Journal of Fish Biology (2005) **66,** 499–512
doi:10.1111/j.1095-8649.2005.00618.x, available online at http://www.blackwell-synergy.com

Reproductive ecology of the river lamprey

M.-H. JANG AND M. C. LUCAS*

School of Biological and Biomedical Sciences, University of Durham, Science Laboratories, South Road, Durham, DH1 3LE, U.K.

(Received 12 April 2004, Accepted 29 October 2004)

The reproductive ecology of river lamprey *Lampetra fluviatilis* was investigated during the spawning period 2003 in the River Derwent, north-east England. Over this period 1199 ± 104 individuals day^{-1} (mean $\pm$ S.D.) were counted on one spawning site (area *c.* 450 m^2), but mark-recapture estimates suggested that >5000 river lamprey used this site over the same period and egg deposition was estimated as 168 000 eggs m^{-2}. The operational sex ratio of river lamprey in spawning clusters changed between spawning phases, from domination by females during the nest-building phase (male : female ratio, 1 : 3·46), to a preponderance of males during the spawning phase (male : female, 1 : 0·37), followed by a return to a majority of females after spawning (male : female, 1 : 3·74). Recapture data showed that >97% of recaptured, tagged males were recorded at two or more nests, whereas almost 50% of recaptured, tagged females were recorded at the same nest, suggesting a promiscuous mating system, with a tendency towards polygyny within the population. Within the lower 80 km of the River Derwent and its tributaries, evidence of river lamprey spawning was found at only six sites, and most spawning (>80% of the observed spawning population) was at one site.

Key words: *Lampetra fluviatilis*; mating system; reproductive ecology; sex ratio; spawning habitat.

INTRODUCTION

Throughout their distribution, lampreys (Petromyzontiformes) are of significant ecological, cultural and economic importance (Hardisty, 1986*a*; Renaud, 1997; Kelly & King, 2001; Lucas & Baras, 2001). The river lamprey *Lampetra fluviatilis* (L.) is a parasitic species, formerly widespread through western Europe (Maitland, 1980; Hardisty, 1986*b*) and typically anadromous, although permanently freshwater populations are known (Maitland *et al.*, 1994; Renaud, 1997). It is an endangered species (Lelek, 1987) and receives conservation protection in Europe through the Bern Convention (Renaud, 1997) and through the European Habitats Directive 92/43/EEC, as a species whose conservation requires the designation of special areas of conservation (SACs) (EC, 1992; Kelly & King, 2001; Maitland, 2003). Populations of river lamprey have been impacted by pollution of rivers and estuaries, overexploitation, loss of spawning and

*Author to whom correspondence should be addressed. Tel.: +44 (0) 191 334 1345; fax: +44 (0) 191 334 1201; email: m.c.lucas@durham.ac.uk

larval habitat and by physical barriers to migration (Lelek, 1987; Ojutkangas *et al*., 1995).

Lampreys aggregate in pairs or larger groups to spawn in crude nests or depressions formed in gravel, pebbles or stony substrata with swift-running water in spring or early summer (Applegate, 1950; Malmqvist, 1983; Hardisty, 1986*a*). Field descriptions (Hardisty, 1986*b*), together with laboratory observations (Hagelin & Steffner, 1958; Hagelin, 1959; Maitland *et al*., 1994), indicate that male river lamprey have a tendency to begin 'nest-building' and are joined by females, that spawning is in a cluster and that mating is promiscuous. Adults die after a single spawning, following endocrine-mediated changes in physiology (Larsen, 1980). Recent studies have demonstrated highly structured, pheromone-mediated reproductive behaviour in sea lamprey *Petromyzon marinus* L. (Li *et al*., 2002). Limited information, however, is available on the mating systems and the factors involved in site selection and reproductive behaviour in lamprey species.

The aim of this study was to characterize population structure, spawning habitat characteristics, nest building and use, sex ratio and individual movements on the spawning grounds of adult river lamprey in their natural environment.

MATERIALS AND METHODS

STUDY AREA

The study was carried out on the candidate SAC lower River Derwent (mean discharge of *c*. 15 $m^3 s^{-1}$), a tributary of the River Ouse that then joins with the River Trent to form the proposed SAC River Humber (mean discharge of 250 $m^3 s^{-1}$) which flows to join the North Sea in north-east England (Law *et al*., 1997). The tidal River Ouse maintains a river lamprey fishery that takes *c*. 20 000–40 000 adult river lamprey per year and is believed to hold one of the most important river lamprey populations in Great Britain (M. Lucas, unpubl. data). It has an extensive, shallow and productive estuary and coastal zone and this, combined with freshwater spawning and larval river lamprey habitats, particularly within the River Ouse system, provides suitable conditions for a substantial river lamprey population (Whitton & Lucas, 1997; Lucas *et al*., 1998). The lower 80 km of the Derwent is distinctly lowland in character (overall gradient of *c*. 0·3 m km^{-1}), but much of this drop occurs locally at the five weirs (>1 m height) and one tidal barrage along the main channel over this distance.

The main spawning study was carried out immediately downstream of Stamford Bridge weir (53°59′30″ N; 0°54′30″ W), the third river obstruction counting in an upstream direction and 35·4 km upstream from the River Ouse confluence. The area provides one of the first known locations of significant gravel substratum in the main channel of the River Derwent and is a known site for river lamprey spawning (D. Hopkins, pers. comm.). The weir has a near-vertical headloss of 2·1 m at a median discharge (Q_{50}) flow, a sluiced bypass canal and a Denil-type baffled flume fishway (Lucas *et al*., 1999). The river is relatively shallow (*c*. 0·3–0·8 m at Q_{50}), with a gravel substratum below the weirpool, but deepens (mostly 2–5 m) and becomes siltier, with little in-stream vegetation 100 m further downstream.

