Demography of sea lamprey (*Petromyzon marinus*) ammocoete populations in relation to potential spawning-migration obstructions

A. D. Nunn*, R. J. Taylor, I. G. Cowx, R. A. A. Noble, J. D. Bolland and J. P. Harvey

Hull International Fisheries Institute, School of Environmental Sciences, University of Hull, Hull, HU6 7RX, UK

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*Author to whom correspondence should be addressed. Tel.: +44 (0)1482 466429; email: a.d.nunn@hull.ac.uk

ABSTRACT

1. Recent advances in the understanding of lamprey migrations have led to concerns over the impacts of obstructions on the demography of many species. This study investigated sea lamprey (*Petromyzon marinus*) larvae (ammocoetes) in two adjacent but contrasting rivers, both designated Special Areas of Conservation under the EC Habitats Directive (92/43/EEC), one (the River Wye) with a small number of potential migration obstructions in its upper reaches and one (the River Usk) with obstacles along its course. The geographical distributions, densities and age structures of the ammocoete populations were examined in relation to the locations of potential obstructions to the spawning migrations of anadromous adults.

2. A minimum of three age classes was recorded as far as 200 km upstream of the mouth of the River Wye (93% of the length of the mainstem), demonstrating that adults regularly migrate to the upper reaches of the catchment (downstream of a natural waterfall). By contrast, sea lamprey ammocoetes appeared to be absent (in suitable habitat) from 20 km (17%) of the River Usk, and there was a reduction in density, prevalence and the number of age classes upstream of two putative spawning-migration obstructions.

3. This study highlights some of the potential impacts of habitat fragmentation by obstructions on the spawning migrations of anadromous species, as inferred from ammocoete demography. When used in combination to compare contiguous reaches, ammocoete densities, prevalence and age structure may be a useful indicator of which structures are likely to be important migration obstructions, and where further studies or mitigation efforts should be focussed. It is likely that passage past some obstructions is enhanced if high river levels occur during the spawning migration, but

there is a need to facilitate passage during all conditions, to improve access to under-exploited spawning and nursery areas.

INTRODUCTION

Lampreys can face a range of threats throughout their life cycle, including river regulation, pollution, habitat degradation, exploitation, predation, entrainment, impingement and barriers to migration (Masters *et al*., 2006; Lucas *et al.*, 2009; Mateus *et al*., 2012; Bracken and Lucas, 2013; Foulds and Lucas, 2014; Guo *et al*., 2016). Indeed, in 1997, ten of the 34 nominal lamprey species in the Northern Hemisphere were classified as endangered, eight were vulnerable at least in part of their range and one was extinct, with pollution and stream regulation being major causes (Renaud, 1997). Migration between marine and freshwater environments is essential for anadromous species to complete their life cycle, and is therefore a prerequisite for effective conservation (Lucas *et al.*, 2009). However, recent advances in the understanding of lamprey migrations have led to concerns over the impacts of obstructions on the demography of many species (Almeida *et al.*, 2002; Kemp *et al.*, 2011; Nunn and Cowx, 2012; Moser *et al*., 2015a). Although 'low-head' obstructions may have less dramatic local effects than large barriers such as dams, they are far more numerous and their cumulative ecological impacts can be significant (Lucas *et al.*, 2009). Indeed, several studies have suggested that the number of obstructions is the most important factor preventing lampreys from reaching spawning grounds in the upper reaches of rivers (Moser *et al.*, 2007; Goodwin *et al.*, 2008; Russon *et al.*, 2011). Furthermore, even when lampreys are able to overcome obstructions, the energy expended can result in delayed spawning and/or reduced spawning success (Mesa *et al.*, 2003; Quintella *et al.*, 2004, 2009).

The sea lamprey (*Petromyzon marinus* L.) is listed under Annex IIa of the EC Habitats Directive (92/43/EEC) as species whose conservation requires the designation of Special Areas of Conservation (SACs), Appendix III of the Bern Convention, which requires signatory countries to take "appropriate and necessary legislative and administrative measures" to ensure their protection, and is a UK Biodiversity Action Plan species. The species is widespread along the Atlantic coasts of Europe and North America, but has declined in many parts of its native range (Renaud, 1997; Maitland, 2003; Mateus *et al*., 2012; Guo *et al*., 2016; Hansen *et al*., 2016). The decline has been attributed to a number of factors, including habitat degradation, pollution, overexploitation and, especially, migration barriers (Oliveira *et al*., 2004; Andrade *et al*., 2007; Lasne *et al*., 2015; Maitland *et al*., 2015; Hansen *et al*., 2016). Conversely, migration barriers have been used in attempts to control the species in parts of its introduced range, such as the Laurentian Great Lakes in North America, where it is invasive and considered a pest (Lavis *et al*., 2003; McLaughlin *et al*., 2007; Hansen *et al*., 2016). Although it is known that obstructions impede the migrations of adult lampreys, there appear to have been few studies of their influence, if any, on the demography of lamprey larvae (ammocoetes). This study investigated sea lamprey ammocoetes in two adjacent but contrasting rivers, one (the River Wye) with a small number of potential migration obstructions in its upper reaches and one (the River Usk) with obstacles along its course. Both rivers are designated SACs for their population of sea lamprey. The aim was to examine the demography of the sea lamprey ammocoete populations in relation to potential obstructions to the spawning migrations of anadromous adults. The hypothesis was that there would be reductions in ammocoete density, prevalence and the number of age classes upstream of putative migration obstructions.

