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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 (*Entosphenus 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($CPUE_{d,yr}$), 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($CPUE_{d-1,yr}$) 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.

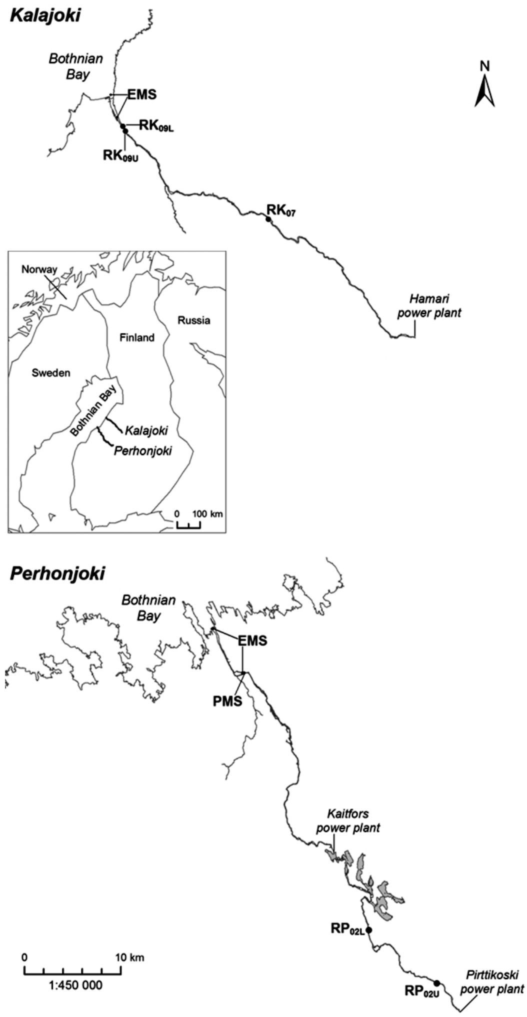

Fig. 1. Map of the study area showing the locations of the lamprey catching areas from where the data for the regression analyses were acquired (PMS = peak migration season, EMS = early migration season), and of the release sites in the telemetry experiments P_{02} (release sites RP_{02L} and RP_{02U}),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

Illumination intensity of the moon ($MII_{d,yr}$) 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 ($NL_{d,yr}$) 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 ($T_{d,yr}$) 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 $TDS_{d,yr}$ 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

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

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

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

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 ($WVC_{d,yr}$).

Sea water level ($SWL_{d,yr}$) 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 $SWL_{d,yr}$ for a given night was the average of the measurements of previous afternoon and following morning.

Thus, the regression model was

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

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 β 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 $\varepsilon_{d,yr}$ 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 $reCPUE_{yr}$.

The mean discharge of the rivers was measured daily by the Kokkola Water District with an accuracy of 0.1 $m^3 s^{-1}$. 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 ($reDIS_{yr}$). 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 (TA_{yr}), maximum ($TMAX_{yr}$) and minimum temperatures ($TMIN_{yr}$) 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 (TD_{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