TRAPPING AND MARKING OF RIVER LAMPREY

To characterize the size and sex distribution during the main migration period (November 2002 to February 2003) and the prespawning-spawning period (March to

April 2003), adult river lamprey were trapped in the lower River Derwent between 19 November 2002 and 30 April 2003, using meshed 1 m long, two-funnel eel pots. Mesh-size to the first funnel was 12 mm, knot-to-knot, sufficiently small to catch river lamprey >26 cm total length, L_T (M.-H. Jang, unpubl. data). Mesh-size after the first funnel was 10 mm, knot-to-knot. Traps were located at Barmby Barrage, Loftsome Bridge (4 km upstream from the Ouse confluence), Sutton-upon-Derwent (25 km upstream), Stamford Bridge (35·4 km upstream) and Kirkham (50·3 km upstream). Sampling at the sites downstream of Sutton-upon-Derwent halted at the end of February 2003 because catches were low, while sampling at Kirkham began on 8 March 2003. River lamprey captured were sedated in a 0·5 ml l^{-1} solution of 2-phenoxyethanol, measured for L_T, weighed, sexed by examination of secondary sexual characteristics (Hardisty, 1986*a*, *b*) which was possible from early March onwards, marked with a uniquely numbered mini T-bar anchor tag (FD-68B FF, Floy Tag, U.S.A.) inserted into the dorsal musculature at the rear of the anterior dorsal fin, fin-clipped on the posterior dorsal fin (for purposes of double-marking to assess floy tag loss) and released at the site of capture.

From 17 March 2003 to 30 April 2003 a modified, wingless, two-funnel fyke net (12 and 8 mm mesh) was set at the upstream exit of the fishway at Stamford Bridge weir to capture river lamprey passing upstream through the fishway immediately prior to and during the spawning period. The entrance frame of this net was secured closely to the fishway exit and the water level did not go over the top of the net during the period of study until 27 April when high flows occurred. Any river lamprey present were examined for marks, tagged if unmarked and released immediately upstream. Two additional 1 m long, two-funnel river lamprey traps were set 3–5 m downstream of the entrance to the fishway at the weir from the beginning of April onwards for mark-recapture purposes and to assess river lamprey activity in the vicinity of the fishway entrance.

SPAWNING SITE OBSERVATIONS

From 17 March to 30 April 2003 daily inspections of the field site at Stamford Bridge were made from the bank and by wading, to locate spawning river lamprey. These were made in daylight, but often at night also, using a hand-held spotlight. On the first day that spawning activity was noted (13 April 2003), locations and approximate size of nests were noted and drawn on a scale map of the site. This was repeated daily, during daytime (between 1300 and 1800 hours), until the last day on which river lamprey spawning was observed, 27 April 2003. During the spawning period, the river was surveyed from bank to bank in *c*. 2 m transects, moving in an upstream direction and counting the number of river lamprey individuals and clusters (discrete aggregations associated with nests). The precision of counting, nest recording and fish capture was facilitated by carrying this out during the day, since earlier observations suggested no apparent differences in behaviour or numbers of spawning river lamprey by day or night. River lamprey lose their negative phototaxic behaviour during the spawning period (Claridge *et al*., 1973; Sjöberg, 1977) and daytime activity may be nearly as extensive as at night (Hardisty, 1986*b*). Nests were identified as depressions in the gravel surrounded, at the rear and sides, by gravel moved outside the depression. Nests were also characterized by clean gravel and sand from the overturned and disturbed material, compared to the surrounding gravel that was covered with epilithic algae. Where nests were relatively large, more than one distinct cluster of river lamprey could occur in the same nest, particularly later in the spawning period when old and fresh nests often became joined together.

Each day, over the same time period, two to three clusters of river lamprey were sampled randomly from the spawning area. A total of 35 clusters were sampled during the study. Visual observations of each cluster were made over a 5 min period, in some cases supplemented by digital photographs. If approached carefully from downstream, the cluster was not disturbed by human presence. In most cases, males and females could by distinguished from above by the swelling of the anterior portion of the first dorsal fin in males, or as river lamprey tilted their bodies to the side, by the swollen post-cloacal ventral fin in females (Hardisty, 1986*b*).

Each cluster was preliminarily classified as nest-building, spawning or postspawning, reflecting the three behaviour types observed. Nest-building refers to that phase where river lamprey constructed nests using their oral discs and tails and were not spawning or exhibiting any behaviours related with spawning, such as attachment of the oral disc to conspecifics, body entwinement and vibration of the body during egg deposition and fertilization (Hardisty, 1986*a*, *b*). The spawning phase describes that stage where river lamprey were engaged in spawning behaviour as defined above, but during which nest excavation continued. The postspawning phase is defined as that in which a cluster of river lamprey was resting within a well-excavated nest, without evidence of nest excavation or spawning behaviour. These descriptions were subsequently confirmed as valid by capture, examination and gentle stripping of river lamprey; the first two categories comprised unspawned river lamprey and ovulated females and spermiating males, while the last category comprised partly spent or fully spent males and females.

