non-odour driven rheotaxis also promotes upstream migration. Many studies have revealed that migratory activity of river lampreys which have already entered the river is positively correlated with river flow (Masters *et al*. 2006, Lucas *et al*. 2009, Foulds and Lucas 2013). Furthermore, sea lampreys with occuled nasopores have been shown to migrate upriver, even though not as actively as lampreys with functional olfaction (Vrieze *et al*. 2010).

Given that river lampreys are negatively phototactic during their autumn migration (e.g. Enequist 1937, Sjöberg 1980), and that during high discharge column light attenuation is increased due to increased water depth and turbidity, it is possible that increased discharge also enhances migratory activity by reducing light penetration to river bed, where adult lampreys tend to swim during the spawning migration (Lucas *et al*. 2009, Kemp *et al*. 2011). For instance, in the Kalajoki turbidity is strictly regulated by discharge, and during high discharges turbidity is typically over 10 FTU while the normal turbidity level during low discharges is 3–5 FTU (Tuohino *et al*. 2008). The reduced light intensity on the river bed may extend the daily hours suitable for migration. Furthermore, increased light attenuation may enhance the intensity of migration, if it is depressed due to moonlight or artificial illumination.

In contrast to our results, the run of the Pacific lamprey takes place later in high-discharge years than low-discharge years (Keefer *et al*. 2009), and river lamprey catches have been found to be depressed during the highest flows (Masters *et al*. 2006). Migration velocity of the sea lamprey has also been demonstrated to decrease during elevated discharge, although it stimulated lampreys to move (Almeida *et al*. 2002). In our regression analysis, we examined changes in the number of lampreys entering the river or estuaries, but not the migration behaviour in the rivers, where in steep and/or narrow river sections highest discharges may increase the current velocity up to the level where it starts to restrict migration by reducing ground speed of lampreys (*see* Almeida *et al*. 2002) or by preventing upstream migration due to excessive flow velocity (*see* Kemp *et al*. 2011). In addition, when studying migratory intensity during the early migration season, the years with highest discharge were rejected from the data and in the telemetry experiments the highest discharges were only three times higher than MQ. These facts likely explain why we did not detect any indications of high discharges depressing migration.

The regression analysis indicated that the number of lampreys entering the river correlates negatively with the nighttime light intensity of the moon. These results support the observations in earlier studies that low migratory activity occurs at or near the time of full moon (Asplund and Södergren 1975), and that high river lamprey catches are connected to moonless, dark nights (e.g. Abakumov 1956, Asplund and Södergren 1975). Intense migration of *Geotria australis* has also been associated with extensive cloud cover or the dark phase of the moon (Potter *et al*. 1983).

It is possible that, in addition to or instead of the illumination factor, migration could be entrained to the lunar cycle or, alternatively, migratory behaviour could be affected by the gravitational changes due to lunar phases. However, in most studies the effect of the lunar cycle has been linked to illumination (e.g. Abou-Seedo and Potter 1979, Binder *et al*. 2010) as the anti-predatory behaviour of light avoidance is an obvious explanation for nocturnal animals (*see* Keefer *et al*. 2013b). According to our results, near full moon cloud cover correlated positively with catch, which supports the suggestion that the moon affects the migratory activity of river lamprey primarily by regulating the nighttime light level.

Sea lampreys showed a behavioural response when the dermal photoreceptors of the tail were illuminated with a light intensity of 1 lux (Binder and McDonald 2008a). Our results suggest that river lampreys are sensitive to even lower light intensities than that. Light intensity on the river surface during the full moon is only around 0.2 lux and, furthermore, light attenuation within the water-column diminishes the amount of light reaching lamprey photoreceptors.

Wind was also found to affect migration. In the peak migration season, more lampreys migrated into the river during onshore than offshore winds. It has been suggested that *Lampetra planeri* also migrates more actively during onshore winds (Malmqvist 1980). Onshore winds give rise to surface currents parallel to the wind direction, and we hypothesize that they speed up the migration towards the shore or towards the river mouth when a lamprey has already detected the plume. Similarly, offshore winds may slow down the migration. Wind-driven surface currents have also been found to affect migration patterns of blue fin tuna (*Thunnus thynnus*) (Addis *et al*. 2013). Furthermore, wind is an important factor controlling the short-term sea level changes in the Bothnian Bay (Lisitzin 1967), and wind forcing affects the pattern of horizontal river water dispersal, including the spreading of river water over ambient, more saline water (Choi and Wilkin 2007). Therefore, it is possible that wind influences migratory activity also via sea level changes and the dispersal of the river plume.

Actual river water temperature did not significantly affect migratory activity in the early or peak migration season. This result was consistent with earlier observations that discharge is more important than river temperature in controlling migratory activity of river lampreys (e.g. Abou-Seedo and Potter 1979, Masters *et al*. 2006, Foulds and Lucas 2013). Abou-Seedo and Potter (1979) reported that the first conspicuous influx of river lampreys into estuary generally occurred when the temperature was 12–16 °C. Our result indicates that if river discharge is high, a significant number of lampreys may already enter the estuary at the beginning of the catching season after mid-August despite the high river water temperature (> 18 °C). Lucas *et al*. (2009) estimated that the upper limit for temperature, where migration into the rivers normally occurs, is probably 8–12 °C. In the peak migration season in 1982–1984, the river water temperature varied between 1.4 and 16.2 °C, and was above 12 °C for 35% of the days. Yet we did not see any effect of temperature on migratory activity, suggesting that the upper limit for active migration may be higher than Lucas *et al*. (2009) suggested. It is possible, however, that northern populations have adapted to the local environment and start their migration at higher temperatures due to the relatively short migratory period before the river water temperature becomes too cold. In $K_{09}$, lampreys from the first RO (temp. 16.5 °C) showed low migratory activity, which may be linked to too high river water temperature and/or to the fact that the river water did not cool down during the two-week period after release. Applegate (1950) reported that sea lampreys arrive at the estuaries days or even weeks before they start to migrate into the river. Overall, it seems possible that river lampreys also aggregate in the estuary in the early season if the river discharge is high, but start intensive migration into the river only when the temperature of the river water is low enough.