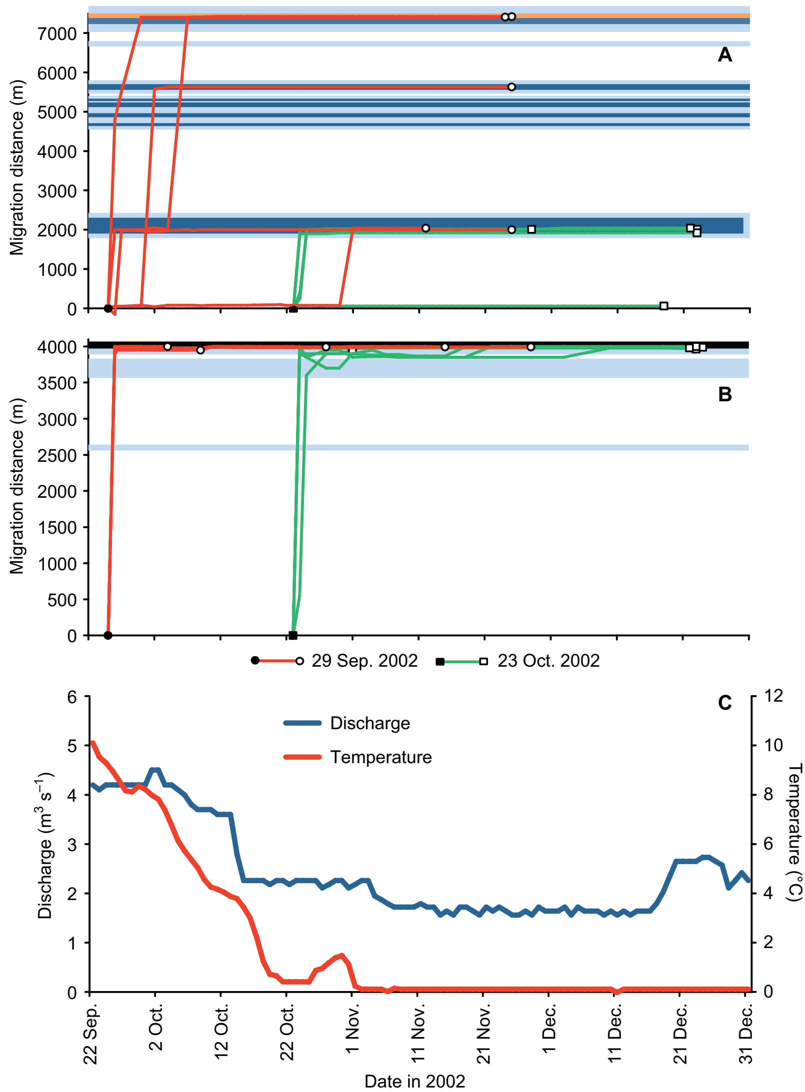

Fig. 2. The movements of radio-tagged river lampreys released at sites RP_{02L} (**A**) and RP_{02U} (**B**) on 29 Sep. 2002 (red lines) and 23 Oct. 2002 (green lines). Filled symbols represent release date/site and open symbols the last observation date/site for an individual lamprey. The mesohabitat 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},