After observation, a hand-net (2 mm mesh-size) was used to catch all members of the cluster. This was successful if carried out carefully and <5% of river lamprey escaped. All river lamprey from each cluster were sedated and L_T, mass and sex of each individual were recorded. A uniquely numbered T-bar anchor tag was externally attached to the river lamprey, to identify each individual on subsequent recapture. All tagged river lamprey were double-marked by fin clipping in order to assess tag retention. The identities of all recaptured river lamprey were noted. Following recovery in well-oxygenated water, the whole cluster was released at the site from which it had been captured, within *c.* 1 h of capture. Most river lamprey immediately adhered to the substratum at the nest although several typically moved a few metres away. Usually within 1 h of release a cluster of tagged river lamprey was observed re-engaging in their original behaviour at the nest site.

Daily mark and recapture data were used to estimate population size at the site over the 15 day study period using the Jolly-Seber stochastic method for estimating population, survival and immigration in open populations (Jolly, 1965). This was carried out using the programme 'Jolly' (http://www.phidot.org). Recapture data were also used to analyse movements of river lamprey between clusters at the site.

During the spawning period, characteristics of spawning habitat and numbers of spawning river lamprey were recorded in the middle and lower River Derwent. From the distribution of possible spawning habitat (submerged gravel, pebble, cobble in flowing water), 66 sites were selected and searched for river lamprey and evidence of river lamprey spawning during the spawning period. When river lamprey spawning was observed at a site, the numbers of river lamprey spawning and physical characteristics (*i.e.* composition of substratum, water depth, river width, surface water velocity and gradient) of the site were recorded.

Water temperature was measured at 1 h intervals with a temperature logger (Tinytag, Gemini Data Loggers, Chichester, U.K.) at Stamford Bridge during the study period. Water flow data at the Buttercrambe gauging station (40·2 km upstream) were supplied by the Environment Agency (pers. comm.). Statistical analyses were carried out using *t*-tests and one-way ANOVA (SPSS Release 11.0).

RESULTS

SIZE AND SEX CHARACTERISTICS

A total of 124 adult river lamprey were caught in traps in the River Derwent between November 2002 and the end of February 2003 and 77 were caught in traps of the same design in the River Derwent between 1 March and 30 April 2003, as well as three captured in the trap at the upstream exit of the fishway at Stamford Bridge. River lamprey captured in identical traps over the period November to February were significantly longer than those captured over the period March to April (ANOVA, $F_{1,200}$, $P < 0{\cdot}001$) [Fig. 1(a)].

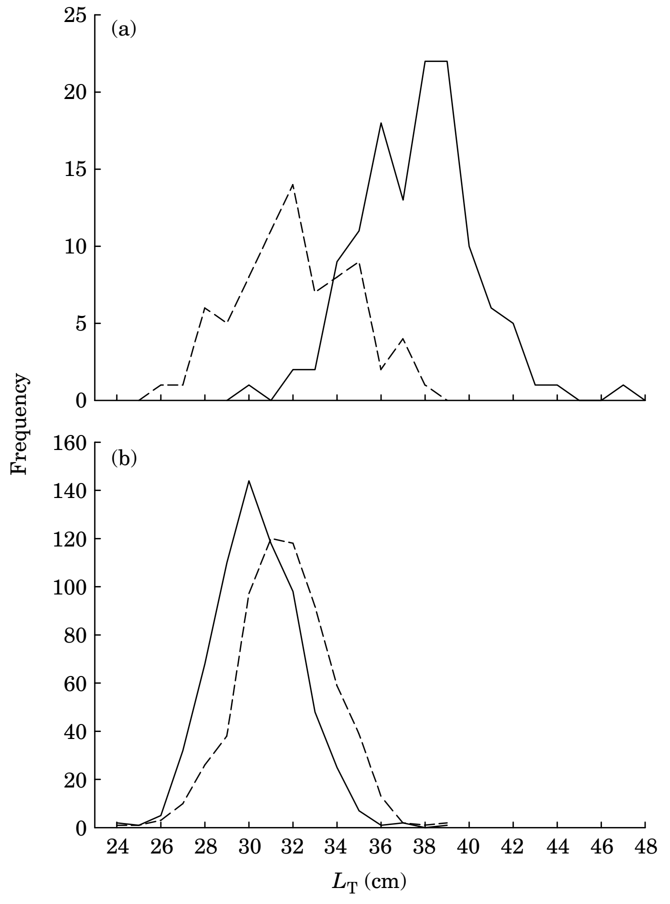

FIG. 1. Total length (L_T) distribution of adult river lamprey in the lower River Derwent caught by (a) traps [November 2002 to February 2003 (—), $n = 124$ (sex indeterminate); March to April 2003 (– – –), $n = 77$ of which 21 female, 55 male and one indeterminate] and (b) hand-net (—, female; – – –, male) below Stamford Bridge weir ($n = 1284$) during the spawning period (13–27 April 2003).

A total of 1284 (male, $n = 622$; female, $n = 662$) individual river lamprey were hand-netted during the spawning period (15 days; 13–27 April 2003), giving an estimated sex ratio (male : female) for the spawning population of 1 : 1·06. Mean L_T and mass of river lamprey captured were 30·8 cm (male, 31·5 cm; female, 30·2 cm) and 73·2 g (male, 74·7 g; female, 72·6 g) respectively. Males were slightly, but significantly, longer than females (ANOVA, $F_{1,1283}$, $P < 0.001$) [Fig. 1(b)].