Although actual river-water temperature did not affect migratory activity, speed (in peak migration season) and magnitude (in early migration season) of cooling of the river water were positively correlated with migratory activity. In earlier studies the effect of temperature change has not been included among the factors which could affect the migratory activity of the river lamprey, but the migratory activity of the sea lamprey has been shown to be affected by temperature change (Binder and McDonald 2008b, Binder *et al*. 2010). However, opposite to the behaviour of the river lamprey, migratory activity of the sea lamprey, which begin their migration in spring, increased with the increase in temperature and declined with the decrease (Binder *et al*. 2010). It seems that sudden and/or large changes in water temperature may act as a trigger for lampreys to start their migration. As sea-water temperatures change in parallel with changes in river-water temperatures, it is also possible that changes in sea-water temperature may have an effect on migratory activity.

In telemetry experiments $P_{02}$ and $K_{09}$, the lampreys from the latest release occasions were less active than those from earlier ROs. The probable reason for that was the low river-water temperature during release, 1.0 and 1.6 °C, respectively. Moreover, no lampreys from other ROs passed marked riffle sections after temperature had dropped near to or below 1 °C. When lampreys moved at low temperatures, they mainly migrated to the lower end of the nearest fast-flowing section. The depressed activity is probably connected to the reduced swimming endurance at low temperatures (*see* e.g. Beamish 1974, Huusko *et al*. 2007). However, in late November 2009, when we already stopped tracking the lampreys in $K_{09}$, the discharge of the Kalajoki increased during a few days from 8 to 90 $m^3$ $s^{-1}$ and water temperature from near 0 to 3 °C. At the same time, one of the lamprey fishermen, who recorded his basket catches for monitoring, restarted catching. During 22–24 November, when the discharge was 34–62 $m^3$ $s^{-1}$ and temperature 1.2–2.1 °C, he caught 168 lampreys (including one telemetry-tagged individual) with 21 baskets and CPUEs were among the highest of the whole catching season (own unpubl. data). This indicates that the increase in discharge and/or temperature activated lampreys to migrate, even though we expected that they had already started the winter holding period, and they actively migrated in rather low temperatures. Starcevich *et al*. (2013) observed similar behaviour among the Pacific lamprey and concluded that winter is not strictly a holding period, and increased discharge may still induce upstream movements. In the River Derwent, England, elevated discharge episodes tended to stimulate upriver movement of the river lamprey until the end of January, but after that river lampreys that have migrated substantial distance upriver were not stimulated to continue upriver migration despite discharge elevations (M. Lucas pers. comm.).

As sea-water level and night length correlated strongly with many other explanatory variables, they had to be rejected from the final models. However, as changes in sea-water level affect flow conditions in the lowermost part of the river and estuary, and longer nights mean longer period suitable for migration for nocturnal animals, we cannot rule out some effect of these variables on migratory activity.

The migration distances of lampreys in the telemetry experiments were short. In the late 1970s and early 1980s, before the major river regulation measures, aggregations of river lamprey larvae in the Kalajoki and Perhonjoki had been detected as far as 45 to 55 km from the sea (Kainua and Valtonen 1980, Ojutkangas *et al*. 1995) indicating that at least some lampreys had migrated up to 55 km. Lucas *et al*. (2009) reported migration distances of over 100 km in the English rivers. There are many potential reasons why lampreys in our telemetry experiments migrated much shorter distances than mentioned above.

First of all, most lampreys which met an illuminated bridge on their migration route halted by it. Most of these did not continue migration, and migration of those individuals which did continue was delayed. According to preliminary measurements by three illuminated bridges in the Kalajoki, there are 25 to 50 m sections on both sides of the bridges where light intensity just above water surface exceeds 1 lux, and light intensities higher than 10 lux exist just by the bridge (own unpubl. data). Combining these observations with the results of the regression analysis that even moonlight with intensity ≤ 0.2 lux depresses migratory activity, implies that illumination of bridges markedly obstructed upstream movements of lampreys. To our knowledge, there are no other studies revealing that light pollution may affect migratory behaviour of river lamprey. However, the juvenile Pacific lamprey has been shown to exhibit a strong light avoidance, but acclimate to white light in relatively short time periods (Moser and Russon 2009). Furthermore, Riley *et al*. (2012) demonstrated that street lightning disrupts the diel migratory pattern of wild Atlantic salmon (*Salmo salar*) smolts leaving their natal stream. Given that the sites nearby the bridges offered good holding habitats, we cannot completely rule out the possibility that halting by the bridges was, at least to some extent, normal behaviour rather than light avoidance.

In $P_{02}$, a morphological migration barrier (the Pirttikoski power plant) also restricted migratory distances.

