Catchment-scale distribution, abundance, habitat use, and movements of European eel (*Anguilla anguilla* L.) in a small UK river: implications for conservation management

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Title:

Catchment-scale distribution, abundance, habitat use, and movements of European eel (*Anguilla anguilla* L.) in a small UK river: implications for conservation management

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Abstract

1. Effective conservation management of the critically endangered European eel (*Anguilla anguilla*) is hindered by incomplete understanding of distribution, abundance, and habitat requirements at the catchment-scale.
2. Here, all habitats available to eels within a small, highly regulated river catchment, representative of many utilised across the species' range, were sampled using several methods (including point-abundance sample electric fishing and fyke nets) and supplemented by individual telemetry to investigate movements. A similar approach is recommended for use elsewhere.
3. Eels were found throughout the catchment (59% of *n* = 131 sites) from the coastal marshes to the headwaters, although the probability of presence declined with distance from the estuary. The lack of a clear relationship with perceived barriers may illustrate a mismatch with the reality experienced by eels, as telemetry identified connectivity across obstacles between paludal habitat and estuary and detected escapement of mature silver eels from both lotic and lacustrine habitat.
4. Different size/age classes utilised different parts of the catchment, partly linked to different habitat associations, with coastal paludal habitat supporting >50% of the catchment population and especially smaller (possibly male dominated) yellow eels.

Recently recruited elvers were most abundant in the lower reaches of lotic habitat. The largest (likely female) eels were concentrated in lacustrine sites, especially at the ‘end-of-the-line’ in the headwaters.

5. Experiences here suggest conservation management for eels in small catchments is best focussed on improving connectivity and assisting migration of elvers across ‘problem’ barriers that cannot be removed or modified. River restoration and rewilding, especially measures that increase instream woody material, could benefit elvers and provide refuge for larger eels. Enhancement or, where absent, creation of suitable lacustrine habitat would benefit important female stocks. Such action across numerous small river catchments may ultimately help support the recovery of eel stocks.

Key words:

Anguilla anguilla, anthropogenic barriers, catchment-scale, connectivity, electric fishing, fyke netting, habitat use, river management, telemetry.

1 Introduction

The European eel (*Anguilla anguilla*, Linnaeus, 1758) is a facultatively catadromous fish species that spawns in the Sargasso Sea in the West Atlantic. Larvae (leptocephali) drift to Europe and North Africa before metamorphosising into 'glass' eels which then pigment as they move into estuaries, rivers and connected lakes. Here, they develop as 'yellow' eels before maturation as 'silver' eels that migrate back across the Atlantic (Schmidt, 1923; Tesch, 2003). Glass eel recruitment crashed in the 1980s and currently ranges between 1–10% of pre-1980 levels (Dekker & Beaulaton, 2015; ICES, 2018). As a result, the species was classified as Critically Endangered on the IUCN Red List in 2008 (Jacoby & Gollock, 2014) and is listed under Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (Convention on International Trade in Endangered Species of Wild Fauna and Flora, 2021) and Appendix II of the Convention on Migratory Species (Convention on Migratory Species, 2020). Reasons for sustained population declines across the species range are multifactorial, including the impacts migration barriers, habitat degradation, pollution, overfishing, infection by the introduced parasite (*Anguillicolloides crassus*) and effects of climate change (see review by Jacoby et al., 2015). In 2007, the European Union (EU) established measures for the recovery of stocks under the Eel Recovery Plan (Council Regulation No. 1100/2007/ EC). Accordingly, member states are required to create national Eel Management Plans (EMPs) to achieve, or maintain, escapement to the sea of ≥ 40% of the adult eel biomass relative to undisturbed conditions. There have been widespread efforts to facilitate eel recovery which generally focus on reducing fishing pressure, restoring connectivity, restocking and improving habitat (Moriarty & Dekker, 1997; Feunteun, 2002; ICES, 2018; Tamario et al., 2018; Tamario et al., 2019; Rohtla et al., 2021).

Eels exhibit phenotypic plasticity in their use of a wide range of estuarine and freshwater habitats (Moriarty & Dekker, 1997; Feunteun et al., 1999; Laffaille et al., 2003; Arai, Kotake & McCarthy, 2006). Spatial distribution and habitat use may be influenced by density-dependent dispersal (Feunteun et al., 2003), habitat accessibility (Laffaille, Lasne & Baisez, 2009) and water quality (Degerman et al., 1986). Ontogenetic, or size-related, shifts may also determine habitat preferences (Laffaille et al., 2003). Eels are generally nocturnal (Walker, Godard & Davison, 2014; Verhelst et al., 2018) and refuge by day in soft sediments and amongst vegetation and woody material (Knights et al., 2001; Acou et al., 2011). They may occupy definable home ranges according to individual size (Herrera et al., 2019), morphology, and diet (Barry et al., 2016a), but may also readily disperse between habitats. The timing and extent of movements is generally influenced by individual size and environmental conditions (Daverat et al., 2006; Jellyman & Arai, 2016). However, they are especially rapid and complex during upstream or downstream migration according to light conditions, lunar phase and tidal direction, and can famously involve crossing wet ground (Daverat et al., 2006; Jellyman & Arai, 2016; Barry et al., 2016b).

Despite a wealth of research, relatively little is known about the scale and importance of different habitats at the catchment-scale, particularly in the face of fragmentation of aquatic landscapes (Sayer, 2014). Accordingly, in contrast to species with more specific and readily defined habitat needs, it remains difficult to prescribe tailored habitat improvement measures for eels with confidence (Lasne & Laffaile, 2008). Furthermore, a lack of robust monitoring, linked to challenges in sampling eels across a range of habitats (Dekker, 2003; Degerman et al., 2019), often constrains evaluation of eel conservation measures at the local scale (e.g. Birnie-Gauvin et al., 2018).

This study aimed to integrate investigations of distribution, population size, habitat use and movements of European eel across all habitats within a whole river catchment. The River Glaven catchment in eastern England (Figure 1) was chosen for the study as it is a small (17 km long), groundwater-fed calcareous and mixed bed substrate lowland river (<100 m asl), representative of the most abundant river type (R-05) in the UK (36% of 6,761 waterbodies classified) and Europe (17% of 65,840 waterbodies classified including the UK) (Lyche Solheim et al., 2019). As is typical of many such rivers, the Glaven has been heavily modified with numerous water control structures that may operate as barriers to eel migration (Figure 1) and suffers from habitat degradation through previous channelisation and creation of embankments (Clilverd et al., 2013).

A combination of methods including electric fishing and fyke netting was used to investigate eel presence across the catchment. Quantitative electric fishing was then used to provide estimates of relative population sizes across lotic (riverine), lacustrine (lake and pond) and coastal paludal (marsh ditch and pool) habitats and to describe microhabitat use by daytime refuging eels. An existing acoustic and passive integrated transponder (PIT) telemetry array, used in a separate study of brown trout (*Salmo trutta*), was expanded to examine the movements and escapement of eels tagged in different habitats across the catchment. Survey work was funded for three-years (2017 to 2019), by a European Maritime and Fisheries Fund (EMFF) grant however, the study makes use of historic survey data where possible. Results are discussed in relation to the wider applicability of the methods and catchment-scale conservation management of eels in the Glaven and numerous similar European rivers across the species' range.