NEST BUILDING AND HABITAT CHARACTERISTICS

Flows in March and April 2003, were relatively low (daily mean $\pm$ S.D. $= 14.0 \pm 4.2$ m^3 s^{-1}; daily mean $\pm$ S.D. for preceding 10 year period $= 21.8 \pm 18.7$ m^3 s^{-1}). The resulting clear water aided field observation. Flow, however, was higher than the 10 year mean during the main upstream migration period of November to February 2002–2003 (daily mean $\pm$ S.D. $= 40{\cdot}4 \pm 16{\cdot}0\ m^3\ s^{-1}$; daily mean $\pm$ S.D. for preceding 10 year period $= 25{\cdot}6 \pm 3{\cdot}7\ m^3\ s^{-1}$).

River lamprey were first observed to begin building several spawning nests on 13 April 2003 at Stamford Bridge, when the water temperature was *c.* 8° C and flow was relatively low and stable [Fig. 2(a)]. but radio-tracked river lamprey had arrived and remained within 200 m of the spawning area for several months previously (M.-H. Jang, unpubl. data). Nests typically measured 0·5–1·0 m long × 0·2–0·4 m wide, with the longest dimension usually oriented across the river (Fig. 2).

The only other fish species in this river that makes similar spawning depressions at this time of the year is the grayling *Thymallus thymallus* (L.), but this occurs at a low density at the site (pers. obs.) and no grayling were observed spawning on the shallows during the study period. In the nests themselves, and below them, minnow *Phoxinus phoxinus* (L.) and stone loach *Barbatula barbatula* (L.) congregated in large numbers and consumed deposited eggs and those swept from the nests by the current.

Later in the spawning period, nests tended to be built further upstream on the area of gravel below the weir (Fig. 2); from the downstream boundary of spawning at this site, there was a significant difference in mean longitudinal nest position between days 1, 5, 10 and 13 (ANOVA, $F_{3,132}$, $P < 0{\cdot}001$) with nests significantly further upstream on days 5, 10 and 13 than on day 1. Old nests were often expanded in size for spawning as time progressed and these

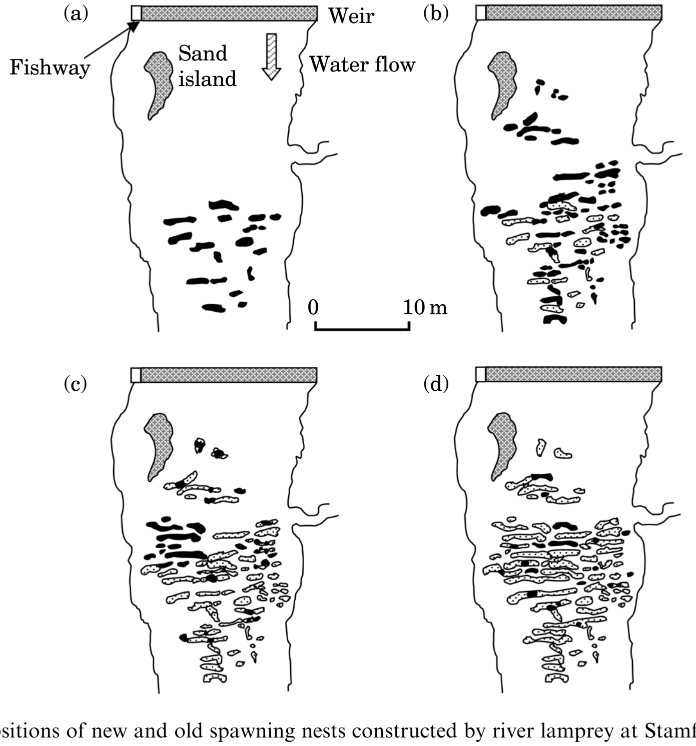

FIG. 2. The positions of new and old spawning nests constructed by river lamprey at Stamford Bridge on (a) 13 April, (b) 18 April, (c) 23 April and (d) 27 April 2003 (▨, old nest; ■, new nest).

tended to become linked to form lines oriented across the river [Fig. 2(b), (c), (d)]. After 20 April, the number of new nests decreased, whereas the frequency of used or expanded old nests increased [Fig. 2(d)]. The total area over which spawning occurred was *c*. 30 m long and 15 m wide, an area of 450 m^2. By 27 April, few new nests were apparent [Fig. 2(d)] and on this day heavy rain fell, causing high flows and turbid water. Despite repeated observation over successive days as flows subsided and the water cleared no further spawning river lamprey could be observed at the site.

NUMBERS OF SPAWNERS AND CLUSTERS

A cumulative total of 17 990 river lamprey was counted at the spawning site over 15 days (13–27 April) and the number of individuals counted each day varied between 336 and 1804 (mean $\pm$ S.D. $= 1199 \pm 104$ individuals day^{-1}) on 13 and 23 April respectively. The daily number of river lamprey clusters varied between 27 on 13 April and 102 clusters on 20 April, respectively. The mean number of river lamprey per cluster varied between 12 on 13 April and 24 on 16 April. Thirty five river lamprey (27 males and eight females) were caught in the traps set near the entrance of the fishway, one of which was subsequently recaptured by hand-net on the spawning area.

Of 1284 river lamprey hand-netted and tagged at the spawning site, a total of 180 recaptures (including second or third recaptures) were made of 145 individuals (11·3% of river lamprey marked at the site). Daily numbers of marked and recaptured river lamprey are shown in Table I. No river lamprey tagged at sites other than Stamford Bridge were recaptured at that site. One river lamprey with a fin clip, but without a floy tag, was recaptured at the spawning site. The rate of recapture of river lamprey marked on any one day tended to decrease exponentially in the days following release, suggesting that river lamprey left the spawning site in a downstream direction, presumably after spawning, within *c*. 8 days (Fig. 3).