MATERIALS AND METHODS

Study area

Upstream migration by lampreys is potentially impeded by at least 11 structures along the mainstem of the River Usk (Figure 1). By contrast, the mainstem of the Wye has only four potential obstructions, all in the upper reaches and the most downstream of which is a natural waterfall with a fish pass, and consequently the majority of the catchment should be accessible to migrating lampreys (Figure 1). Indeed, sea lamprey spawning has been recorded along approximately 160 km (74%) of the mainstem of the Wye, from ~15 km above the tidal limit (Monmouth) to 207 km upstream (just downstream of Rhayader), as well as in the rivers Irfon and Ithon (Harvey *et al.*, 2006, 2010); the river increases in acidity and gradient and there are water-quality issues related to forestry and abandoned metal mines upstream of Rhayader (T. Hatton-Ellis, pers. comm.). In the Usk, spawning has been recorded along approximately 40 km (33%) of the mainstem, from ~3 km above the tidal limit (Llantrisant) to ~70 km upstream (Crickhowell), with the majority of records from near Abergavenny (Harvey *et al.*, 2006). The upper reaches of the mainstems and tributaries of both the Wye and Usk have mainly ‘sub-optimal’ lamprey ammocoete habitat (<15 cm depth of fine sediment, interspersed among coarser substrata; APEM, 2002), which is patchily distributed and restricted to areas of slow-flowing or still water; ‘optimal’ habitat (stable, fine sediment with organic matter, ≥15 cm sediment depth, low water velocity; APEM, 2002) is generally restricted to the lower reaches of the mainstems and tributaries (Harvey *et al*., 2006).

Sampling strategy and data collection

Sampling sites were selected to encompass as much of the catchments as possible in the vicinity of known spawning areas, in areas with previous records of lamprey ammocoetes and areas above and below potential spawning-migration obstructions (Figure 1). The locations of potential barriers to migration were provided by Environment Agency Wales. It is generally believed that there are two significant obstacles to migration in the Usk (Crickhowell Bridge and Brecon Weir; T. Hatton-Ellis, pers. comm.), but for the purposes of this study, all weirs, waterfalls and bridge footings were regarded as potential obstructions to the spawning migration of sea lamprey.

A total of 54 sites (130 points) on the River Wye and 35 sites (83 points) on the River Usk were sampled for lamprey ammocoetes in October and November 2005 (Figure 1), with sampling points being selected in areas of suitable lamprey ammocoete habitat (APEM, 2002; Harvey and Cowx, 2003; Maitland, 2003) at each site. The sampling strategy followed the EU Life in UK Rivers protocol (Harvey and Cowx, 2003; Cowx *et al*., 2009), with quantitative or semi-quantitative samples taken at each site, depending upon habitat availability and access. Lamprey were sampled by electric fishing (2 kVA generator, 220 V, 50 Hz pulsed DC). For quantitative surveys, a delimiting framework (equivalent to a quadrat base area 1 m^2) was used (Harvey and Cowx, 2003). The framework was placed at the selected sampling point and left to allow any disturbed sediment to settle. A single anode (40-cm diameter) was immersed 10-15 cm above the substratum, energized for 20 seconds, then turned off for 5 seconds. This process was repeated for 2 minutes. This technique draws lamprey out of the sediment and into the water column. Immobilized lamprey were removed using a fine-meshed net, and transferred to a water-filled container. The sampling process was repeated twice (i.e. three samples in total), with a resting period of 5 minutes between each sample. Samples were kept separate for analysis.

Where deployment of the framework was not possible (e.g. narrow marginal areas, near overhanging trees, and deep or fast-flowing areas), a semi-quantitative sampling approach was used, with sampling points of a known area fished only once, rather than three times. Sea lamprey ammocoetes were identified according to Gardiner (2003) and measured (total length, L_T, mm). The microhabitat at each sampling point was classified as either 'optimal' or 'sub-optimal', irrespective of whether sea lamprey were captured.