2 Methods

2.1 Study area

The River Glaven is fed by two small tributaries (Gunthorpe Stream and Stody Beck) (Figure 1 and Figure 2a) and has a catchment of approximately 115 km^2. Land use is mainly arable agriculture with patches of coniferous/deciduous secondary woodland in the upper and middle reaches, grazing meadows and fen patches along the middle river course and low-lying remnants of former estuarine marshland in the lower reaches. The freshwater catchment contains an estimated 132 lacustrine waterbodies, including at least nine small lakes (>1 hectares) and many small ponds (Figure 2a). Downstream of the Glaven Outfall Sluice (two tidal gates and a penstock gate, see Figure 1), the river is tidal with several connections to a network of both saline and freshwater channels (ditches), shallow scrapes and ponds (Cley and Salthouse Marshes). The major connection closet to the coast is via a sluice (three top-hung and one side-hung gate) on the largest channel (the New Cut). To the west of the main river, paludal habitat continues with an extensive (160 hectares) freshwater grazing marsh (Blakeney Freshes) and its numerous channels (Figure 1, Figure 2a and 2b). The river discharges into a shared estuary with the River Stiffkey, behind Blakeney Point, a 6.4 km shingle spit.

Eels must navigate at least one tidal flow control before entering the river or paludal system. Otherwise, there are c. 42 water control structures throughout the system (Figure 2a). These include five water mills, of which only Letheringsett Mill (Figure 1) remains operational, c. 11 weirs, two flow gauging stations and a variety of smaller structures including perched culverts and lacustrine sluices. The UK Environment Agency (EA) previously identified seven ‘hard’ barriers (highly restrictive to free passage) to eels in the system: two crayfish barriers (modified weirs), four of the mills and a weir/silt trap in the upper reaches (J. Wood, EA, pers comm). During the current field surveys, an extended elevated culvert, several lake sluices and land barriers to unconnected ponds and lakes were also idenitfied as ‘hard’ barriers.

Given its small size, and the lack of a significant commercial or recreational fishery, the Glaven does not feature heavily in EMPs for the Anglian River Basin District (Department for Environment, Food and Rural Affairs, 2010). Nevertheless, the River Glaven and its wider catchment has been the subject of several local restoration initiatives to address impacts of habitat modification and degradation, pollution, soil erosion and siltation, water abstraction, limitations to fish passage and the introduction of non-native species (Clilverd et al., 2013; Sayer, 2014; Champkin et al., 2017; Sayer & Greaves, 2020).

2.2 Survey methods

2.2.1 Electric fishing surveys

Electric fishing was undertaken between May and October, during 2016-2019 inclusive, and sampled a total of 50 independent sites throughout the catchment (Figure 2c). Use of electric-fishing equipment was authorised under section 27A of the Salmon and Freshwater Fisheries Act 1975, by the EA. Electric fishing focused on lotic (n = 30) and lacustrine sites (n = 16) with a limited number (n = 4) of paludal sites where water conductivity was sufficiently low (< 1000 $\mu s/cm^2$) to enable effective sampling. Five of the lotic sites were also surveyed annually between 2016 and 2018 inclusive, to assess temporal variability in eel numbers. This resulted in a total dataset of 60 surveys (45 sites sampled once and 5 sites sampled three times). Both quantitative point-abundance sampling (PAS) (Copp & Peňáz, 1988; Perrow, Jowitt & Zambrano González, 1996; Laffaille et al., 2005a; Perrow et al., 2017), and semi-quantitative continuous electric fishing along a single littoral margin were undertaken at each site. The latter sampling was undertaken after a recovery time of at least one hour, to detect eels when present in low densities. Surveys were undertaken in daylight hours during the summer months and are assumed to have sampled refuging eels (Knights et al., 2001).

Surveys of lotic and paludal sites aimed to cover a 200 m stretch of channel (mean length = 178 m, range 45–280 m), in which approximately 50 (mean = 48.8) randomly stratified points were sampled. Points were spaced approximately 4 m apart and sampled by moving upstream from bank to bank, with the number of sample points in the littoral margin reflecting the ratio of marginal to open water habitat (typically 1:3 or 1:4). Subsequent continuous fishing runs aimed to cover 100 m (mean = 119 m, range = 40–215 m) of the margin along one randomly selected bank within the same site. In lacustrine sites, the open water and littoral margin were sampled separately, with point spacing along systematic transects in open water being roughly proportional to its size. The entire area of open water and length of littoral margin was covered by 20–80 points (mean = 48) and 11–90 points (mean = 45) respectively. Subsequent continuous runs (mean length = 357 m) sampled the whole margin of a small pond (minimum of 45 m) or randomly distributed sections of larger lakes (maximum of 910 m).

Electric fishing, using low voltage (20–40 V) and current (1.2–2 A) at 50 Hz applied through a single 40 cm diameter anode, was undertaken by wading (n = 23 sites), or from a small boat (n = 27 sites) powered by 'push-rowing' (Perrow, Jowitt & Zambrano González, 1996). During PAS, the anode was activated and rapidly immersed at each point, with any stunned fish collected with a hand-net (5 mm Fryma Mesh) swept through the affected area. On continuous marginal runs, the anode was swept through the margin ahead of the operator. All captured eels were measured (total length in mm) and weighed (nearest g). An estimate of length was recorded for an eel that was seen but evaded capture or was not weighed, with its biomass estimated by the length-weight relationship established from eels weighed during electric fishing (n = 174).

Individual point densities were calculated by dividing the number, or biomass, of eels by the effective area. This was estimated to be ~1.3 m^2 based on measurements of distance from the anode where the voltage gradient decreased to 0.12 volts (V) and the minimum effective voltage at which inhibited swimming occurs (Copp & Peňáz, 1988), and confirmed by observations. Mean (± 1 standard error [SE]), numerical (ind. m^{-2}) and biomass (g m^{-2}) density estimates of eels were calculated based on all points in lotic or paludal channels. For lacustrine sites, separate estimates for the margins and open water were combined after weighting their relative contribution to the overall wetted area. A catch-per-unit-effort (CPUE) estimate (ind. m^{-1}) was calculated for the littoral run by dividing the total catch of eels by the length of margin fished.

Habitat was described at each point sampled. Water depth (cm) and surface flow (cm sec^{-1}) were measured at the centre of the point with other descriptors estimated over the entire visualised point area. Substrate was categorised as clay, earth, silt, sand, gravel, stone, cobble, and rock following Bain et al. (1985) and expressed as a percentage of the sampled area. In-stream submerged, emergent, and floating plants, and filamentous algae were recorded as percentage cover (to the nearest 5%). Similarly, benthic debris (e.g. small twigs and leaf litter), large woody material (fallen tree parts and live submerged tree roots), overhanging vegetation (< 1 m above the water) and tree canopy cover (> 1 m above the water) were recorded as percentage cover.

2.2.2 Fyke net surveys

Fyke net surveys were conducted between April and October, from 2013–2019 inclusive, in lacustrine (n = 37), paludal (n = 25) and lotic sites (n = 7) with relatively deep and slow-flowing water. In 2018–2019, 21 of the 69 sites (Figure 2c) were also sampled by electric fishing within a two-month period, to assess agreement of eel detection between methods.

Traditional, commercial standard double-ended fykes, with a stretched mesh size of 15 mm, expected to retain eels ≥ 300 mm (Bark, Williams & Knights, 2007), were used throughout. All fyke nets were fitted with otter guards and carried EA registered tags. Effort was roughly proportional to the size of a site, to a maximum of 45 ends. For lacustrine sites, fykes were positioned in strings of 11–253 m in length to bisect the maximum dimension. In lotic and paludal sites, nets were deployed in continuous strings of 11–209 m along the centre of the channel. Nets were set before dusk and deployed for approximately 16 hours before retrieval the following morning and thus passively captured active eels. All eels were measured before release and weight was estimated from the length-weight relationship derived from captures made by electric fishing. Fyke net catches were expressed as CPUE (number of eels per net per 16 hours).