It is likely that environmental factors during the experiments also induced the low migratory activity. As shown in our regression analysis and many earlier studies (e.g. Masters *et al*. 2006, Lucas *et al*. 2009), discharge is an important factor stimulating upstream movements of river lampreys. Especially during $P_{02}$, but also during $K_{09}$, discharge was low, which probably lowered migratory intensity. Low larval densities above the release sites (< 1 larvae $m^{-2}$, own unpubl. data) in experiments $P_{02}$ and $K_{07}$ may also have depressed the migratory activity. Even though lampreys have been demonstrated to migrate upriver without a pheromonal cue (Vrieze *et al*. 2010), concentrations of larval pheromones affect their migratory behaviour and activity (Wagner *et al*. 2009, Vrieze *et al*. 2010). In addition, low water temperature during the last release occasions in $P_{02}$ and $K_{09}$ most likely inactivated lampreys.

It is possible that the tagging procedure and tags also reduced migratory distances in the telemetry experiments. However, laboratory experiments with the Pacific lamprey have revealed that surgically implanted tags have only a minimal effect on swimming performance and physiology (Close *et al*. 2003, Mesa *et al*. 2003). Close *et al*. (2003) suggested that tags weighing 7.4 g (max. 2.5% of the body weight) could be used for the Pacific lamprey. Furthermore, many studies with fish have confirmed that tags < 2% of the fish body mass can be used without significant effect on fish behaviour (Jepsen *et al*. 2002). On the other hand, Moser *et al*. (2007) concluded that tags even smaller than 1% of the body mass have an effect on migratory behaviour of Pacific lamprey. Recently, Keefer *et al*. (2013a) demonstrated that the results of Moser *et al*. (2007) could be at least partly explained by actual size of tagged lampreys, not by the relative size of the tag. In our experiments, the tag weight averaged 1.7% of the body mass and exceeded 2% of the body mass in the case of eight lampreys (13%). Five of these were lampreys from second RO in $K_{09}$. Lampreys of that RO had the highest rate of upstream movement in $K_{09}$ indicating that relative tag size did not have a significant negative effect on migratory activity, or at least it did not mask the effect of other factors that influenced the migratory behaviour. The relative impact of tagging compared with that of the other factors affecting migratory behaviour in our experiments remains unknown. However it should be taken into account that handling, the implantation procedure, rather long holding period before release and the tag itself may all have, to some extent, affected behaviour and swimming performance of the tagged lampreys.

## Holding habitats

The general migration patterns of radio-tagged river lampreys were similar in all telemetry experiments. Most of the lampreys tended to pass slow-flowing as well as steep riffle sections quickly during one night and halt in the fast-flowing river section, where they typically held for long periods. According to the telemetry experiments, lampreys may already become sedentary and start a prolonged holding phase during the early migration season, and migration of all lampreys ceases at the latest when temperature drops close to zero. However, during the formation of ice cover some lampreys were still observed to move short distances from the river margin to the deeper part of the river, and as in November 2009, increased discharge or/and temperature still induced lampreys to change location, at least in early winter.

Given that in boreal rivers the period of water temperatures near 0 °C lasts typically 6–7 months and river lampreys are shown to be in energy saving hypometabolic state during winter months (Gamber and Savina 2000), the wintering site should offer a safe, energy saving and stable position in a harsh environment with various ice phenomena. According to the mesohabitat observations, temporary resting sites and more permanent locations at low temperatures, which were considered wintering sites, resembled each other. The river lampreys were typically holding in a run at the lower end of a riffle or in the glide above a riffle, but lampreys were only occasionally observed to hold in slow-flowing river sections or in the middle or upper part of riffle sections. Furthermore, the holding sites were associated with boulders as cover. Our results are consistent with observations on wintering habitats of Pacific lampreys in coastal rivers in Oregon, where run and glide habitats with boulders were the most selected mesohabitats for the wintering Pacific lamprey, which rejected the middle parts of riffles (Starcevich *et al*. 2013; R. Lampman pers. comm.).

It is likely that river lampreys preferred holding sites dominated by large boulders (diameter > 256 mm) because these sites offered large enough crevices between and under boulders in which to hide. Using an underwater view tube, lampreys were observed only after removing some boulders from the upper layer of boulder piles, indicating that the lampreys were under and/or between the crevices of boulders, not on them. This observation is supported by Binder and McDonald (2007, 2008a) who suggested that sea lampreys use tactile and/or hydraulic cues to search for refuges before dawn, but after dawn the dermal photoreceptors ensure that the animal's tail remains fully concealed from the light. Pacific lampreys (Robinson and Bayer 2005, Starcevich *et al*. 2013) and *Geotria australis* (Kelso and Glova 1993) also use boulders as a cover while holding. The sea lamprey in a creek in Canada used more variable refuge types (Binder and McDonald 2007), including overhanging banks and fallen branches used in the same proportion as large rocks. Furthermore, Jellyman *et al*. (2002) reported that *Geotria australis* mainly used logs as a refuge in a river where the abundance of boulders was low. According to our field observations, the amount of possible refuge types other than boulders is limited in the Perhonjoki and Kalajoki, so in this study their suitability for river lampreys remained unknown. However, in the River Derwent, England, river lampreys have been observed to hold in areas associated with riparian willows with large underwater root masses (M. Lucas pers. comm.).

River lampreys avoid slow-flowing river sections as holding sites. The potential reason for this behaviour is that in these sections substrata like silt, clay and sand, which do not provide any refuge, are dominant. Lampreys halting in river sections categorized as pool usually selected sites where boulders were dominant, although the availability of boulder substratum was low. It is likely that factors other than refuge availability also explain why the river lamprey prefer fast-flowing areas. This behaviour may be connected to water quality, water temperature, ice conditions, anti-predatory behaviour or proximity of potential spawning sites. Thus, further studies are needed to understand better the reasons for mesohabitat selection.