Data analysis

Sea lamprey ammocoete densities (no. m^{-2}) were calculated for each sampling point. For quantitative sampling points (Wye n = 1, Usk n = 1), absolute density estimates were calculated using depletion methodology (Carle and Strub, 1978), while gear calibration was used for semi-quantitative sampling points (Wye n = 129, Usk n = 82). This involved calculating the efficiency of sampling effort or probability of capture (p) from the quantitative samples. The derived probability of capture (Wye p = 0.93, Usk p = 0.71) was used to calibrate the gear for sampling points where only one sample was taken. From this, a measure of relative density was derived: $N = (C / p) A^{-1}$, where C is the total number of ammocoetes caught in one sample at each sampling point, and *A* is the sampling area (Cowx, 1996). Mean sea lamprey ammocoete densities were calculated for all sites combined and optimal microhabitats only within reaches between potential migration obstructions (Figure 1) by summing the individual sample densities (quantitative and semi-quantitative samples combined) and dividing by the number of samples. In the UK, for the purpose of condition assessment – establishing the conservation status of designated species against predetermined objectives – the original criteria to achieve "favourable" status were mean densities of ≥ 0.1 m^{-2} (all sites combined) and ≥ 0.2 m^{-2} in optimal microhabitats (Harvey and Cowx, 2003), but this was later revised to a presence in at least four sampling sites, each not less than 5 km apart (Joint Nature Conservation Committee, 2005), and no criterion is included in the latest guidance (Joint Nature Conservation Committee, 2015); the original criteria were employed in this study, to allow a comparison of densities between reaches and because the geographical distribution of sea lamprey ammocoetes was assessed using prevalence (see below). Median densities were compared between contiguous reaches using Mann-Whitney *U*-tests.

The prevalence of sea lamprey ammocoetes (the number of samples containing sea lamprey divided by the number of samples, expressed as a percentage) was calculated for reaches between potential migration obstructions. For the purpose of condition assessment, sea lamprey ammocoetes should be present at $\geq 66\%$ of sites surveyed to achieve favourable status (Joint Nature Conservation Committee, 2005).

Length distributions of sea lamprey ammocoetes were determined for reaches between potential barriers to facilitate interpretation of the age structure of the populations. When catches were sufficient, modal groups ($\approx$ age classes) were identified using modal progression analysis (Bhattacharya, 1967; Gayanilo *et al*., 1997) in FiSAT (FAO/ICLARM Stock Assessment Tools), otherwise the *minimum* number of age classes present was estimated by eye (Nunn *et al*., 2008) or from the literature (e.g. Hardisty, 1969; Quintella *et al*., 2003; Dawson *et al*., 2015; Hansen *et al*., 2016). In contrast to *Lampetra* spp., there is no age structure criterion for sea lamprey to achieve favourable condition (Harvey and Cowx, 2003; Joint Nature Conservation Committee, 2005, 2015; Cowx *et al*., 2009). Thus, for the purposes of this study, any reduction in the number of sea lamprey ammocoete age classes upstream of a structure was taken as an indicator that it may be an obstruction to adult migration. In addition, length distributions were compared between contiguous reaches using two-sample Kolmogorov-Smirnov tests.

RESULTS

A total of 619 sea lamprey ammocoetes was captured in the study, with 423 from the River Wye (18 points) and 196 from the River Usk (16 points). In addition, 2910 *Lampetra* spp. ammocoetes were captured (1030 from the Wye, 1880 from the Usk), but were excluded from the analysis as it is not possible to separate the ammocoetes of (anadromous) river lamprey (*Lampetra fluviatilis* (L.)) and (potamodromous) brook lamprey (*Lampetra planeri* (Bloch)) in the field (Gardiner, 2003). Sea lamprey ammocoetes were recorded up to 208 km upstream of the mouth of the River Wye (97% of the length of the mainstem) and up to 92 km upstream of the mouth of the River Usk (77% of the mainstem).

Sea lamprey ammocoetes were recorded at mean (± SD) densities of 2.3 (± 10.7) and 1.9 (± 8.9) m^{-2} in the rivers Wye and Usk, respectively, and 16.8 (± 15.2) and 8.0 (± 19.4) m^{-2} in optimal habitat, indicating that the populations in both catchments were in favourable condition. Notwithstanding, densities declined upstream of putative migration obstructions. In the Wye, sea lamprey ammocoete density in reach 1 (mainstem downstream of Rhayader Waterfall) was significantly higher than in reach 2 (mainstem upstream of Rhayader Waterfall) (Table 1). By contrast, although substantial, the differences in the densities in reaches 1 vs. 2a (River Irfon) and 1 vs. 2b (River Ithon) were not statistically significant due to high variance in the samples (Table 1). In the Usk, sea lamprey ammocoete density in reach 1 (downstream of Prioress Mill Weir) was significantly lower than in reach 2 (Trostrey Weir to Llanfoist Bridge), which was significantly higher than in reach 3 (Crickhowell Bridge to Cwmcrawnon Weir), but there was no significant difference in the densities in reaches 3 and 4 (Cwmcrawnon Weir to Brecon Weir) (Table 1).

There was a reduction in the prevalence of sea lamprey ammocoetes upstream of putative migration obstructions in both the Wye and Usk (Table 1). A minimum of three age classes of sea lamprey ammocoetes was recorded as far as 200 km upstream of the mouth of the River Wye (reach 1), including in a major tributary in the upper catchment (reach 2a), whereas just a singleton was captured in reach 2 (Table 1; Figure 2). There were significant differences in sea lamprey ammocoete lengths and length distributions in reaches 1 vs. 2a and 1 vs. 2b, due largely to a low absolute and relative abundance of 0+ individuals in the tributaries (Figure 2). Two age classes were recorded up to 84 km upstream of the mouth of the River Usk (reach 4), but three were found only in the lower 55 km of the river (reach 2) (Table 1; Figure 3).