2.2.3 Single run and catch-depletion electric fishing

Spatial coverage of the study area (Figure 2c) was extended across the upper catchment and tributary streams by including electric fishing surveys conducted by the EA from 2003 to 2017, at a further 35 sites extracted from the National Fish Populations Database. Repeated surveys (in 1999, 2003, 2008, 2014 and 2017), carried out at six lotic sites, were used to investigate temporal variation in the relative abundance of eels. Surveys of two of these six sites, were superseded by more contemporary PAS surveys for the analysis of catchment eel distribution based on detection in surveys.

Each site (mean width = 2.0 m, mean length = 77.5 m) was demarcated by stop-nets and the entire enclosed area was fished using one or two anodes. A single run was used at 14 sites where the wetted channel was very narrow (generally <1 m), and two (n = 17) or three (n = 4) consecutive runs were used where the channel was larger. Eel densities (ind. m^{-2}) were derived from the estimated site area and population size based on the minimum catch or estimates based on the model of Carle & Strub (1978).

2.3 Tagging and telemetry

To investigate eel movements and escapement, a total of 76 individuals were fitted with acoustic tags from 21 May to 20 September 2018 (Table 1) following capture in fyke nets or electric fishing surveys at six sites in the main river (n = 25), five sites in the coastal marshes (n = 28), and three lacustrine sites (n = 23). Only eels in good condition and of sufficient size to accommodate respective tags were selected for the study. Prior to tagging, eels were anaesthetised (Benzocaine 0.2 g L^{-1}), weighed and measured. An incision (≤ 15 mm length) was made approximately 50 mm anterior to the ventral opening. An acoustic tag (Vemco, model V9–2L, 29 mm × 9 mm, 4.7 g in air, 476 d life expectancy or V5–2H, 12.7 × 5.8 mm, 0.77 g in air, 185 or 207 d life expectancy, dependent on eel size) and PIT tag (23 × 4 mm, 0.6 g in air, Texas Instruments) were inserted through the opening into the peritoneal cavity and the incision closed with two sutures (Resolon™, Advanced Medical Solutions, UK). In 2018, a further 139 eels were tagged with an intraperitoneal PIT tag only (23 × 4 mm and 0.6 g in air or 12 x 2.12 mm and 0.1 g in air, dependent on eel size) using a smaller incision (≤4 mm) and without suturing (Table 1). No mortality occurred during the procedures and eels were released at the site of capture within 1.5 h of recovery. The study was reviewed and approved by the Zoological Society of London Ethics Committee. Tagging and associated fish capture and holding were carried out under UK Home Office licence (PPL 7008909) and conformed with the Animals (Scientific Procedures) Act 1986 Amendment Regulations (SI 2012/3039).

Eel movements were monitored using an array of 36 fixed acoustic receivers (Vemco, model VR2W). Eight sets of paired 69 and 180 kHz receivers were strategically placed at mill structures and tidal sluices, while an existing array of 69 kHz receivers (n = 20) covered the lower reaches and estuary (Figure 2d). Acoustic tag detection ranges varied between receiver locations can be affected by variables including channel width and depth, local bedform and presence of obstructions, including submerged vegetation. Regular range testing throughout the study demonstrated that, in the lotic and paludal locations, detection range encompassed the full width of the channel and a minimum longitudinal distance of 16.8 m (mid-catchment) and maximum of 64.0 m (at the Glaven Outfall). Detection range in the estuary typically ranged from 112 to > 200 m within 1 hour either side of high water (conducted during first or last quarter of lunar period). The array was configured to include sufficient redundancy to ensure that tagged individuals could not escape detection during passage to the outer estuary. Data was retrieved at approximately four-month intervals between deployment in May/June 2018 and removal in August 2019. A single 69 kHz acoustic receiver was retained at the lowest water mill site until July 2020. Manual tracking was also conducted from the bank using a portable unit (Vemco, VR100 unit with 69 and 180 kHz hydrophones) at weekly intervals across 11 locations along the main river and in the coastal marshes from 9 June to 4 November 2018. Two single swim-through PIT antennas located immediately up (2.2 m width x 0.7 m height) and downstream (2.2 m width x 0.95 m height) of Glandford Mill, in the lower catchment, monitored movements past this structure. All eels captured in surveys after the commencement of tagging activities were scanned for PIT tags using a handheld reader (Oregon radio frequency identification reader).

2.4 Data analysis

2.4.1 Catchment population estimates

Mean PAS densities, and associated confidence intervals, derived from the most recent surveys of that habitat, were used to calculate indicative population estimates for eels in paludal, lotic and lacustrine habitats based on surface area following a similar approach to Meulenbroek et al. (2020). Areas were estimated using QGIS (QGIS Development Team 2021) based on Ordnance Survey vector map surface water and watercourse data (Ordnance Survey data © Crown copyright and database right 2021). The combined area of unsampled minor tributaries was estimated by multiplying their length by the mean estimated width of surveyed tributaries (1.5 m). Coefficients of variations were calculated alongside the mean density estimates as an indicator of survey precision. Overall catchment densities and population size were estimated from the sum of the component habitats weighted by area.

2.4.2 Catchment-scale distribution

Potential variables influencing the catchment-scale distribution of eels were investigated by modelling probability of eel occurrence using a similar approach to Degerman et al. (2019). Eel presence-absence was determined from any method employed at n = 131 independent survey sites (n = 50 PAS sites, n = 48 fyke net sites not also surveyed by PAS, and n = 33 single run or catch-depletion sites not also surveyed by PAS). Further, survey method was included as a factor in the model framework to assess whether it influenced probability of occurrence. Other available covariates included 'distance from estuary', 'distance from main river channel' (along tributaries or overland) and 'site area' (log transformed). The cumulative number of all possible obstacles to eels, or those barriers assessed as 'hard' for eel passage alone, were also considered as alternative covariates to 'distance from the estuary'. Due to their proximity to each other, and lack of survey data between them, three 'hard' barriers in the middle reaches (around Letheringsett Mill) were combined for the analysis.

Generalised Additive Models (GAMs), with a binomial distribution and a logit-link function, using the *gam* function in the mgcv package (Wood, 2017) in R 3.6.3 (R Core Team, 2021), were used to investigate eel occurrence as the response variable. Prior to modelling, exploratory analyses confirmed a high degree of multicollinearity, according to variance inflation factor (VIF) scores (see Zuur, Ieno & Elphick, 2010), between the variables 'distance to estuary', 'cumulative number of barriers' and 'cumulative number of hard barriers'. Comparison of models using these different descriptors, using Akaike's information criteria (AIC) scores, suggested 'distance to estuary' performed best, and this was taken forward in the model framework. Model selection was performed using the *dredge* function in the MuMIn package (Bartoń, 2017). The 'best' model was chosen based on AIC for models containing only significant explanatory variables. Variables, other than survey method, were fitted with smooth splines, with degrees of freedom limited to 4 knots ($k = 4$) to prevent overfitting.

Two-tailed Fisher's exact tests of independence were also run on the contemporaneous fyke net and PAS, or littoral margin run, surveys undertaken at the same sites (n = 21) to investigate agreement in eel detection between methods. Additionally, Kruskal-Wallis rank sum tests (Kruskal & Wallis, 1952) were used to investigate whether there was an effect of survey year on eel abundance (ind. m^{-2} or CPUE) at the five sites sampled over successive years (2016–2018) by PAS, or littoral margin run, electric fishing, and at the six sites sampled by the EA on five occasions (from 1999 to 2017).