In addition to slow-flowing sections, river lampreys seemed to avoid steep riffles and high current speed for holding sites. It is possible that holding under very high current speed is too energy demanding, although refuge from high current speed could probably be found inside boulder piles. Avoidance of shallow, steep and fast-flowing river sections for holding could also have evolved in response to harsh and unstable conditions during the winter. These areas develop permanent ice cover last if at all, and consequently formation of anchor ice may frequently fill the potential holding sites (*see* Huusko *et al*. 2013).

Lampreys selected various depths for holding, but as the availability of the deepest class (> 80 cm) was low its selection ratio was highest. As habitat determination for two lampreys was impossible because of too-deep water it is possible that lampreys may prefer deep sites, but we suggest that refuge availability and current speed are more important factors in directing the selection.

The Pacific lamprey has been reported to select wintering sites near the river margin (Robinson and Bayer 2005), but according to our results closeness of the river margin may not be important for the river lamprey if refuge is available in the mid-channel.

### Rehabilitation aspects

As discharge is an important factor controlling migration of lampreys, the regulation patterns of river flow may affect migration of lampreys considerably. In flow-regulated rivers, it is usual that reservoirs or regulated lakes are filled during autumn. This reduces discharge during the migration season and may also decrease the number of lampreys migrating to a regulated river compared with unregulated rivers. Also short-term regulation may reduce the number of migrating lampreys if discharge is lower during the night than during the day (*see* also Andrade *et al*. 2007). Flow-regulation may even be beneficial for lampreys if they are directed to unregulated rivers where wintering, spawning and larval habitats are more suitable. However, if lamprey migration into regulated rivers is desired, then ensuring sufficient discharge during the migration season seems to be a key factor.

Our results suggest that illumination of bridges, especially at shallow areas, may reduce the migratory activity of river lampreys. Cumulative effects of migration delays due to illuminated bridges may have as severe consequences on lamprey populations as low-head morphological barriers (*see* Jackson and Moser 2012, Foulds and Lucas 2013), and more studies on the effect of artificial illumination on migratory behaviour are needed. If further studies support our observations, some solutions to bridge lighting are required. For example, covers could be used to prevent the river from being illuminated or the lights could be switched off for some period if it is safe for traffic.

Transplanting adults above migration barriers during the autumn migration is the most usual way of rehabilitating lamprey populations in Finland. Annually, over 200 000 adults are released above barriers (Sjöberg 2011). As lampreys need refuges for holding, lampreys transplanted during daylight should preferably be released at sites offering refuge from predation pressure and stress. There were some indications that predation risk increases, if lampreys aggregate below migration obstructions. Therefore, transplanting lampreys below migration barriers should be avoided; if it is necessary to transplant lampreys into such areas, spring release after keeping lampreys in holding facilities over the winter could be one solution (*see* Close *et al*. 2009).

As migratory activity of lampreys seems to diminish at low temperatures, we recommend that river lampreys transplanted in water temperatures < 2 °C are released near potential wintering/spawning sites, because they are likely to migrate only to the nearest fast-flowing river section. According to telemetry experiments conducted in 2003 (own unpubl. data), lampreys may not migrate long distances in the spring after winter holding, but mainly stay to spawn in the nearest fast-flowing area. This emphasizes the importance of the selection of transplantation sites at low temperatures.

In projects to restore previously dredged fast-flowing areas, it is important to place boulders in run/glide sections to enhance wintering habitats for lampreys. It is likely that piles of boulders provide a better refuge for lampreys than individual stones.

$K_{07}$ demonstrated preference of lampreys for the natural-like fish-way over the technical one and 100% efficiency of passing it. During the experiment, the flow through the fish ramp was more than 10 times higher than the flow through the technical fish-way (own unpubl. data). It is likely that the high flow through the fish-ramp directed lampreys to select it and, therefore, the suitability of the super-active baffle fish-way for lamprey remained unknown. However, technical fish-ways are known to be challenging for river lampreys (Laine *et al*. 1998, Lucas *et al*. 2009, Foulds and Lucas 2013). The results suggest that a natural-like fish ramp may be a good solution to enhance passage of river lampreys over low-head barriers.

## Conclusions

The river lamprey migratory behaviour is associated with many environmental factors, but the causal mechanisms are still more or less speculative. However, it is likely that many behavioural responses influence migration of river lampreys including at least: (1) chemotaxis (attraction to migratory pheromones), (2) positive rheotaxis,

(3) negative phototaxis, and (4) thermotaxis (increased activity triggered by fast and large temperature decrease and inactivity at low temperatures). River regulation measures and water flow regulation may have a marked effect on larval densities (i.e. amount of migratory pheromones) and flow conditions. Furthermore, in addition to dams and other man-made solid barriers, artificial lighting may create illumination barriers for migration. Consequently, anthropogenic activities may have a serious effect on migratory patterns and dispersal of lampreys to different rivers. In the long run, climate change may change migration patterns markedly; due to warming, the potential migration period, especially in boreal areas, will be prolonged and river flow as well as wind conditions are predicted to change. Our study has increased the general understanding of migratory behaviour and holding habitats of river lamprey, but more precise information is needed to select the best measures for conserving and rehabilitating river lamprey populations in a changing environment.