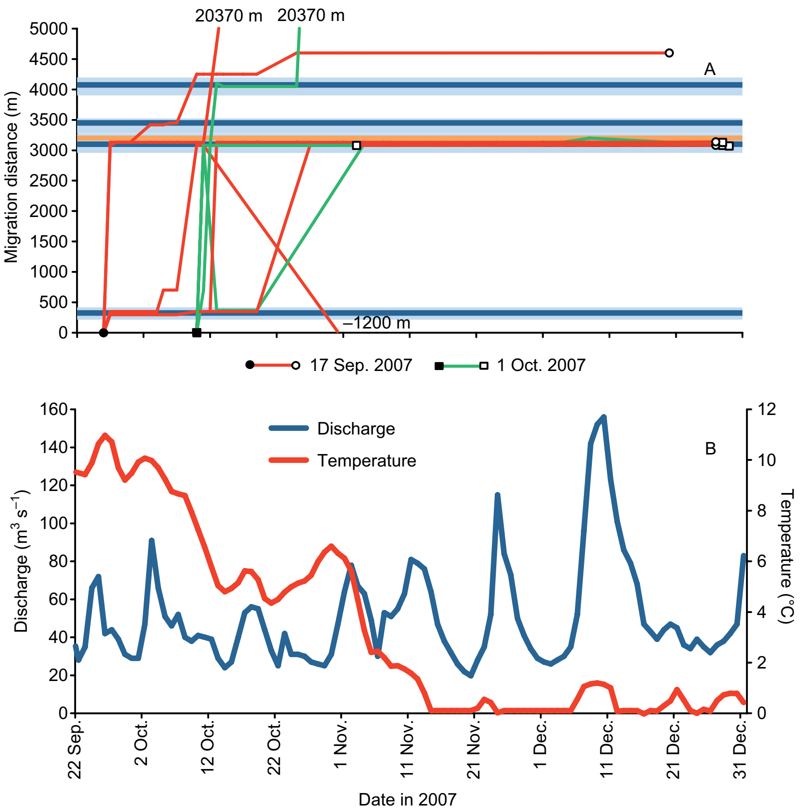

Fig. 3. (**A**) The movements of radio-tagged river lampreys released at site RK_{07} on 17 Sep. 2007 (red lines) and 1 Oct. 2007 (green lines). 20 370 m and –1200 m denote the exceptionally long upstream and downstream migrations. Other symbols as in Fig. 2. (**B**) The river water temperature (°C)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

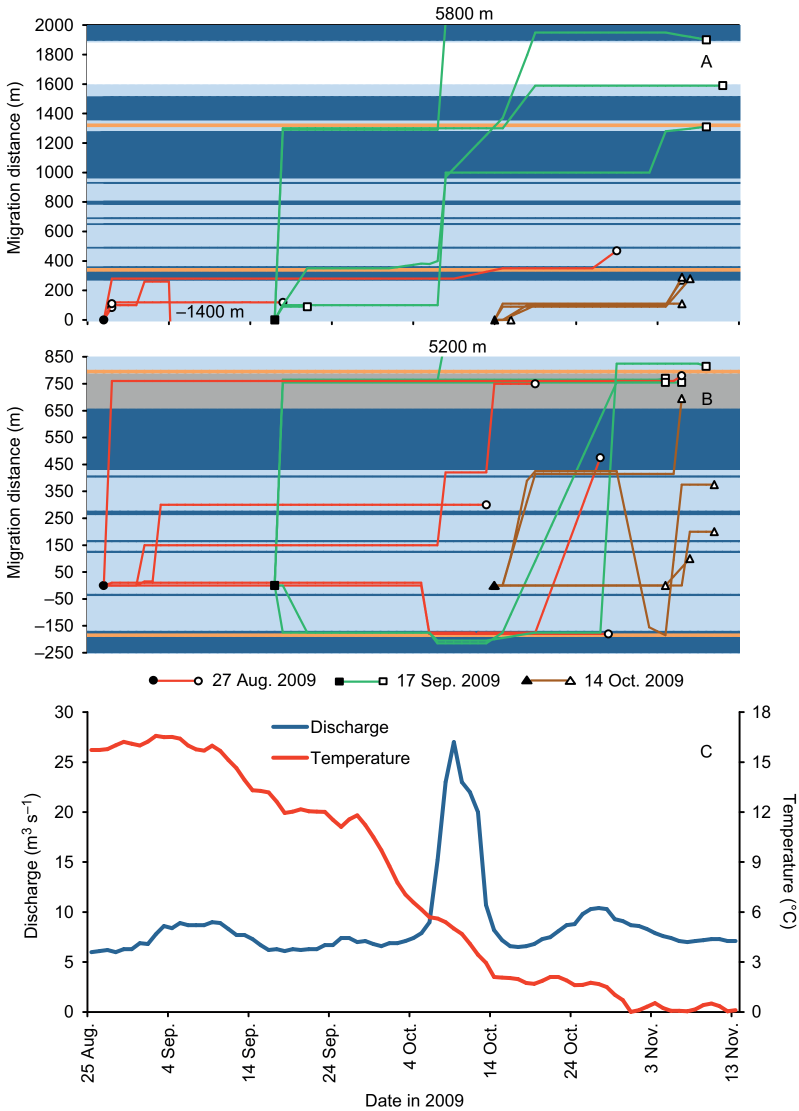

Fig. 4. The movements of radio-tagged river lampreys released at sites RK_{09L} (**A**) and RK_{09U} (**B**) on 27 Aug. 2009 (red lines), 17 Sep. 2009 (green lines) and 14 Oct. 2009 (brown lines). 5800 m, 5200 m and –1400 m denote the exceptionally long upstream and downstream migrations. Other symbols 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