Length frequency data were compared between combined PAS and littoral margin electric fishing run eel data and fyke net derived data, and variation in length with distance from the estuary was visualised by fitting smooth local regression (loess) lines (span = 1). Trends in abundance (PAS) or CPUE estimates (littoral margin runs or fyke net surveys) with distance from the estuary were also visualised by fitting loess lines. All analyses were carried out in R 3.6.3 (R Core Team, 2021).

2.4.3 Habitat associations

Given the ordinal nature of many of habitat descriptors, habitat associations were investigated using two-tailed Fisher's exact tests of independence. Here, the difference in occurrence of eels at PAS points with specific habitats was compared with the expected occurrence based on habitat availability in all points. The repeat surveys at five of the sites were deemed to be temporally independent and were included in the analysis. Given the small number of samples from paludal sites, only lotic and lacustrine habitats were considered for this analysis. For lotic sites, analyses were repeated for recently recruited elvers (≤ 160 mm) and yellow, or mature, eels (>160 mm) based on length frequency distributions (Figure 3), sample sizes and previous studies (e.g. Laffaille et al., 2004). A lack of eels of ≤ 160 mm in points in lacustrine sites precluded a similar analysis.

Habitat descriptors were initially placed into the following categories: 1) water depth aggregated into 20 cm categories up to 100 cm and >100 cm, 2) flow for riverine sites only categorised as 0, in 10 m sec^{-1} intervals up to 60 m sec^{-1} and >60 m sec^{-1}, 3) dominant substrate type: solid (clay and earth), fine (sand and silt), coarse (gravel and stone) and large (cobble and rock), 4) submerged, emergent and floating plants, filamentous algae, benthic debris, large woody material, overhanging vegetation, and canopy cover were categorised as '0' presence, followed by 20% intervals. Where necessary, categories were combined to provide a minimum of n = 50 sample points for each analysis. Post-hoc pairwise comparisons, with Bonferroni correction of P-values for multiple tests, were carried out following significant results using the RVAideMemoire package in R (Hervé, 2020). Where tests yielded a significant result for any of the data groupings (i.e. lotic, ≤160, >160 mm and lacustrine), plots of the proportions of points sampled containing eels were used to visualise relative use of available habitat.

2.4.4 Telemetry data

Detections from all data collection methods were collated and analysed to identify site residency, local movements between adjacent sites, and large-scale movements between several sites. Potential barrier delay to downstream migration was investigated at two structures, Letheringsett Mill (middle catchment) and Glandford Mill (lower catchment), and was calculated as the time difference between the last eel detection upstream of the structure and first eel detection downstream.

3 Results

3.1 Catch statistics and abundance estimates

Contemporary electric fishing surveys sampled 3,663 points (c. 4,762 m^2) and c. 11 km of littoral margin, resulting in the capture of 75 eels in 60 PAS surveys (including the repeated surveys of five sites) and 180 eels during continuous littoral runs (Table 2). Fyke netting yielded a total of 142 eels in n = 775 fyke ends at 69 sites (Table 2). Eels were recorded in 81% of lotic (82% of main river sites and 21% of tributary sites), 78% of paludal and 51% of all lacustrine sites (59% overall). The length-weight relationship derived from electric fishing data (n = 174 from all sexes) resulted in a (coefficient relative to body form) and b (an exponent of indicating isometric growth when equal to 3.0) estimates of 0.0018 and 2.985 respectively (r^2 = 0.96). These were akin to those derived from 13 catchments across six countries in Europe, where a was 0.0010 and b was 3.148 (Boulenger et al., 2015). Eel length-frequency data from contemporary surveys (Figure 3) inferred the presence of a range of eel cohorts, ranging from recently recruited elvers of ~70 mm to large (likely female) specimens of 940 mm (~1.38 kg). Mean lengths of all fish caught during the electric fishing averaged 253 mm in comparison with 384 mm for fyke nets (Figure 3a, b). The mean length of eels captured by electric fishing varied between habitats, with smaller eels captured in lotic habitats (215 mm ± 9 SE, n = 167), slightly larger in paludal sites (273 mm ± 14 SE, n = 11) and the largest eels captured in lacustrine sites (333 mm ± 13 SE, n = 77). Lengths of eels caught in fyke nets showed similar trends, with larger eels present in lacustrine habitat (490 mm ± 25 SE, n = 41) compared to paludal (342 mm ± 7 SE, n = 94) and lotic habitats (327 mm ± 18 SE, n = 7). The length of eels captured by both electric fishing and fyke nets generally increased with distance from the estuary (Figures 3c, 3d). However, there was a notable reduction in size of eels caught in fyke nets at the top of the catchment (Figure 3d).

Fyke net surveys delivered the highest CPUE estimates in coastal paludal habitat, with CPUE ~2.7–3.3 times higher on average than for lacustrine sites and the small number of lotic sites surveyed (Table 2). Lotic habitat sampled by PAS supported an average eel density of 0.020 ind. m^{-2} (± 0.001 SE), ~2-4 times higher than the mean densities of 0.008 ind. m^{-2} (± 0.001 SE) for paludal, and 0.005 ind m^{-2} (± 0.0003 SE) for lacustrine waterbodies. Here, the small number of paludal sites sampled reduces confidence in these estimates. Otherwise, average biomass estimates from PAS were highest in lacustrine sites, indicative of the capture of larger fish. PAS surveys delivered overall mean density and biomass estimates of 0.015 ind. m^{-2} (± 0.001 SE) and 0.516 g m^{-2} (± 0.018 SE), with maximum estimates of 0.185 ind. m^{-2} and 5.438

g m^{-2} respectively (Table 2). Mean CPUEs from continuous littoral runs generally mirrored these trends (Table 2). Mean lotic PAS density estimates were comparable to the estimate of 0.014 ind. m^{-2} (± 0.006 SE) delivered by EA methods (n = 35).

The total area of habitat available to eels in the catchment was calculated to be in the order of 116 hectares, comprised mainly of paludal habitat (Table 3). Overall weighted catchment density and biomass of eels were estimated at 0.009 ind. m^{-2} and 0.397 g m^{-2} respectively. The whole catchment eel stock was estimated to be in the order of 10,000 eels, with around 54% of the population in paludal habitat, 30% in lotic and 16% in lacustrine habitats (Table 3).

3.2 Catchment-scale distribution of eels

There was 81% agreement between electric fishing (PAS/continuous littoral margin runs combined) and fyke netting on eel detection at the 21 sites. This declined slightly to 76% using only littoral runs, and 67% for PAS alone. Fisher's exact tests detected no effect of method on eel detectability at a site (PAS/littoral margin run *vs* fyke netting, P = 0.763; littoral margin runs *vs* fyke netting, P = 1.000; PAS *vs* fyke netting, P = 0.567). Furthermore, Kruskal-Wallis rank sums tests detected no significant effect of year on repeated eel abundance estimates at the five key sites based on PAS (χ^2 = 4.044, df = 2, P = 0.132) or continuous runs (χ^2 = 1.119, df = 2, P = 0.572). Similarly, the analysis of longer-term repeat sampling carried out by the EA, spanning the entire period of all data used in the modelling, also suggest no significant difference between years across the sites (χ^2 = 2.060, df = 4, P = 0.725). As such, the approach of including data from different methods and time periods in the modelling framework appears justified.