There were no significant differences in lengths or length distributions in reaches 1 and 2, but no sea lamprey were captured in reach 3 and only small numbers of ≥1+ ammocoetes were captured in reach 4 (Figure 3).

Using the original condition assessment criteria (Harvey and Cowx, 2003), the sea lamprey populations in the rivers Wye and Usk were judged to be in a favourable condition at the catchment scale (Harvey *et al.*, 2006, 2010). By contrast, using adjusted criteria, to allow comparisons between reaches, only reach 2 on the River Usk achieved favourable condition, due mainly to the low prevalence of sea lamprey ammocoetes in the other reaches and reductions in the numbers of age classes upstream of putative migration obstructions (Table 1).

DISCUSSION

A minimum of three sea lamprey ammocoete age classes was recorded as far as 200 km upstream of the mouth of the Wye, demonstrating that adults regularly migrate to the upper reaches of the catchment. However, densities, prevalences and the numbers of age classes of sea lamprey ammocoetes (in suitable habitat, as demonstrated by the presence of large numbers of *Lampetra* spp. ammocoetes; Maitland, 2003; Taverny *et al.*, 2012) were lower in reaches 2, 2a and 2b than reach 1, due largely to a low absolute and relative abundance of 0+ individuals, suggesting that the structures (artificial or natural) at the downstream limits of these reaches impede the upstream migration of adults to some extent. Indeed, just a single sea lamprey ammocoete was captured from reach 2, suggesting that the waterfall at its downstream limit (at Rhayader) is almost a total barrier, but also that small numbers of adults must occasionally use the fish pass or high flows to migrate upstream. It is also possible that increases in gradient and water-quality issues upstream of Rhayader (T. Hatton-Ellis, pers. comm.) are influential, but the presence of large numbers of *Lampetra* spp. ammocoetes suggests that the issue is not severe.

Sea lamprey ammocoetes appeared to be absent (in suitable habitat) from 20 km (17%) of the River Usk, and there was a reduction in density, prevalence and the number of age classes upstream of two putative spawning-migration obstructions (i.e. Crickhowell Bridge and Brecon Weir). Similarly, Andrade *et al*. (2007) observed that the abundance and age-class diversity of sea lamprey ammocoetes in the Vouga river basin, Portugal, was lower upstream than downstream of weirs suggested by telemetry data to be migration obstructions. In this study, there were no reductions in the density, prevalence or number of age classes of ammocoetes when moving from reach 1 upstream to reach 2, suggesting that the weirs at the upstream limit of reach 1 (Prioress Mill [a boulder weir with a 10-m-wide low-flow channel, 1.12 m mean water depth, 1.43 m s^{-1} mean water velocity] and Trostrey [a crump weir with a 0.27 m mean head-loss, 0.38 m mean water depth, 1.94 m s^{-1} mean water velocity]; Atkins Ltd, 2004) are passable by adults in most years. By contrast, no sea lamprey ammocoetes were captured in reach 3, perhaps suggesting that one or both of the structures at the upstream limit of reach 2 (Llanfoist Bridge and, especially, Crickhowell Bridge [0.3-0.7 m head-loss, 0.05-0.2 m mean water depth, 2.06 m s^{-1} mean water velocity] footings; Atkins Ltd, 2004) are migration barriers. However, small numbers of sea lamprey ammocoetes were recorded from reach 4, demonstrating that at least some adults must pass through reach 3. Observations of adults suggest that, despite there being a fish pass, the weir at the upstream limit of reach 4 (Brecon, 2.17 m head-loss) is the upstream limit for sea lamprey in most years (Harvey *et al*., 2006), which was reflected in this study by the apparent absence of ammocoetes (in suitable habitat) upstream. Although Brecon Weir is likely to be a significant obstruction (T. Hatton-Ellis, pers. comm.), the failure to record sea lamprey ammocoetes upstream of reach 4 does not necessarily mean that Brecon Weir itself is a total barrier, as the cumulative impacts of obstructions downstream could have a similar affect; assessments of passage efficiency (Kemp *et al*., 2011; Russon & Kemp, 2011) are required to determine whether individual structures are total or only partial obstructions.

It is likely that sea lamprey passage past some obstructions is enhanced if high flows occur during the spawning migration, as has been found for river lamprey (Nunn *et al*., 2008; Lucas *et al*., 2009). However, sea lamprey migrate in spring and early summer (Hardisty, 1969), when river levels in the UK are invariably lower and more stable than in winter, when river lamprey migrate, and high flows may not coincide with the spawning migration in all years or at all obstructions. There is therefore a need to facilitate upstream passage at potential obstructions during all conditions, to improve access of migrating sea lamprey to under-exploited spawning and nursery areas. The effectiveness of fish passes for lampreys can vary widely, however, and is often low (Keefer *et al.*, 2010, 2011; Foulds and Lucas, 2013; Moser *et al.*, 2015a; Tummers *et al*., 2016). It is therefore necessary to adjust existing passes (e.g. by reducing water velocity, removing or modifying vertical steps and/or providing suitable refuge areas) to increase passage success at artificial obstructions (see Keefer *et al*., 2010, 2011; Moser *et al*., 2015a; Pereira *et al*., 2016; Tummers *et al*., 2016).