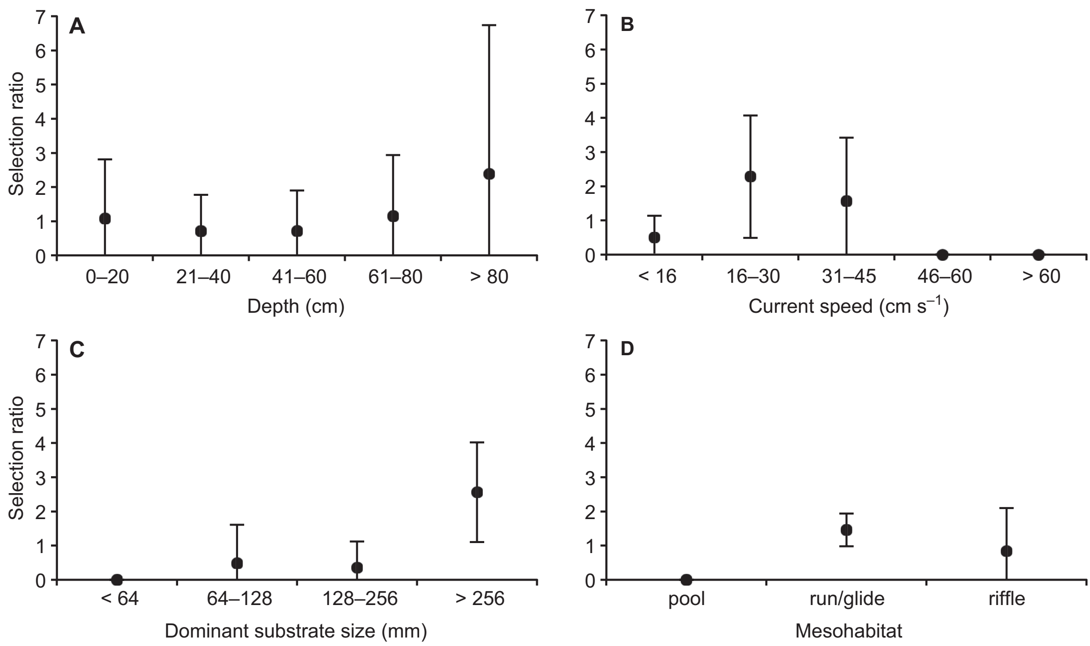

Fig. 5. Selection ratios (± 90%CI) for holding sites of 10 river lampreys for different categories of (**A**) water depth, (**B**) surface current speed, (**C**) prevailing substrate type, and (**D**) mesohabitat.

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 β	t	p	VIF
	β	SE				
Adjusted r^2 = 0.752						
Constant	0.227	0.078		2.917	0.004	
log($CPUE_{d-1,yr}$)	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($DIS_{d,yr}$)	0.185	0.068	0.118	2.716	0.007	1.377
$MII_{d,yr}$	–2.366	0.523	–0.188	–4.524	< 0.001	1.260
$TDS_{d,yr}$	0.143	0.068	0.089	2.089	0.038	1.320
$WVC_{d,yr}$	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 β	t	p	VIF
	β	SE				
Model 1: Adjusted r^2 = 0.769						
Constant	0.134	0.113		1.192	0.237	
log($CPUE_{d-1,yr}$)	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($DIS_{d,yr}$)	0.282	0.101	0.162	2.800	0.006	1.358
$TDS_{d,yr}$	0.158	0.118	0.086	1.337	0.185	1.649
$WVC_{d,yr}$	0.028	0.010	0.177	2.938	0.004	1.461
$MII_{d,yr}$	–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($CPUE_{d-1,yr}$)	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($DIS_{d,yr}$)	0.274	0.104	0.158	2.637	0.010	1.377
$TDS_{d,yr}$	0.177	0.121	0.096	1.465	0.147	1.654
$WVC_{d,yr}$	0.032	0.010	0.205	3.237	0.002	1.548
$MPI_{d,yr}$	–0.005	0.002	–0.158	–2.511	0.014	1.519
$CC_{d,yr}$	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 β	t	p	VIF
	β	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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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