Daily Jolly-Seber population estimates and numbers of immigrants, with their 95% CI are given in Table I. By summing the first Jolly-Seber (open population) estimate with subsequent estimates of immigration, the cumulative number of individual river lamprey estimated to have used the spawning site over this period was *c*. 5800. The daily population estimate varied from daily observed numbers by a mean of 19%. Even if a conservative figure of 5000 river lamprey using the spawning site is adopted, this gives a cumulative density of 11 adult river lamprey per m^2 using the 450 m^2 site over the spawning period, suggesting extremely intensive use of this limited area of spawning habitat. Using the overall sex ratio at the spawning site (male : female, 1 : 1·18) it is estimated that 2706 female river lamprey used the spawning site. The average mass of females at the spawning site was 72 g. Using an average fecundity of 28 000 eggs for a river lamprey of this size (Hardisty, 1964) yields an estimated total egg deposition at the spawning site in 2003 of $7{\cdot}58 \times 10^7$ eggs or *c*. 168 000 eggs m^{-2}.

OCCURRENCE OF SPAWNING RIVER LAMPREY IN THE LOWER DERWENT

Evidence of river lamprey spawning was found at six out of 66 possible sites investigated (Table II). Principally, river lamprey spawning occurred below

TABLE I. The numbers of adult river lamprey marked and recaptured daily, and Jolly-Seber population estimate during the river lamprey spawning survey

Day	n_i	M_i	m_i	N	S.E.	95% CI		B	S.E.	95% CI	
1	139	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
2	77	139	8	1572	789	25	3119	326	281	−224	876
3	93	216	8	738	281	187	1289	−73	367	−792	646
4	102	309	23	775	239	306	1243	57	98	−134	249
5	92	411	27	446	146	160	732	583	273	48	1117
6	128	503	17	833	341	164	1502	734	452	−153	1620
7	92	631	8	1118	527	86	2150	586	475	−345	1517
8	164	723	16	1387	602	208	2567	148	243	−329	625
9	59	887	9	639	321	9	1269	747	479	−191	1685
10	103	946	9	1175	579	40	2301	833	634	−411	2076
11	100	1049	7	1462	725	41	2882	81	377	−658	819
12	125	1149	16	897	383	145	1648	66	126	−182	313
13	54	1274	11	366	174	25	706	173	163	−146	491
14	47	1328	9	412	251	−80	904	ND	ND	ND	ND
15	89	1375	12	ND	ND	ND	ND	ND	ND	ND	ND
Total	1464		180								
Mean				909	127	659	1159	355	56	245	464

n_i, number of river lamprey captured including recaptures; M_i, cumulative number of marked river lamprey available for recapture; m_i, number of recaptured river lamprey; N, estimated number of individuals; B, immigrant river lamprey to population; ND, no data.

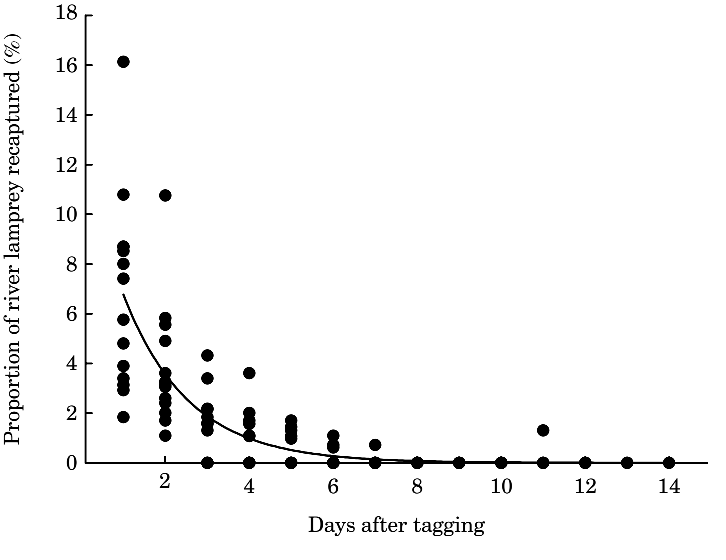

FIG. 3. The proportion of river lamprey recaptured on Stamford Bridge spawning site in successive days after tagging and release over the period 13–26 April 2003 together with fitted exponential function ($y = 7{\cdot}476e^{-0{\cdot}643x} + 5{\cdot}406e^{-0{\cdot}644x}$, $n = 180$, $r^2 = 0{\cdot}631$, $P < 0{\cdot}001$).

TABLE II. Characteristics of river lamprey spawning habitats at spawning sites on the River Derwent system, 2003

	Stamford Bridge	Buttercrambe	Howsham	Kirkham	Malton	Newsham
Distance upstream of river mouth (km)	35·4	40·2	45·7	50·3	61·3	77·7
Area used in spawning (m^2)	*c.* 450	<10	*c.* 200	*c.* 10	<10	*c.* 1
Mean width (m)	18	15	20	25	18	10
Depth range (cm)	19–120	50–150	30–150	40–100	30–120	20–100
Surface velocity (mean ± S.D. $m\,s^{-1}$)	$0·67 \pm 0·17$	$0·82 \pm 0·23$	$0·57 \pm 0·05$	$0·47 \pm 0·15$	$0·50 \pm 0·20$	$0·80 \pm 0·28$
Locality gradient* ($m\,km^{-1}$)	0·21	0·89	0·24	0·26	1·12	1·03
Substratum composition (M : S : G : C : B : Bd)	10 : 10 : 30 : 40 : 10 : 0	5 : 5 : 20 : 30 :40 : 0	7 : 8 : 10: 50 : 25 : 0	10 : 10 : 5 : 20 55 : 0	25 : 25 :10 : 20 : 15 : 5	0 : 10 : 20: 60 : 10 : 0
Maximum daily number of spawning river lamprey recorded	1804	134	243	96	10	4