Key factors determining the distribution and abundance of lamprey ammocoetes are the availability of suitable sediments, typically fine particulate matter with a high organic content, and the locations of spawning areas (Almeida and Quintella, 2002; Derosier *et al*., 2007; Goodwin *et al.*, 2008; Dawson *et al*., 2015; Silva *et al*., 2015; Hansen *et al*., 2016). The low densities, prevalence and number of age classes in reach 1 and the apparent absence of sea lamprey from reach 3 of the Usk could therefore be linked to a lower quality of nursery habitat and/or lesser availability of spawning habitat compared with upstream reaches. Indeed, it may be of relevance that only sub-optimal ammocoete habitat was located in reaches 1 and 3 and that the densities, prevalences and numbers of age classes of *Lampetra* spp. ammocoetes were also low; the majority of sea lamprey spawning records are from reach 2 (Harvey *et al*., 2006). The largest quantities of fine sediments generally accumulate in the margins or backwaters of rivers, where water velocity is slowest, but can sometimes occur in mid-channel in slow-flowing reaches. Although the habitat requirements of river and sea lamprey ammocoetes are extremely similar (Maitland, 2003), the latter species sometimes occurs in deeper water (Taverny *et al*., 2012). It is therefore possible that the abundance of sea lamprey ammocoetes is underestimated in water that is too deep to sample effectively by electric fishing, and it may be appropriate to use other methods, such as air-lift/suction dredge (Moser *et al*., 2007; Taverny *et al*., 2012); such methods may also increase the capture efficiency of 0+ individuals in shallow water, particularly in turbid conditions (Lasne *et al*., 2010). It should be noted, however, that supplementary methods need to be calibrated (in shallow water) against electric fishing if they are to be included in monitoring programmes (Silva *et al*., 2014), and that catches using air-lift/suction dredge are usually only qualitative and often small.

In addition to the impacts of migration barriers on the rivers Wye and Usk themselves, there could be impacts on the status of sea lamprey in the Severn Estuary SAC. Given that there is little, if any, evidence of active homing to natal watercourses in sea lamprey (Bergstedt and Seeyle, 1995; Waldman *et al*., 2008), it is possible that all the tributaries of the Severn Estuary (including the Wye and Usk) share a single, panmictic population. Indeed, sea lamprey populations have been found to be largely genetically homogeneous across the whole of Western Europe (Almada *et al*., 2008; Genner *et al*., 2012). Actions to conserve sea lamprey must therefore be implemented from at least a catchment perspective, because many of the issues are not localised. The Severn Estuary population could potentially be enhanced by facilitating spawning migrations in tributaries at the tidal limit, particularly watercourses with extensive spawning and nursery habitats but numerous putative migration obstructions; data on adult runs, the extent of spawning and recruitment, and the distribution of potential spawning and nursery habitats would be required to assess the relative contributions of the tributaries and how many are required to support a healthy population in the Severn Estuary.

Many lamprey populations are affected by river regulation, pollution, habitat degradation, exploitation, predation, entrainment, impingement or barriers to migration (Masters *et al*., 2006; Lucas *et al.*, 2009; Mateus *et al*., 2012; Bracken and Lucas, 2013; Foulds and Lucas, 2014). This study highlights some of the potential impacts of habitat fragmentation by obstructions to the spawning migrations of sea lamprey, as inferred from ammocoete demography. Low densities, low prevalence or missing age classes in suitable habitat do not alone prove that adults struggle to access particular river reaches, because sea lamprey ammocoetes are often patchily distributed, even in unimpounded rivers, and may disperse downstream over time (Quintella *et al*., 2005; Derosier *et al*., 2007; Dawson *et al*., 2015; Moser *et al*., 2015b). Notwithstanding, when used in combination to compare contiguous reaches, they may be a useful indicator of which structures are likely to be important migration obstructions, and where further studies or mitigation efforts should be focussed. Ideally, adult sea lamprey should also be included in the condition assessment process, to provide a proxy for spawning effort and potentially a link between adult and ammocoete abundance, and also to quantify the impacts of putative migration obstructions (Moser *et al*., 2007; Guo *et al*., 2016; Pinder *et al*., 2016).

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Table 1. Mean density, prevalence, age structure, length and condition of the sea lamprey ammocoete populations in reaches, between potential migration obstructions, of the rivers Wye and Usk, UK.