According to both electric fishing and fyke net surveys, eel abundance broadly declined with increasing distance from the estuary (Figure 4). However, some lakes in the headwaters of the catchment also supported relatively high eel densities. The selected catchment-scale eel occurrence GAM included the log of the site area (edf = 2.084, P = <0.001) and distance from the estuary (edf = 2.681, P = 0.001) as significant terms (Table 4, Fig. 5). The model explained 28% of deviance and had an adjusted r^2 of 0.32. The next best model had a ΔAIC of 0.52 but included 'distance to main river' as a non-significant (edf = 1.707, P = 0.192) covariate, with minimal improvement in deviance explained (28.2%) and no improvement in adjusted r^2 (0.32). The full model, which also included 'survey method' as a factor, was ranked fourth, with a ΔAIC of 2.69, and neither 'survey method' (P = 0.340) or 'distance to main river' (P = 0.357) were significant covariates. The model inferred there was an increased probability of encountering eels in surveys of larger sites, though the increase was not as pronounced for sites with a log area larger than six (approximately 400 m^2) where surveys were more likely than not to detect an eel (Figure 5a). The chance of capturing an eel at a survey site also decreased non-linearly with distance from the estuary (Figure 5b). Sites less than 15 km from the estuary were generally more likely than not to yield a detection, with the probability of detection declining rapidly beyond this.

3.3 Habitat associations

A total of n = 1,951 lotic PAS points (including repeat surveys) yielded only 44 points (2.3%) with eels (n = 24 for ≤ 160 mm and n = 22 for > 160 mm, n = 2 points for eels of both sizes). In lacustrine habitats, eels were recorded in 1.3% (n = 20) of the points (n = 1,491). Only two points recorded eels in the open water habitat and hence the analysis was limited to points in the littoral margins (n = 753), with eels (all > 160 mm in length) caught in 2.4% (n = 18) of these.

In lotic habitat, water depth (P = 0.004), submerged plant cover (P = 0.003) and cover of large woody material (P = 0.008) had a significant effect on the presence of all eels (Table 5 and Figure 6). The effect of water depth and submerged plant cover was limited to recently recruited elvers (≤ 160 mm) and influence of woody material to larger (> 160 mm) eels (Table 5). Post-hoc tests, suggested a significant effect on occupancy between sites with depths of > 0-20 cm and > 60–80 cm for all eels (P = 0.015) and elvers (P = 0.036), with peaks in the proportional use of lotic habitat at depths of > 60-80 cm (Figure 6). Similarly, post-hoc tests on submerged plant cover inferred a preference for moderate levels of cover relative to no cover for all eels (P = 0.024), driven by small eels (P < 0.001), with a peak in proportional use of habitat with > 20-40% cover (Figure 6). Conversely, the presence of larger eels was significantly influenced by overhanging vegetation cover and quantity of large woody material. Post-hoc tests suggested significant effects on site occupancy between 0% and 60-80% overhanging vegetation cover (P = 0.048) and between > 0–20% and > 60–80% (P = 0.009), with a peak in proportional use at >60-80%. Post-hoc tests for woody material inferred significant effects on occupancy between 0% and > 20% cover for all sizes (P = 0.025) and large eels alone (P = 0.003), with peaks in proportional use of sites with > 20 % cover (Figure 6).

In lacustrine habitats, the dominance of large substrate (P = 0.004) and overhanging vegetation (P = 0.005) alone appeared to have a significant effect on the presence of typically larger eels (Figure 3) relative to availability (Table 5 and Figure 6). Here, eels were more likely to be present at sites where large substrate was dominant and with increasing overhanging vegetation cover. Post-hoc tests suggested a significant effect on occupancy (P = 0.048) between 0–20% and > 60% overhanging vegetation cover, with a peak in proportional use of sites with the maximum cover.

3.4 Movements and migration

The detection rate among acoustically tagged eels was 56.6%. Of the 43 eels detected, 55.8% were detected by the acoustic array only, 25.6% by manual tracking only, 11.6% by both the PIT station and acoustic array, and c. 2% each by combinations of PIT station/manual tracking or acoustic array/manual tracking or the PIT station only. Detection rates for eels with PIT tags alone was low (9.4%), a result of the reliance on detection at a single PIT station and given a single recapture during surveys (Table 6). Moreover, many PIT tagged eels were caught and released below the PIT station, limiting the prospects of subsequent detection.

Overall, 51.8% of all eels detected (n = 56) had remained at their release site, 28.6% exhibited net downstream movement within freshwater and 19.6% moved into the estuary. Based on all detections, the mean maximum distance moved during net downstream movement, or movement into the estuary, was much higher for lacustrine eels (6.8 km, range = 4.2–15.5 km), smaller but more variable for lotic eels (2.9 km, range = 0.5–17 km), with a more constrained range of movement from paludal eels (3.2 km, range = 0.2–7.5 km).

Five of the 23 tagged lacustrine eels migrated downstream. Four of these five eels carried PIT tags alone and were detected at the lowest mill where the PIT loops were installed. One of these fish had travelled 15.5 km from the upper catchment in June 2019, one year after tagging. Three moved downstream in October or November, either within the same year as tagging (n = 1), or the following year (n = 2). The acoustically tagged eel, moved down to the river mouth before returning upstream. However, no out-migration was detected at one lake in the upper catchment where several of the 17 eels tagged in July 2018 showed signs of migratory readiness.

Of the 16 lotic fish detected, 15 showed limited net downstream movement to the lowest mill, from sites up to 6.3 km upstream. Three of these (> 400 mm), carrying acoustic tags, were subsequently recorded below the Glaven Outfall Sluice. One of these three eels also spent two months (December and January) in the Cley-Salthouse Marshes before continuing to the outer estuary where it was last detected in January 2019. Despite the presence of a large tidal sluice, detections from eels released in paludal sites indicated relatively high connectivity with the river and estuary. Seven of the 16 acoustically tagged eels (43.8%) passed into the estuary, mainly during summer and autumn. Of the seven, three were recorded at the Glaven Outfall Sluice, with one briefly moving upstream before descending into the estuary again. One large individual (549 mm length), showing signs of migratory readiness when tagged in June 2018, moved into the estuary shortly after tagging where it resided for two weeks, briefly moving to the mouth of the neighbouring River Stiffkey, before migrating to the outer estuary where it was last recorded at the start of July 2018.

Downstream movements of eels (n = 14) were not delayed at the lowest mill at Glandford (Figure 1), where passage times ranged from 13 to 85 seconds (median = 23 seconds). Two eels, both tagged in the river 2 km upstream in June 2018, were recorded passing the only working mill at Letheringsett (Figure 1). One individual (368 mm length) was first recorded upstream of the mill in August 2018, where it remained for 11 hours before moving back upstream out of detection range. It returned two months later and passed after around 5 hours. Six weeks later, the same eel passed Glandford Mill. The second eel (457 mm length) was detected intermittently just above Letheringsett Mill for 6 days in October 2018 before eventually passing the mill. It also then passed Glandford Mill in November in just 43 seconds.

4 Discussion

4.1 Use and integration of different survey methods

The cryptic nature and nocturnal habits of eels, combined with possible differences in catch efficiency across size ranges, amongst habitats and between methods, limit quantitative studies of spatio-temporal abundance. For example, the use of standard fyke nets, a traditional commercial means of capture, is generally qualitative or semi-quantitative at best (i.e. providing CPUE statistics) and highly size-selective in nature, with variable performance according to environmental conditions and eel behaviour (Naismith & Knights, 1990; Tesch, 2003). Thus, in this study it has principally been used to investigate eel presence, with close agreement in detection of eels during fyke net and electric fishing surveys providing confidence in the results of the modelling based on the integrated data. However, because absence at any site could not be fully verified, it is accepted that both methods more correctly describe presence-pseudo absence of eels (Royle, Nichols & Kery, 2005). Nevertheless, surveys were designed to maximise the chance of capturing eels and the modelling is unlikely to be sensitive to 'false-negative' errors (Lasne & Laffaille, 2008).