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## References

Abakumov V.A. [Абакумов В.А.] 1956. [The mode of life of the Baltic River Lamprey.] *J. Vopr. Ikhtiol.* 6: 122–128. [In Russian].

Abou-Seedo F.S. & Potter I.C. 1979. The estuarine phase of the spawning run of the river lamprey *Lampetra fluviatilis*. *J. Zool.* 188: 5–25.

Addis P., Secci M. & Cau A. 2013. The effect of Mistral (a strong NW wind) episodes on the occurrence and abundance of Atlantic bluefin tuna (*Thunnus thynnus*) in the trap fishery of Sardinia (W Mediterranean). *Sci. Mar.* 77: 419–427.

Almeida P.R., Quintella B.R. & Dias N.M. 2002. Movement of radio-tagged anadromous sea lamprey during the spawning migration in the River Mondego (Portugal). *Hydrobiologia* 483: 1–8.

Andrade N.O., Quintella B.R., Ferreira J., Pinela S., Póvoa I., Pedro P. & Almeida P.R. 2007. Sea lamprey (*Petromyzon marinus* L.) spawning migration in the Vouga river basin (Portugal): poaching impact, preferential resting sites and spawning grounds. *Hydrobiologia* 582: 121–132.

Applegate V.C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. *Spec. Sci. Rept. U.S. Fish and Wildlife Serv.* 55: 1–237.

Aronsuu K. & Virkkala P. 2014. Substrate selection by subyearling European river lampreys (*Lampetra fluviatilis*) and older larvae (*Lampetra* spp.). *Ecol. Freshw. Fish* 23: 644–655.

Asplund C. & Södergren S. 1975. Flodnejonögats (*Lampetra fluviatilis* L.) lekvandring I Rickleån. *Zool. Revy* 36: 111–119.

Beamish F.W.H. 1974. Swimming performance of adult sea lamprey, *Petromyzon marinus*, in relation to weight and temperature. *Trans. Am. Fish. Soc.* 103: 355–358.

Bergstedt R.A. & Seelye J.G. 1995. Evidence for lack of homing by sea lampreys. *Trans. Am. Fish. Soc.* 124: 235–239.

Binder T.R. & McDonald D.G. 2007. Is there role for vision in the behaviour of sea lampreys (*Petromyzon marinus*) during their upstream spawning migration? *Can. J. Aquat. Sci.* 64: 1403–1412.

Binder T.R. & McDonald D.G. 2008a. The role of dermal photoreceptors during the sea lamprey (*Petromyzon marinus*) spawning migration. *J. Comp. Physiol. A* 194: 921–928.

Binder T.R. & McDonald D.G. 2008b. The role of temperature in controlling diel activity in upstream migrant sea lampreys (*Petromyzon marinus*). *Can. J. Fish. Aquat. Sci.* 65: 1113–1121.

Binder T.R., McLaughlin R.L. & McDonald D.G. 2010. Relative importance of water temperature, water level, and lunar cycle to migratory activity in spawning-phase sea lampreys in Lake Ontario. *Trans. Am. Fish. Soc.* 139: 700–712.

Choi B.-J. & Wilkin J.L. 2007. The effect of wind on the dispersal of the Hudson River plume. *J. Phys. Oceanogr.* 37: 1878–1897.

Clemens B.J., Mesa M.G., Magie R.J., Young D.A. & Schreck C.B. 2012. Pre-spawning migration of adult Pacific lamprey, *Entosphenus tridentatus*, in the Wilamette River, Oregon, U.S.A. *Environ. Biol. Fish.* 93: 245–254.

Close A.D., Fitzpatrick M.S., Christopher M.L., Li H.W. & Schreck C.B. 2003. Effects of Intraperitoneally Implanted Radio Transmitters on the Swimming Performance and Physiology of Pacific Lamprey. *N. Am. J. Fish. Manage.* 23: 1184–1192.

Close D.A., Currens K.P., Jackson A., Wildbill A.J., Hansen J., Bronson P. & Aronsuu K. 2009. Lessons from the reintroduction of a noncharismatic, migratory fish: Pacific lamprey in the upper Umatilla River, Oregon. In: Brown L.R., Chase S.D., Mesa M.G., Beamish R.J. & Moyle P.B. (eds.), *Biology, management, and conservation of lampreys in North America*, American Fisheries Society, Symposium 72, Bethesda, Maryland, pp. 233–254.

Enequist P. 1937. Das Bachneunauge als ökologische modification des Flussneunauges. Über die Fluss- und Bachneunaugen Schwedens. *Arkiv für zoology* 29 A: 1–22.

Fine J.M., Vrieze L.A. & Sorensen P.W. 2004. Evidence that petromyzontid lampreys employ a common migratory pheromone that is partially comprised of bile acids. *J. Chem. Ecol.* 30: 2091–2110.

Foulds W.L. & Lucas M.C. 2013. Extreme inefficiency of two conventional, technical fish-ways used by European river lamprey (*Lameptra fluviatilis*). *Ecol. Eng.* 58: 423–433.

Gamper N. & Savina M.V. 2000. Reversible metabolic depression in hepatocytes of lamprey (*Lampetra fluviatilis*) during pre-spawning: regulation by substrate availability. *Comp. Biochem. Physiol.* 127: 147–154.

Gaudron S.M. & Lucas M.C. 2006. First evidence of attraction of adult river lamprey in the migratory phase to larval odour. *J. Fish Biol.* 68: 640–644.