River	**Reach**	**Density**[1] **(no. m^{-2})**	***U***	***P***	**Density**[2] **(no. m^{-2})**	**Prevalence (% sites)**	**No. age classes**	***Z***	***P***	**Length (mm)**	***U***	***P***	**Population condition**
Wye	1	15.0			27.3	59	3+			47.7			Unfavourable
	2	0.2	28	0.047*	n/a	14	1	–	–	–	–	–	Unfavourable
	2a	2.0	44	0.318	2.2	43	3+	2.096	<0.001**	101.4	4052	<0.001**	Unfavourable
	2b	2.7	60	0.204	n/a	40	2+	4.422	<0.001**	89.1	13229	<0.001**	Unfavourable
Usk	1	1.3			n/a	40	2+			67.8			Unfavourable
	2	18.8	41	0.012*	21.4	100	3+	0.684	0.738	62.4	358	0.456	Favourable
	3	0	0	0.003**	n/a	0	0	–	–	–	–	–	Unfavourable
	4	1.2	26	0.109	0.2	63	2+	–	–	–	–	–	Unfavourable

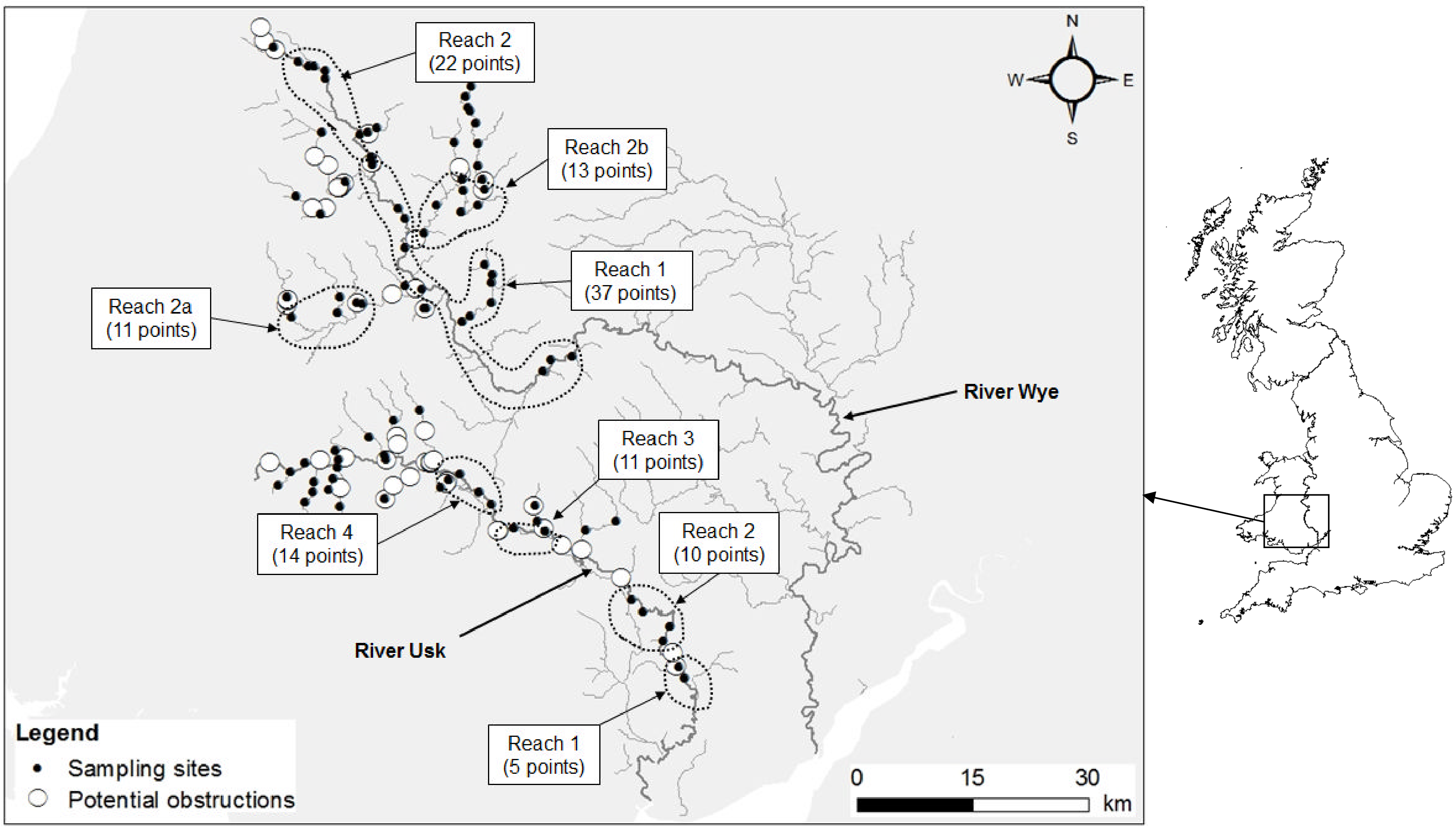
1 = mean density in the reach, 2 = mean density in 'optimal habitat' in the reach; *U* = Mann-Whitney *U*-statistic; *Z* = two-sample Kolmogorov-Smirnov *Z*-statistic; n/a = no 'optimal habitat' present. Reach numbers as in Figure 1. Parameters were compared between contiguous reaches; *$P<0.05$, **$P<0.01$, – insufficient data. Parameters failing the respective condition assessment criterion (see text for details) are shaded.