M, mud; S, sand; G, gravel; C, cobbles and stones; B, boulder; Bd, bedrock; *, measured from altitude estimates at 1 km intervals.

weirs and bridges in areas of locally elevated gradient and water velocity. The hydraulic conditions of the spawning areas were shallow and fast water with areas of gravel and cobble (Table II). At Stamford Bridge spawning river lamprey were more than three times as abundant, as at all other sites combined.

OPERATIONAL SEX RATIO AND MOVEMENTS BETWEEN CLUSTERS

From the 35 river lamprey clusters that were intensively investigated, *c* 3·4 times as many females as males were present in clusters in the nest-building phase (Table III). During nest building, males tended to be distributed 1–2 m downstream of nests, usually clearly out of the nest itself. During the spawning phase, the operational sex ratio reversed dramatically in favour of males, then for postspawning clusters the ratio of males to females returned to a value similar to that for prespawning clusters (Table III). Differences in sex ratio between spawning phases were significant (ANOVA, $F_{2,34}$, $P < 0{\cdot}001$) for spawning clusters *v*. nest building or postspawning (Tukey's HSD, $P < 0{\cdot}001$) but not for nest building *v*. postspawning categories (Tukey's HSD, $P = 0{\cdot}991$).

A total of 180 river lamprey recaptures, including multiple (second or third) recaptures, were made. The sex ratio of recaptured river lamprey varied between nest-building (male : female, 1 : 2·50, 21 individuals), spawning (male : female, 1 : 0·29, 40 individuals), and postspawning (male : female, 1 : 7·50, 119 individuals) behaviours. Recapture data showed that >97% of all males recaptured once ($n = 41$) were located at a different nest site from where they were tagged (Fig. 4). Of male river lamprey recaptured twice ($n = 9$), six were captured at two nests different from the site at which they originated and two at one other nest. By contrast, 48% of all females recaptured once only ($n = 104$) were recorded at the same nest as where they were tagged (Fig. 4). Of females recaptured twice ($n = 22$) 36% were found at the same nest site on all occasions. Three females and one male were recaptured three times.

DISCUSSION

Males of several lamprey species, including river lamprey, tend to reach the spawning grounds first and begin preliminary nest building, while females join later (Applegate, 1950; Hagelin & Steffner, 1958; Hagelin, 1959; Malmqvist, 1983; Hardisty, 1986*b*, *c*). Spermiating male sea lamprey (Li *et al*., 2002) produce a sex pheromone from the gill region that is highly attractive to

TABLE III. Changes in sex ratio of river lamprey clusters sampled during the nest-building, spawning and postspawning phases

	Nest-building	Spawning	Postspawning	Total
Sex ratio* (M : F)	1 : 3·46	1 : 0·37	1 : 3·74	1 : 1·18
Number of clusters	7	15	13	35
Number of individuals*	357	690	417	1464

*, includes recaptured individuals.

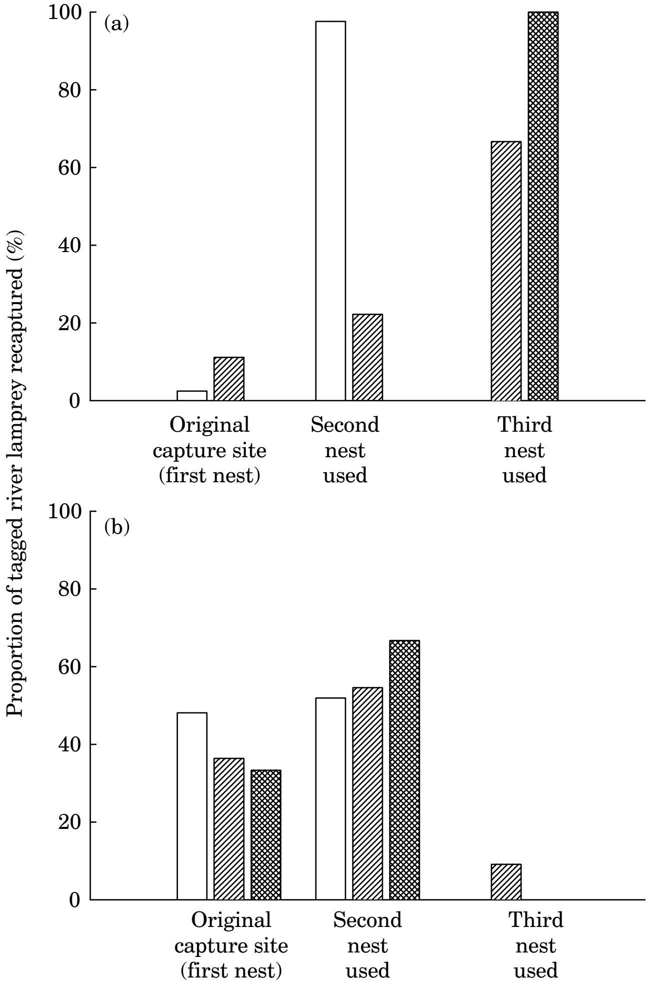

FIG. 4. The percentage of tagged river lamprey recaptured at the same nest where they were originally captured, tagged and released or at different nests on subsequent occasions for (a) first (□, $n = 41$), second (▨, $n = 9$) and third recapture (▩, $n = 1$) for males and (b) first (□, $n = 104$), second (▨, $n = 22$) and third recapture (▩, $n = 3$) for females.