Stock assessments tend to be based on commercial catch data, traps, or densities delivered by targeted surveys in key catchments (Bark, Williams & Knights, 2007; ICES 2018). Thus, the estimation of indicative total eel population sizes across a whole catchment, which may be considered an important step in developing specific conservation strategies, has rarely been attempted (e.g. Meulenbroek et al., 2020). However, in theory, population estimates may be derived using several methods, including mark-recapture analysis (e.g. Naismith & Knights, 1990; Jessop, 2000) and model-based inference (e.g. Aprahamian et al., 2007). Here, a simple approach was adopted by which PAS was used to estimate mean densities for each principal habitat and these were scaled according to the area of each to provide indicative population estimates.

As the catch efficiency of electric fishing methods may vary according to water conductivity, temperature, turbidity, depth and habitat complexity (Zalewski & Cowx, 1989), the abundance estimates derived in this study may underestimate the true abundance of eels. However, the long thin body morphology of eels means they respond well to electric fishing and their daytime refuging behaviour may mean catch efficiency is high relative to fast-swimming midwater shoaling fish (Perrow et al., 1996). Baldwin & Aprahamian (2012) suggested catch efficiencies of around 0.6 could be achieved during catch-depletion electric fishing, with little effect of site width, eel length or fishing method (coarse, salmonid or eel specific surveys). Furthermore, Laffaille et al. (2005a) found PAS to be strongly correlated (r^2 = 94%, $P < 0.001$) with catch-depletion methods and lotic PAS densities were generally comparable with estimates derived from the catch-depletion sampling in the Glaven. PAS aims to be a surprise application of current, covering a small sampling area, and it seems likely that efficiency is very high (perhaps approaching 1) for eels, especially given the shallow and clear nature of the waters generally sampled during this study. However, the precision of the density estimates for the principal habitats was relatively, possibly reflecting habitat heterogeneity between sample sites, the small numbers of sample sites (especially within paludal habitat) and numbers of eels encountered. Nevertheless, the extrapolation of densities to provide indicative population estimates for the principal habitats illustrated the relative importance of each and is seen as a valuable step for conservation planning (see below). Thus, the approach warrants further development, with improvements to accuracy and precision being achievable through increased survey effort, segregation of the catchment into smaller survey compartments with more homogenous habitat, and consideration of variability in catch-efficiency. Studies in similar situations should also consider the use of tailored electric fishing equipment to allow sampling of highly conductive brackish waters to advance our understanding of paludal habitat use (e.g. Warry et al., 2013).

4.2 Abundance and eel distribution across the catchment

The Glaven catchment, on the east coast of the UK, is relatively isolated from the supplies of eel leptocephali brought to Europe on the Gulf Stream. Thus, coupled with historic lows in the glass eel supplies since the early 2000s (ICES 2018), it was not unexpected that the overall weighted density (0.009 ind. m^{-2}) and biomass (0.516 g m^{-2}) of eels for the catchment were low. Further, evidence from repeated catch-depletion electric fishing suggests this is a relatively stable position with no significant reduction over the last 20 years. Like-for-like comparisons with other rivers were undertaken using lotic density, as sampling elsewhere is typically limited to the river alone. While the mean lotic density of eels in the Glaven (0.02 ind. m^{-2}) appears broadly comparable with the <0.05 ind. m^{-2} reported from the majority (71%, n = 1,464) of river sites in England (Carss et al., 1999), it is below the lower end of the range of

0.03–0.50 ind. m^{-2} reported by Bark, Williams & Knights (2007) for 11 rivers in England and Wales sampled in the early 2000s. Moreover, the lotic biomass estimate (0.462 g m^{-2}) is far below the suggested carrying capacity of 25 g m^{-2} for small lowland rivers in the UK (Aprahamian, 2000), suggesting that lotic habitat for eels in the Glaven is generally poor. Indeed, all major habitat types in the Glaven supported <1 g m^{-2}, suggesting considerable scope for improving what would appear to be a vulnerable stock. The low abundance was reinforced by generally low presence in available habitat (e.g. presence at 2.3% of lotic and 1.3% of lacustrine points), although the relative site-level occurrence of eels was high in both paludal (78% of sites) and lotic (81% of sites) habitat, but lower for lacustrine sites (51% of sites) that typically lie in the floodplain and may not be directly connected to the river or are isolated by water control structures. This pattern is further reflected by the overall catchment distribution, with confirmed presence at 59% of the 131 locations sampled. However, in agreement with other studies (e.g. Ibbotson et al. 2002; Feunteun et al., 2003; Lasne & Laffaille, 2008), both the probability of presence and density of eels across the catchment generally declined with distance from the estuary. Collinearity between distance from the estuary and cumulative numbers of barriers confounded investigation of the relative effects of each factor in isolation on the probability of eel occurrence. Thus, in keeping with the known abilities of eel to navigate obstructions, potential barriers to migration did not appear to be the principal driver of the observed distribution patterns, although this does not discount the effects of specific barriers on eel abundance (see below).

To help highlight specific limitations and thus areas of potential conservation effort here, each of the principal habitats (paludal, lotic and lacustrine) are considered in turn. This also broadly fits both with a river continuum approach, the sequence of habitats encountered by colonising elvers and likely accessibility of the habitats. It is also noted that different habitats may also be important for different life stages and availability and quality could also influence overall catchment sex-ratios (Davey & Jellyman, 2005).

4.2.1 Paludal habitat

In agreement with Steele et al. (2018), working in the Thames estuary, the coastal paludal network of ditches and pools appears to be an important habitat for eels in the Glaven. This was indicated by the highest fyke net catches here which suggested densities, particularly of yellow eels, may be higher than those estimated from the limited PAS surveys. Despite this, the large area of paludal habitat, representing ~60% of all surface water in the Glaven, meant that it could be supporting over half of the overall catchment eel population. Concentrated at the coast, paludal habitat is likely to be important for elvers recruiting to the catchment, although the limited sampling by electric fishing captured very few and the standard fykes were unable to retain elvers. The large tidal sluice controlling water movement to the marshes to the east, and outfall sluices regulating water levels in the marshes to the west, may also impede elver access. However, the presence of elvers in the lower river after crossing a similar structure (the Glaven Outfall Sluice – see Figure 1) suggests these barriers are unlikely to prevent access and that elvers were perhaps underrepresented in surveys.

Telemetry also suggested relatively good connectivity between paludal habitat and the estuary for larger eels at least. Indeed, the patterns of movement suggested that many paludal eels might be so-called 'founders' or 'nomads' (Feuteun et al., 2003; Daverat et al., 2006), that retain a high degree of ecological plasticity and exhibit relatively free interchange between different habitats. The lengths of eels caught in fykes in paludal habitat (342 mm ± 7 SE) suggested relatively few large female fish (>450 mm) were present and thus a dominance of smaller, possibly male, yellow eels is likely. This aligns with theories of density-dependent sex determination (Davey & Jellyman, 2005; Geffroy & Bardonnet, 2016), with the larger numbers of eels suggested by fyke net surveys potentially driving a bias towards males. Further, the abundance of older conspecifics may be sufficient to discourage or even prevent settling by elvers due to the risk of predation or competition for resources. However, competition may be mitigated by size-specific differentiation of habitat use (Feuteun et al., 2003; Domingos, Costa & Costa, 2006; Acou et al., 2011; Jellyman & Arai, 2016). Unfortunately, information on microhabitat use was limited by the lack of PAS survey coverage. However, paludal habitat was highly variable, ranging from small channels with abundant macrophytes in clear waters to larger structureless channels with turbid waters. It is of note that Steele et al. (2018) were unable to link eel abundance with habitat characteristics, other than a lack of channel management (i.e. dredging and weed-cutting) being beneficial. Further research into the use of this important habitat by eels is required.