FIGURE CAPTIONS

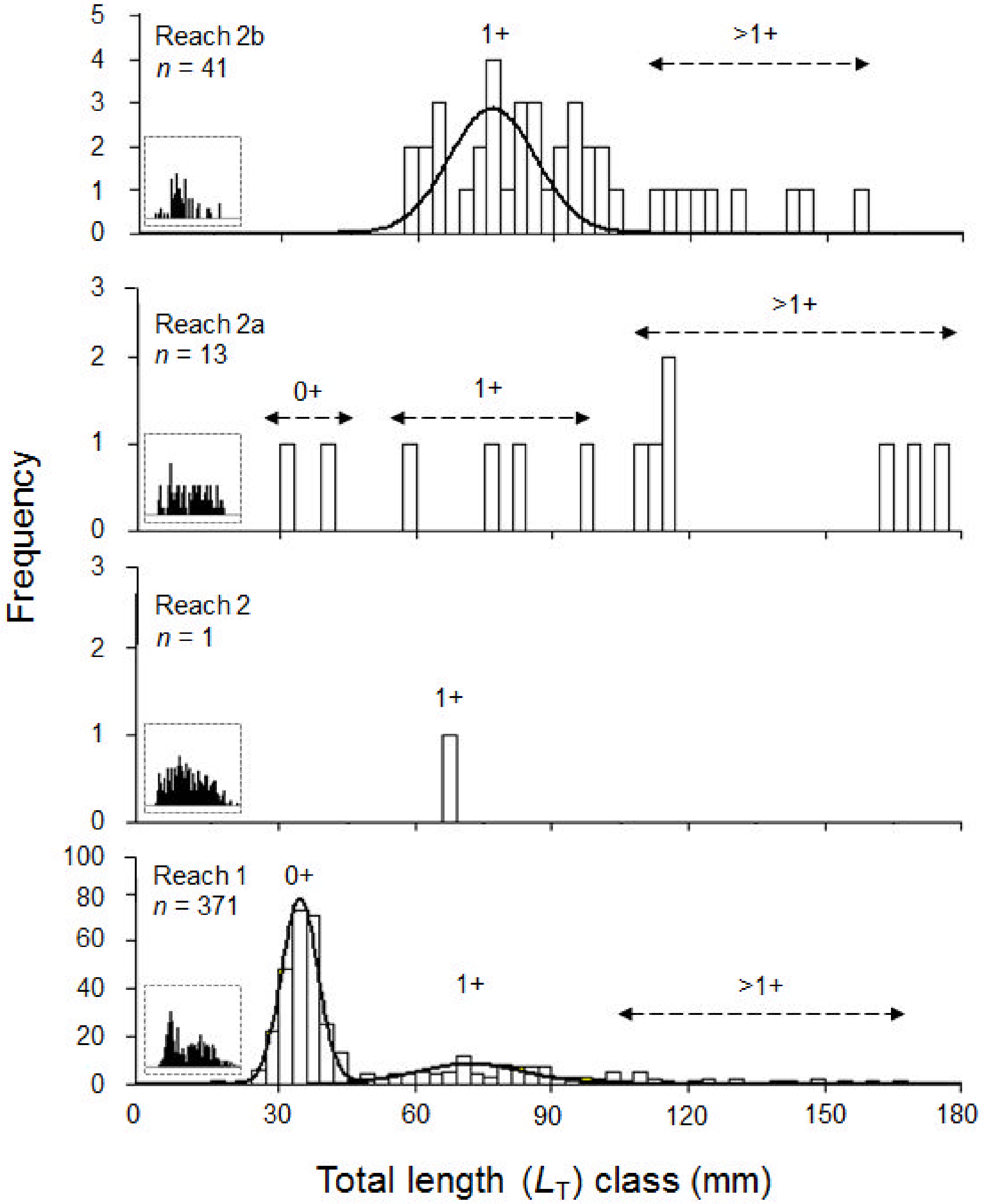
Figure 1. Lamprey ammocoete sampling locations (black circles) and potential migration obstructions (white circles) on the rivers Wye and Usk, UK. Study reaches, between potential migration obstructions, encompassing the geographical distribution of sea lamprey are indicated. River Wye reach 1, mainstem downstream of Rhayader Waterfall; reach 2, mainstem upstream of Rhayader Waterfall; reach 2a, River Irfon; reach 2b, River Ithon. River Usk reach 1, downstream of Prioress Mill Weir; reach 2, Trostrey Weir to Llanfoist Bridge; reach 3, Crickhowell Bridge to Cwmcrawnon Weir; reach 4, Cwmcrawnon Weir to Brecon Weir.