Goodwin C.E., Dick J.T.A., Rogowski D.L. & Elwood R.W. 2008. Lamprey (*Lampetra fluviatilis* and *Lampetra planeri*) ammocoete habitat associations at regional, catchment and microhabitat scales in Northern Ireland. *Ecol. Freshw. Fish* 17: 542–553.

Huusko A., Greenberg L., Stickler M., Linnansaari T., Nykänen M., Vehanen T., Koljonen S., Louhi P. & Alfredsen K. 2007. Life in the ice line: the winter ecology of stream salmonids. *River Res. Appl.* 23: 469–491.

Huusko A., Vehanen T. & Stickler M. 2013. Salmonid habitats in riverine winter conditions with ice. In: Maddock I., Harby A., Kemp P. & Wood P. (eds.), *Ecohydraulics: an integrated approach*, Wiley-Blackwell, New Delhi, pp. 177–192.

Jackson A. & Moser M.L. 2012. Low-elevation dams are impediments to adult Pacific lamprey spawning migration in the Umatilla River, Oregon. *N. Am. J. Fish. Manage.* 32: 548–556.

Jang M.H. & Lucas M.C. 2005. Reproductive ecology of the river lamprey. *J. Fish Biol.* 66: 499–512.

Jellyman D.J., Glova G.J. & Sykes J.R.E. 2002. Movements and habitats of adult lamprey (*Geotria australis*) in two New Zealand waterways. *New Zeal. J. Mar. Fresh.* 36: 53–65.

Jepsen N., Schreck C., Clements S. & Thorstad E.B. 2005. A brief discussion on the 2% tag/bodymass rule of thumb. In: Spedicato M.T., Marmulla G. & Lembo G. (eds.), *Aquatic telemetry: advances and applications*, FAO and COISPA, Rome, pp. 255–261.

Kainua K. & Valtonen T. 1980. Distribution and abundance of European river lamprey (*Lampetra fluviatilis*) larvae in three rivers running into Bothnian Bay, Finland. *Can. J. Fish. Aquat. Sci.* 37: 1960–1966.

Keefer M.L., Moser M.L., Boggs C.T., Daigle W.R. & Peery C.A. 2009. Variability in migration timing of adult Pacific lamprey (*Lampetra tridentate*) in the Columbia River, U.S.A. *Environ. Biol. Fish.* 85: 253–264.

Keefer M.L., Boggs C.T., Peery C.A. & Caudill C.C. 2013a. Factors affecting dam passage and upstream distribution of adult Pacific lamprey in the interior Columbia River basin. *Ecol. Freshw. Fish* 22: 1–10.

Keefer M.L., Caudill C.C., Peery C.A. & Moser M.L. 2013b. Context-dependent diel behavior of upstream-migrating anadromous fishes. *Environ. Biol. Fish.* 96: 691–700.

Kelso J.R.M. & Glova G.J. 1993. Distribution, upstream migration and habitat selection of maturing lampreys, *Geotria australis*, in Pigeon Bay Stream, New Zealand. *Aust. J. Mar. Fresh. Res.* 44: 749–759.

Kemp P.S., Russon I.J., Vowles A.S. & Lucas M.C. 2011. The influence of discharge and temperature on the ability of upstream migrant adult river lamprey (*Lampetra fluviatilis*) to pass experimental overshot and undershot weirs. *River Res. Appl.* 27: 488–498.

Laine A., Kamula R. & Hooli J. 1998. Fish and lamprey passage in a combined Denil and vertical slot fish-way. *Fish. Manage. Ecol.* 5: 31–44.

Lisitzin E. 1967. Day-to-day variation in sea level along the Finnish coast. *Geophysica* 9: 259–275.

Lucas M.C., Bubb D.H., Jang M.-H., Ha K. & Masters J.E.G. 2009. Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lampreys. *Freshw. Biol.* 54: 621–634.

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

Malmqvist B. 1980. The spawning migration of the brook lamprey, *Lampetra planeri* Bloch, in a south Swedish stream. *J. Fish Biol.* 16: 105–114.

Manly B.F.J., McDonald L.L., Thomas D.L., McDonald T.L. & Erickson W.P. 2002. *Resource selection by animals*. Kluwer Academic Publishers, Dordrect.

Masters J.E.G., Jang M.-H., Ha K., Bird P.D., Frear P.A. & Lucas M.C. 2006. The commercial exploitation of a protected anadromous species, the river lamprey (*Lampetra fluviatilis* (L.)), in the tidal River Ouse, north-east England. *Aquat. Conserv.* 16: 77–92.

Mateus C.S., Rodríguez-Muñoz R., Quintella B.R., Alves M.J. & Almeida P. 2012. Lampreys of the Iberian Peninsula: distribution, population status and conservation. *Endang. Species Res.* 16: 183–198.

Mesa M.G., Bayer J.M. & Seeley J.G. 2003. Swimming performance and physiological responses to exhaustive exercise in radio-tagged and untagged Pacific lampreys. *Trans. Am. Fish. Soc.* 132: 483–492.

Moser M.L., Odgen D.A. & Sandford B.P. 2007. Effects of surgically implanted transmitters on anguillaform fishes. lessons from lamprey. *J. Fish Biol.* 71: 1847–1852.

Moser M.L. & Russon I.J. 2009. *Development of a separator for juvenile lamprey 2007–2008*. U.S. Army Corps of Engineers, Walla Walla, Washington.