sexually mature females and it appears that males use this pheromone to attract gravid females to the nest. Spawning river lamprey exhibit a similar sexual dimorphism of gill cells (Pickering & Morris, 1977) and the production of a similar sex hormone by spermiating male river lamprey for attraction of gravid females has been hypothesized. Yet the present observations do not conform to these reports. Firstly, mainly females constructed nests before any sign of courtship or spawning behaviour (male : female ratio in nest-building clusters, 1 : 3·46), in contradiction to laboratory studies (Hagelin & Steffner, 1958; Hagelin, 1959). Video observations similar to those reported here have been documented in other rivers of the Yorkshire Ouse system, north-east England (B. Morland, pers. comm.). Secondly, the switch to a preponderance of males in spawning clusters (male : female, 1 : 0·37) suggests an attraction of males to females, not *vice versa*, followed by a predominance of females in 'postspawning' clusters (male : female, 1 : 3·74). Yet overall, the sex ratio at the spawning site was approximately equal. Lastly, analysis of the movements of recaptured river lamprey at the spawning site showed that males moved between nests much more frequently than females. These results strongly indicate a promiscuous mating system, with a tendency towards polygyny, with males locating groups of receptive females, then moving to other clusters. Nevertheless, the close proximity of the sexes on the spawning ground and the high density does not necessarily preclude the production of sex pheromone by male river lamprey. It remains to be determined whether either sex of river lamprey produces a sex pheromone. It is possible that the differences in nest-building and spawning behaviour observed in the current study, compared to those of Hagelin (1959) (typically two to 10 animals), relate to the large clusters on the spawning area in the present study (typically 10–50 animals), particularly since in Hagelin's (1959) study with larger clusters, females contributed greatly to nest-building.

The exponential decline with time of numbers of river lamprey recaptured suggests that relatively few remained on the spawning site for more than a few days. They are presumed to have moved downstream after spawning since only three were caught in the fishway trap. No spawning areas have been identified downstream and so those fish leaving were probably spent river lamprey. River lamprey spawning habitat used was similar to that reported elsewhere in the very few publications that have quantified it (Eglite, 1958).

This study showed that different sizes of adult river lamprey may be captured in a river at different times of the year (Hardisty, 1986*b*). The greatest differences in size were apparent between winter and spring for samples taken using identical traps. Despite the small sample size, traps captured a similar size distribution of river lamprey in spring as obtained by hand-netting at the spawning grounds. It is possible that the substantial differences in fish size taken between winter and spring reflect the presence of different population components, as has reported for river lamprey (Abou-Seedo & Potter, 1979; Hardisty, 1986*b*; Maitland *et al*., 1994). Since 20% of river lamprey captured in traps, between November and February, but 98% of hand-netted spawning lamprey in April 2003, were <36 cm, for this explanation to be true, the vast majority of 'small' lamprey must have entered and migrated upriver without capture in traps before spawning. The seasonal L_T difference might also be due to length shrinkage that occurs during starvation and maturation over the migration and spawning period of river lamprey (Larsen, 1962, 1980; Hardisty, 1986*a*; Maitland *et al*., 1994), although the observed decrease in L_T of *c*. 17% is substantial. None of these possibilities is exclusive of the others and work is needed to elucidate which factors are responsible for the observed differences.

River lamprey have been considered a widespread, long-lived species and have provided significant fisheries in Europe (Renaud, 1997; Kelly & King, 2001). Throughout Europe and elsewhere, however, populations of anadromous river lamprey have declined dramatically over the last 30 years, mainly due to pollution, overexploitation, river barriers, channelization and damage to spawning gravels (Valtonen, 1980; Eklund *et al*., 1984; Ojutkangas *et al*., 1995; Kelly & King, 2001). Although large areas of larval ammocoete habitat are available in the River Derwent and growth habitat for the parasitic stage is abundant in the Humber estuary, there appear to be few spawning sites in the River Derwent. Since gravel areas are only used for courtship and spawning and eggs and hatched larvae drift downstream to the rearing habitat (Potter, 1980), intensive use of small sites for spawning may not, in its own right, present a population bottleneck. Large spawning aggregations at small sites, however, are extremely susceptible to interference, habitat damage or catastrophic effects such as pollution. For rivers with SAC status such as the River Derwent, careful attention needs to be paid to attaining and maintaining effective habitat protection, access to and prevention of exploitation at spawning grounds to help safeguard river lamprey populations. Paradoxically, other River Ouse tributaries with substantial anadromous river lamprey populations (Wharfe, Nidd, Ure, Swale; Whitton & Lucas, 1997; B. Morland, unpubl. data), having better availability of spawning and larval habitat and fewer barriers, but without SAC status, might be more valuable in a conservation context than the River Derwent. Prioritization of sites for river lamprey conservation in the large number of regulated rivers throughout western Europe should take account of issues of habitat availability identified above.