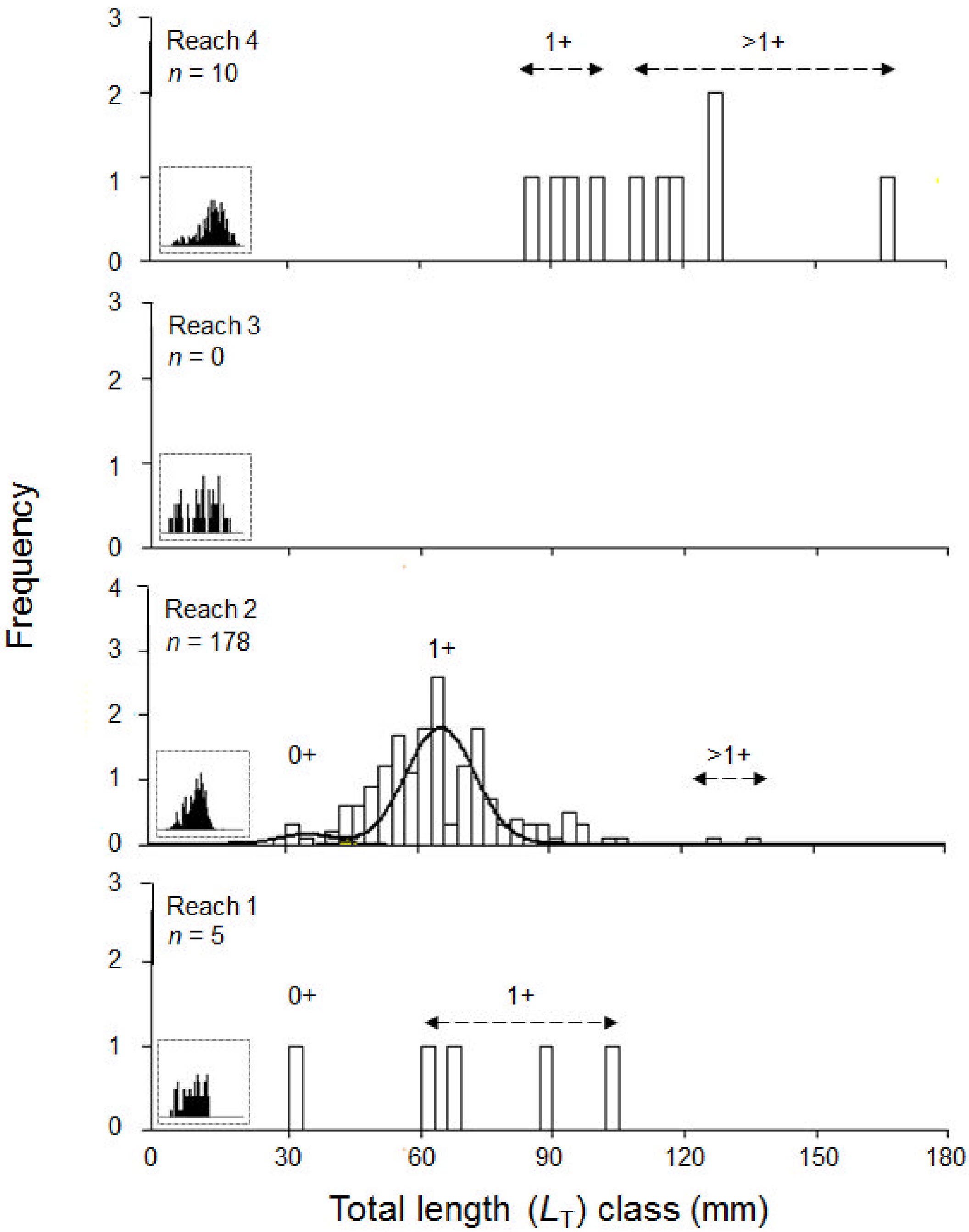
Figure 2. Length distributions of sea lamprey ammocoetes captured from four reaches, separated by potential migration obstructions, of the River Wye, UK. Thumbnail length distributions of *Lampetra* spp. ammocoetes are included near the origins to demonstrate that the habitat is suitable for sea lamprey ammocoetes (Maitland, 2003; Taverny *et al*., 2012).

Figure 3. Length distributions of sea lamprey ammocoetes captured from four reaches, separated by potential migration obstructions, of the River Usk, UK. Thumbnail length distributions of *Lampetra* spp. ammocoetes are included near the origins to demonstrate that the habitat is suitable for sea lamprey ammocoetes (Maitland, 2003; Taverny *et al*., 2012).



Reach 2
(22 points)
Reach 2b
(13 points)
Reach 1
(37 points)
Reach 2a
(11 points)
N
W
E
S
River Wye
Reach 3
(11 points)
Reach 4
(14 points)
Reach 2
(10 points)
River Usk
Reach 1
(5 points)
Legend
Sampling sites
Potential obstructions
0
15
30
km


Reach 2b
n = 41
1+
>1+
Reach 2a
n = 13
0+
1+
>1+
Reach 2
n = 1
1+
Reach 1
n = 371
0+
1+
>1+
Frequency
Total length (L_T) class (mm)



Reach 4
n = 10
1+
>1+
Reach 3
n = 0
Reach 2
n = 178
0+
1+
>1+
Reach 1
n = 5
0+
1+
Frequency
0
30
60
90
120
150
180
Total length (L_T) class (mm)