4.2.2 Lotic habitat

The highest riverine density (0.185 ind. m^{-2}) of eels resulted from the capture of numerous elvers just above the Glaven Outfall Sluice in August 2018. In the lower catchment, where they primarily occurred, elvers were significantly associated with deeper water or submerged plants, but were also found buried in fine sediments, with this habitat offering daytime refuge between upstream migrations. Other studies have suggested elvers prefer shallow depths with coarse substrates (e.g. Laffaille et al., 2003; Christoffersen et al., 2018; Degerman et al., 2019;) and this may reflect differences in habitat availability between catchments. The reduction in densities of eels away from the lower reaches, is likely driven by natural dispersal and settlement in available habitat. Although many of the numerous water control structures (e.g. low weirs) appeared unlikely to strongly impair upstream migration, aggregations of elvers were observed immediately downstream of several larger structures, including two mills and a sluice on one of the online lakes (Bayfield Lake, see Figure 1). The sharp drop-off in overall eel abundance at around 15 km from the estuary also coincides with the location of three mills (including the active Letheringsett Mill, Figure 1) and two recently installed low weirs with overhanging sills. These low weirs have been designed to prevent upstream colonisation of invasive alien signal crayfish (*Pacifastacus leniusculus*) to protect the locally important population of endangered native white-clawed crayfish (*Austropotamobius pallipes*) further upstream. Despite these barriers, 'pioneer' eels (Feunteun et al., 2003) are found in the headwaters of the river and more isolated lacustrine habitat. The size of the smallest eels (~260 mm total length) captured at the top of the catchment suggests it may take two or three years for elvers to navigate the entire river, though the numbers managing to do so may be limited.

The scope for elvers to settle and grow-on within the river itself is likely further limited by its small relative size (c. 13% of surface water area within the catchment) and availability of favourable habitat. In the Glaven, larger, potentially relatively sedentary 'home range dwellers' (Feuteun et al., 2003; Laffaille, Acou & Guillouët, 2005; Ovidio et al., 2013; Bašić et al., 2019) were strongly associated with large woody material or overhanging vegetation that provide cover from predators (Acou et al., 2011). Such habitat is limited, and it is striking that the lotic site with by far the highest biomass (5.6 g m^{-2}) of eels was heavily wooded. Here, the river is characterised by natural riffle-pool form induced by standing bankside and rooted fallen trees (mainly Alder *Alnus glutinosa*) that escaped routine flood defence management due to campaigning by a local conservation group. In accordance with other studies (e.g. Lamouroux et al., 1999) larger eels were also often recorded in deeper sites, although there did not appear to be a significant effect of depth, possibly reflecting the relative lack of variability within the Glaven.

Overall, while lotic habitat supported some 29% of the catchment population, this fraction was dominated (60%) by elvers (≤ 160 mm), suggesting the river is more important as a conduit for upstream and downstream passage rather than as permanent habitat. Telemetry indicated downstream passage of eels, originating both from within the river and from lacustrine habitat, was typically rapid and unimpeded. However, the working mill at Letheringsett, with its specific water management regime, did appear to temporarily delay passage of the two eels recorded attempting to pass it during downstream migration.

4.2.3 Lacustrine habitat

Although lacustrine habitat accounted for 28% of the potential habitat for eels within the catchment, it was estimated to support < 16% of the population (Table 3). Densities were also variable but generally low, with some apparently suitable lakes/ponds containing few, if any eels. Variability may partly reflect accessibility, as some sites were relatively close to the river and presumably readily accessible, whereas others appeared truly isolated or had ephemeral connections to the river via narrow (< 2 m), shallow (< 15 cm) drainage channels. Many also have significant vertical water control structures that could significantly impair access. Although this study did not provide direct evidence of movement into lakes by tagged eels, some insight into out-migration, which is likely to be generally easier (involving 'falling' rather than 'climbing') was provided. For example, what were presumed to be mature silver eels successfully migrated to the river and continued downstream from half of the lacustrine sites where they were tagged. In contrast, none of the 17 large eels tagged at one lake (Brinton Lake, see Figure 1) were recorded by the receiver array, despite several individuals showing indications of migratory readiness in the form of phenotypic change associated with 'silvering' (Durif, Dufour & Elie, 2005) when tagged. Here, escapement was probably restricted by a draw-down, meaning the water level was well below the height of the outflow structure. Reduced water levels also led to marginal tree-roots becoming 'perched' (Figure 1) and inaccessible as refuges, potentially increasing vulnerability to predators, especially Eurasian otter (*Lutra lutra*). The general importance of marginal habitat as refuges to eels in lacustrine habitat was illustrated by their virtually exclusive association with bankside trees and emergent macrophytes as well as some introduced substrates such as large stones or willow piling that have large crevices.

Lacustrine habitat also offered resources in the form of macroinvertebrate and especially fish populations, with the latter including stocked cyprinids that do not occur naturally in the upper catchment. The potential for piscivory increases the capacity for growth and promotes larger size in eels (Moriarty, 1972). Indeed, some lakes in the upper catchment yielded biomass estimates that reflected the dominance of larger eels (mean total length from fyke nets = 490 mm ± 25 SE). While the increase in abundance of larger eels with distance from the tidal limits is consistent with other studies (e.g. Laffaille et al., 2003), a reduction in the size of eels in the upper catchment (Figure 3) was also noted. This reflects the tendency for lacustrine habitat, often at the source of the main river and its tributaries, to operate as points at the 'end-of-the-line' for 'pioneers'. The accumulation of eels in some of these relatively large lacustrine habitats was thought to drive the significant relationship between habitat area and eel presence. Once in such lakes, eels may be resident for 20 years or more to reach the sizes recorded which indicated the dominance of female fish that is also consistent with density-dependent sex determination mechanisms (Tesch, 2003; Davey & Jellyman, 2005; Arai, Kotake & McCarthy, 2006). Considering the relative rarity of large female fish within the rest of catchment, lacustrine habitat is considered of significant conservation value in terms of the potential spawning stock with females classically considered the limiting resource for the males (Geffroy & Bardonnet, 2016).

4.3 Implications for conservation management

River Basin District EMPs across Europe aim to describe the status of eel populations, assess compliance with targets and detail management to improve escapement (Dekker 2008). A lack of reliable monitoring of smaller, more numerous, catchments often means that plans concentrate on larger catchments. This belies the likely collective and cumulative importance of numerous small catchments to eel stocks and overall conservation strategies (Copp, Daverat & Bašić, 2020). This study illustrates the importance of catchment-scale approaches to monitoring using different methods, especially PAS by electric fishing and even the limited tracking of eels (see 4.1 above). Together these provide important insights for eel conservation by identifying important habitats for different life-stages that seem likely to be mirrored in many similar small rivers. In simple terms, lotic habitat is critical for elver dispersal, paludal habitat appears important for high numbers of smaller, possibly male dominated, yellow eels (and presumably elvers) and lacustrine habitat likely supports the bulk of the female spawning stock. In turn, this understanding lends itself to three simple principles for conservation management of eels in small rivers at a catchment scale; defined as follows.