This study was supported by an award from the Environment Agency, U.K. to MCL and by a Postdoctoral Fellowship Program award of the Korea Sciences and Engineering Foundation (KOSEF) and a Hugh Cary Gilson Memorial award of the Freshwater Biological Association (FBA) to MHJ. We are grateful to D. and C. Hind for access to the spawning site at Weir Caravan Park, Stamford Bridge and to the Environment Agency for provision of flow data.

References

Abou-Seedo, F. S. & Potter, I. C. (1979). The estuarine phase in the spawning run of the river lamprey *Lampetra fluviatilis*. *Journal of Zoology, London* **188,** 5–25.

Applegate, V. C. (1950). Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. *U.S. Fish and Wildlife Service Special Scientific Report of Fisheries* **55,** 1–237.

Claridge, P. N., Potter, I. C. & Hughes, G. M. (1973). Circadian rhythms of activity, ventilatory frequency and heart rate in the adult river lamprey, *Lampetra fluviatilis*. *Journal of Zoology, London* **171,** 239–250.

EC (1992). Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. *Official Journal* **L206 22/07/92,** 7–50.

Eglite, R. (1958). Feeding habits of river lamprey in the Latvian SSR. *Gidrol Issle Tallinn* **1,** 234–269 (in Russian).

Eklund, J., Niemi, A. & Ojutkangas, E. (1984). The river lamprey in two regulated Finnish rivers. In *Regulated Rivers*, Vol. 2 (Lillehammer, A. & Saltweit, S., eds), pp. 417–426. Oslo: Universitets for laget.

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. (1964). The fecundity of lampreys. *Archiv für Hydrobiologie* **60,** 340–357.

Hardisty, M. W. (1986*a*). General introduction to lampreys. In *The Freshwater Fishes of Europe*, Vol. 1 (Holcík, J., ed.), pp. 19–83. Wiesbaden: AULA-Verlag.

Hardisty, M. W. (1986*b*). *Lampetra fluviatilis* (Linnaeus, 1758). In *The Freshwater Fishes of Europe*, Vol. 1 (Holcík, J., ed.), pp. 249–278. Wiesbaden: AULA-Verlag.

Hardisty, M. W. (1986*c*). *Lampetra planeri* (Linnaeus, 1758). In *The Freshwater Fishes of Europe*, Vol. 1 (Holcík, J., ed.), pp. 279–304. Wiesbaden: AULA-Verlag.

Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration – stochastic model. *Biometrika* **52,** 225–247.

Kelly, F. L. & King, J. J. (2001). A review of the ecology and distribution of three lamprey species, *Lampetra fluviatilis* (L.), *Lampetra planeri* (Bloch) and *Petromyzon marinus* (L.): a context for conservation and biodiversity considerations in Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy* **101B,** 165–185.

Larsen, L. O. (1962). Weight and length in the river lamprey. *Nature* **194,** 1093.

Larsen, L. O. (1980). Physiology of adult lampreys, with special reference to natural starvation, reproduction and death after spawning. *Canadian Journal of Fisheries and Aquatic Sciences* **37,** 1762–1779.

Law, M., Wass, P. & Grimshaw, D. (1997). The hydrology of the Humber catchment. *The Science of the Total Environment* **194/195,** 119–128.

Lelek, A. (Ed.) (1987). *The Freshwater Fishes of Europe*, Vol. 9. Wiesbaden: AULA-Verlag.

Li, W., Scott, A. P., Siefkes, M. J., Yan, H., Liu, Q., Yun, S.-S. & Gage, D. (2002). Bile acid secreted by male sea lamprey that acts as a sex pheromone. *Science* **296,** 138–141.

Lucas, M. C. & Baras, E. (2001). *Migration of Freshwater Fishes*. Oxford: Blackwell Science.

Lucas, M. C., Mercer, T., Batley, E., Frear, P. A., Peirson, G., Duncan, A. & Kubecka, J. (1998). Spatio-temporal variations in the distribution and abundance of fish in the Yorkshire Ouse system. *The Science of the Total Environment* **210/211,** 437–455.

Lucas, M. C., Mercer, T., McGinty, S. & Armstrong, J. D. (1999). Use of a flat-bed passive integrated transponder antenna array to study the migration and behaviour of lowland river fishes at a fish pass. *Fisheries Research* **44,** 183–191.

Maitland, P. S. (1980). Review of the ecology of lampreys in northern Europe. *Canadian Journal of Fisheries and Aquatic Sciences* **37,** 1944–1952.

Maitland, P. S. (2003). *Ecology of the River, Brook and Sea Lamprey*. Peterborough: English Nature.

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

Malmqvist, B. (1983). Breeding behaviour of brook lampreys *Lampetra planeri*: experiments on mate choice. *Oikos* **41,** 43–48.

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

Pickering, A. D. & Morris, R. (1977). Sexual dimorphism in the gills of the spawning river lamprey, *Lampetra fluviatilis* L. *Cell and Tissue Research* **180,** 1–10.

Potter, I. C. (1980). Ecology of larval metamorphosing lampreys. *Canadian Journal of Fisheries and Aquatic Sciences* **37,** 1641–1657.

Renaud, C. B. (1997). Conservation status of northern hemisphere lampreys (Petromyzontidae). *Journal of Applied Ichthyology* **13,** 143–148.

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

Valtonen, T. (1980). European river lamprey (*Lampetra fluviatilis*) fishing and lamprey populations in some rivers running into Bothnian Bay, Finland. *Canadian Journal of Fisheries and Aquatic Sciences* **37,** 1967–1973.

Whitton, B. A. & Lucas, M. C. (1997). Biology of the Humber rivers. *The Science of the Total Environment* **194/195,** 247–262.