Myllynen K., Ojutkangas E. & Nikinmaa M. 1997. River water with high iron concentration and low pH causes mortality of lamprey roe and newly hatched larvae. *Ecotoxicol. Environ. Safety* 36: 43–48.

Northcote T.G. 1984. Mechanisms of fish migration in rivers. In: McCleave J.D., Arnold G.P., Dodson J.J. & Neil W.H. (eds.), *Mechanisms of migration in fishes*, Plenum Press, New York–London, pp. 317–355.

Nowinszky L., Kiss O., Szentkirályi F., Puskás J. & Ladányi M. 2012. Influence of illumination and polarized moonlight on light-trap catch of caddisflies (Trichoptera). *Res.*

*J. Biol.* 2: 79–90.

Ojutkangas E., Aronen K. & Laukkanen E. 1995. Distribution and abundance of river lamprey (*Lampetra fluviatilis*) ammocoetes in the regulated river Perhonjoki. *Regul. Rivers Res. Manage.* 10: 239–245.

Potter I.C. 1980. Ecology of larval and metamorphosing lampreys. *Can. J. Fish. Aquat. Sci.* 37: 1641–1657.

Potter I.C., Hilliard R.W., Bird D.J. & Macey D.J. 1983. Quantitative data on morphology and organ weights during protracted spawning-run period of the southern hemisphere lamprey *Geotria australis*. *J. Zool.* 200: 1–20.

Quintella B.R., Andrade N.O., Koed A. & Almeida P.R. 2004. Behavioural patterns of sea lampreys' spawning migration through difficult passage areas, studied by electromyogram telemetry. *J. Fish Biol.* 65: 961–972.

Renaud C.B. 1997. Conservation status of northern hemisphere lampreys (Petromyzontidae). *J. Appl. Ichthyol.* 13: 143–148.

Riley W.D., Bendall B., Ives M.J., Edmonds N.J., Maxwell D.L. 2012. Street lightning disrupts the diel migratory pattern of wild Atalantic salmon, *Salmo salar* L., smolts leaving their natal stream. *Aquaculture* 330–333: 74–81.

Robinson T.C. & Bayer J.M. 2005. Upstream migration of Pacific lampreys in the John Day River, Oregon: behavior, timing, and habitat use. *Northwest Science* 79: 106–119.

Russon I.J., Kemp P.S. & Lucas M.C. 2011. Gauging weirs impede the upstream migration of adult river lamprey *Lampetra fluviatilis*. *Fish. Manage. Ecol.* 18: 201–210.

Sjöberg K. 1977. Locomotor activity of river lamprey *Lampetra fluviatilis* (L.) during the spawning season. *Hydrobiologia* 55: 265–270.

Sjöberg K. 1980. Ecology of the European river lamprey (*Lampetra fluviatilis*) in northern Sweden. *Can. J. Fish. Aquat. Sci.* 37: 1974–1980.

Sjöberg K. 2011. River lamprey *Lampetra fluviatilis* (L.) fishing in the area around the Baltic Sea. *J. Northern Stud.* 5: 51–86.

Starcevich S.J., Gunckel S.L. & Jacobs S.E. 2014. Movements, habitat use, and population characteristics of adult Pacific lamprey in a coastal river. *Environ. Biol. Fish.* 97: 939–953.

Taverny G., Lasalle G., Ortusi I., Roqueplo C., Lepage M. & Lambert P. 2012. From shallow to deep waters: habitats used by larval lampreys (genus *Petromyzon* and *Lampetra*) over a western European basin. *Ecol. Freshw. Fish* 21: 87–99.

Tesch F.-W. 1967. Aktivität und Verhalten wandernder Lampetra fluviatilis, Lota lota und Anguilla anguilla im Tidegebiet der Elbe. *Helgoländer wiss. Meeresunters* 16: 92–111.

Tuohino J., Wennman K. & Aronsuu K. 2008: *Kalajoen Juurikosken kunnostuksen vaikutukset veden laatuun, kalastoon ja kalastukseen*. ELY centre for North Ostrobothnia, Oulu.

Tuunainen P., Ikonen E. & Auvinen H. 1980. Lampreys and lamprey fisheries in Finland. *Can. J. Fish. Aquat. Sci.* 37: 1953–1959.

Törmälä S. 1980. *Siikajoen nahkiaisen pyynnistä, nahkiaiskannoista ja nahkiaispopulaatiosta*. M.Sc. thesis, University of Oulu, Finland.

Urho L., Pennanen J.T. & Koljonen M.L. 2010. Fish. In: Rassi P., Hyvärinen E., Juslén A. & Mannerkoski I. (eds.), *The 2010 Red List of Finnish species*, Ympäristöministeriö & Suomen ympäristökeskus, Helsinki, pp. 336–343.

Wagner C.M., Twohey M.B. & Fine J.M. 2009. Conspecific cueing in the sea lamprey: do reproductive migrations consistently follow the most intense larval odour? *Anim. Behav.* 78: 593–599.

Valtonen T. 1980. European river lamprey (*Lampetra fluviatilis*) fishing and lamprey populations in some rivers running into Bothnian Bay, Finland. *Can. J. Fish. Aquat. Sci.* 37: 1967–1973.

Vrieze L.A., Bjerselius R. & Sorensen P.W. 2010. Importance of the olfactory sense to migratory sea lampreys petromyzon marinus seeking riverine spawning habitat. *J. Fish Biol.* 76: 949–964.

Vrieze L.A., Bergstedt R.A & Sorensen P.W. 2011. Olfactory-mediated stream-finding behavior of migratory adult sea lamprey (*Petromyzon marinus*). *Can. J. Fish. Aquat. Sci.* 68: 523–533.

Wentworth C.K. 1922. A scale of grade and class terms for clastic sediments. *J. Geol.* 30: 377–392.

Wikgren B.-J. 1954. Dygnsrytmen hos nejonögat (*Petromyzon fluviatilis* L.) *Mem. Soc. Fauna Flora Fennica* 29: 24–27.

**Appendix**. The proportion (%) of the moon illuminated (MPI) on each night during the peak migration season in 1982, 1983 and 1984. The data were downloaded from http://www.eeki.biz.

| Date | 1982 | 1983 | 1984 | Date | 1982 | 1983 | 1984 |
|---|---|---|---|---|---|---|---|
| 25 Aug | 30 | 99 | 8 | 25 Sep | 42 | 96 | 1 |
| 26 Aug | 40 | 99 | 3 | 26 Sep | 52 | 91 | 0 |
| 27 Aug | 50 | 93 | 0 | 27 Sep | 62 | 84 | 2 |
| 28 Aug | 59 | 87 | 0 | 28 Sep | 71 | 75 | 7 |
| 29 Aug | 68 | 80 | 4 | 29 Sep | 79 | 65 | 15 |
| 30 Aug | 77 | 71 | 10 | 30 Sep | 86 | 55 | 24 |
| 31 Aug | 84 | 62 | 18 | 1 Oct | 92 | 43 | 34 |
| 1 Sep | 91 | 51 | 28 | 2 Oct | 97 | 32 | 45 |
| 2 Sep | 95 | 40 | 38 | 3 Oct | 100 | 22 | 55 |
| 3 Sep | 99 | 29 | 49 | 4 Oct | 100 | 13 | 65 |
| 4 Sep | 100 | 19 | 60 | 5 Oct | 98 | 6 | 74 |
| 5 Sep | 99 | 11 | 70 | 6 Oct | 93 | 2 | 82 |
| 6 Sep | 96 | 5 | 79 | 7 Oct | 86 | 0 | 89 |
| 7 Sep | 91 | 1 | 86 | 8 Oct | 78 | 1 | 94 |
| 8 Sep | 84 | 0 | 92 | 9 Oct | 68 | 5 | 98 |
| 9 Sep | 75 | 2 | 97 | 10 Oct | 56 | 11 | 100 |
| 10 Sep | 65 | 7 | 99 | 11 Oct | 45 | 19 | 100 |
| 11 Sep | 54 | 14 | 100 | 12 Oct | 34 | 27 | 98 |
| 12 Sep | 43 | 23 | 99 | 13 Oct | 24 | 37 | 95 |
| 13 Sep | 32 | 33 | 96 | 14 Oct | 15 | 46 | 90 |
| 14 Sep | 21 | 43 | 92 | 15 Oct | 8 | 56 | 83 |
| 15 Sep | 13 | 53 | 86 | 16 Oct | 3 | 65 | 78 |
| 16 Sep | 6 | 62 | 78 | 17 Oct | 0 | 74 | 65 |
| 17 Sep | 2 | 71 | 70 | 18 Oct | 0 | 82 | 55 |
| 18 Sep | 0 | 80 | 60 | 19 Oct | 2 | 88 | 44 |
| 19 Sep | 1 | 87 | 50 | 20 Oct | 6 | 94 | 33 |
| 20 Sep | 4 | 92 | 40 | 21 Oct | 12 | 98 | 23 |
| 21 Sep | 10 | 97 | 29 | 22 Oct | 19 | 100 | 14 |
| 22 Sep | 16 | 99 | 20 | 23 Oct | 27 | 100 | 7 |
| 23 Sep | 24 | 100 | 11 | 24 Oct | 35 | 98 | 2 |
| 24 Sep | 33 | 99 | 5 | 25 Oct | 45 | 93 | 0 |

# II

# SELECTION OF SPAWNING SUBSTRATUM BY EUROPEAN RIVER LAMPREYS (*LAMPETRA FLUVIATILIS*) IN EXPERIMENTAL TANKS

by

Kimmo Aronsuu & Jermi Tertsunen 2015

Marine and Freshwater Behaviour and Physiology 48: 41–50.

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# III

# SUBSTRATE SELECTION BY SUBYEARLING EUROPEAN RIVER LAMPREYS (*LAMPETRA FLUVIATILIS*) AND OLDER LARVAE (*LAMPETRA* SPP)

by

Kimmo Aronsuu & Pasi Virkkala 2014

Ecology of Freshwater Fish 23: 644–655.

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# IV

# DISTRIBUTION AND ABUNDANCE OF RIVER LAMPREY (*LAMPETRA FLUVIATILIS*) AMMOCOETES IN THE REGULATED RIVER PERHONJOKI

by

Esa Ojutkangas, Kimmo Aronen & Eero Laukkanen 1995

Regulated Rivers: Research & Management 10: 239–245.

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# V

# REHABILITATION OF TWO NORTHERN RIVER LAMPREY (*LAMPETRA FLUVIATILIS*) POPULATIONS IMPACTED BY VARIOUS ANTHROPOGENIC PRESSURES – LESSONS LEARNT IN THE PAST THREE DECADES

by

Kimmo Aronsuu, Risto Vikström, Timo J. Marjomäki, Kim Wennman, Jukka Pakkala, Eero Mäenpää, Jukka Tuohino, Juha Sarell & Esa Ojutkangas 2015

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