4.3.1 Improve connectivity

Where eel populations are not at carrying capacity, as is currently likely in many catchments due to the low supplies of potential recruits, connectivity should be improved to maximise access to the catchment and thence to all available habitat, particularly lakes and ponds. Where barriers cannot be removed, the benefit of eel passes is widely documented (e.g. Briand et al., 2005; Laffaille et al., 2005b; Piper, Wright & Kemp, 2012) with 'nature-like' fishways being a better long-term solution with wider ecological benefits (Tamario et al., 2019). However, this study illustrates that the perception of barriers to eels may not reflect reality and it is important that potential barriers should be fully assessed. Some insight into significant barriers may be provided by specific studies, with telemetry or mark-recapture providing further information on passage. Where suitable, less significant barriers, such as small sluices on ponds or lakes, should be addressed by installing low-cost passes to provide immediate wins. However, significant barriers for both colonisation and escapement are likely to be highly location specific and require tailored solutions.

4.3.2 Restock or relocate

Where engineering solutions cannot be implemented to improve connectivity (e.g. due to prohibitive cost, biosecurity issues or flood protection issues), restocking or relocation (i.e. assisted migration) should be considered. The large degree of uncertainty around the success and indeed appropriateness of restocking (Nzau Matondo et al., 2020; Rohtla et al., 2021) means that assisted migration of elvers within the same catchment is preferred. This could simply involve the deployment of artificial habitat eel collectors (e.g. Silberschneider et al.,

2001) downstream of structures, which are regularly checked and any elvers moved directly upstream. However, translocation over larger distances to the wider catchment, including lacustrine habitat, should be considered where natural passage is limited.

4.3.3 Restore, enhance and create

Habitat improvements should focus on increasing the quality and quantity of refuge and foraging habitat that could increase survival rates and the chance of eels reaching maturity and escaping. However, requirements for habitat enhancement, restoration or even creation are likely to be catchment-specific and should be underpinned by a good understanding of habitat availability. Further research is required to understand the relative importance of paludal microhabitat, including drainage channels and pools, and the role of depth and plant structure in providing optimal eel habitat. Currently, Laffaille et al. (2004) suggests regular rotational dredging of channels to enhance and maintain the diversity, particularly of plant habitat, to combat successional processes in channels. Such management needs to be compatible with the requirements for drainage and other conservation interests, as many coastal marshes are managed as nature reserves, especially for birds.

For lotic habitat, suitable refuges, in which elvers can settle and mature, may be particularly limiting. Thus, where lacking, bankside tree growth that provides living root systems and a supply of woody material to the channel, should be promoted through rewilding techniques (Rideout et al., 2021). Such measures are also likely to confer wider biodiversity benefits (e.g. Thompson et al., 2018). Moreover, natural recovery, through reinstatement of natural channel form (e.g. restoration of meanders), function and complexity, is also likely to benefit eels and provide further biodiversity gains. This could involve the re-introduction of European beaver (*Castor fiber*), whose natural engineering increases supply of large woody material to the channel and slows river flow through the creation of pools and linkages with the floodplain (e.g. Hood & Larson, 2015), all of which are likely to be of considerable benefit to eels.

Management of existing lacustrine habitat should focus on the provision of quality littoral refuges, especially in the form of bankside trees and/or complex emergent margins. In some structural situations such as dam walls, stabilising materials offering large cavities (e.g. stonework, gabions and faggots) may be designed with use by eels in mind. Eel sensitive water management practices should also be encouraged to allow access and escapement of eels. Where lacking, lacustrine habitat may be readily created in the form of floodplain ponds. Ideally, these should be large (to maximise littoral margin habitat) and well connected, with consideration given to the provision of cover for refuging eels and support for prey resources including invertebrates and fish. Stocks of the latter need to be carefully considered in the context of communities native to the catchment concerned.

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Conflict of interest statement:

The authors declare that they have no conflicts of interest associated with this work.

Data sharing and data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

6 References

Acou, A., Rivot, E., van Gils, J.A., Legault, A., Ysnel, F. & Feunteun, E. (2011). Habitat carrying capacity is reached for the European eel in a small coastal catchment: Evidence and implications for managing eel stocks. *Freshwater Biology*, 56(5), 952–968. https://doi.org/10.1111/j.1365-2427.2010.02540.x

Aprahamian, M.W. (2000). The growth rate of eel in tributaries of the lower River Severn, England, and its relationship with stock size. *Journal of Fish Biology*, 56(1), 223-227. https://doi.org/10.1111/j.1095-8649.2000.tb02100.x

Aprahamian, M.W., Walker, A.M., Williams, B., Bark, A. & Knights, B. (2007). On the application of models of European eel Anguilla Anguilla production and escapement to the development of eel management plans: The River Severn. *ICES Journal of Marine Science*, 64(7), 1472-1482. https://doi.org/10.1093/icesjms/fsm131

Arai, T., Kotake, A. & McCarthy, T.K. (2006). Habitat use by the European eel *Anguilla anguilla* in Irish waters. *Estuarine Coastal and Shelf Science*, 67(4), 569–578. https://doi.org/10.1016/j.ecss.2006.01.001

Bain, M.B., Finn, J.T. & Booke H.E. (1985). Quantifying stream substrate for habitat analysis studies. *North American Journal of Fisheries Management,* 5(3B), 499-500. https://doi.org/10.1577/1548-8659(1985)5<499:QSSFHA>2.0.CO;2

Baldwin. L. & Aprahamian, M. (2012). An evaluation of electric fishing for assessment of resident eel in rivers. *Fisheries Research*, 123–124, 4–8. https://doi.org/10.1016/j.fishres.2011.11.011

Bark, A., Williams, B. & Knights, B. (2007). Current status and temporal trends in stocks of European eel in England and Wales. *ICES Journal of Marine Science*, 64(7), 1368-1378. https://doi.org/10.1093/icesjms/fsm117

Barry, J., Newton, M., Dodd, J.A., Hooker, O.E., Boylan, P., Lucas, M.C. et al. (2016a). Foraging specialisms influence space use and movement patterns of the European eel *Anguilla anguilla*. *Hydrobiologia*, 766, 333–348. https://doi.org/10.1007/s10750-015-2466-z

Barry, J., Newton, M., Dodd, J.A., Lucas, M.C., Boylan, P. & Adams, C.E. (2016b). Freshwater and coastal migration patterns in the silver-stage eel *Anguilla anguilla*. *Journal of Fish Biology*, 88(2), 676-689. https://doi.org/10.1111/jfb.12865

Bartoń, K. (2017). MuMIn: Multi-model inference. Vienna, Austria: R Foundation for Statistical Computing. Available at: https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf [Accessed 15 December 2021]

Bašić, T., Aislabie, L., Ives, M., Fronkova, L., Piper, A. & Walker, A. (2019). Spatial and temporal behavioural patterns of the European eel *Anguilla anguilla* in a lacustrine environment. *Aquatic Sciences*, 81(4), 73. https://doi.org/10.1007/s00027-019-0671-y

Birnie-Gauvin, K., Franklin, P., Wilkes, M., & Aarestrup, K. (2018). Moving beyond fitting fish into equations: Progressing the fish passage debate in the Anthropocene. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29(7), 1095-1105. https://doi.org/10.1002/aqc.2946

Boulenger, C., Acou, A., Trancart, T., Crivelli, A.J. & Feunteun, E. (2015). Length-weight relationships of the silver European eel, *Anguilla anguilla* (Linnaeus, 1758), across its geographic range. *Journal of Applied Ichthyology*, 31(2), 1-4. https://doi.org/10.1111/jai.12685

Briand, C., Fatin, D., Fontenelle, G. & Feunteun, E. (2005). Effect of re-opening of a migratory pathway for eel (*Anguilla anguilla*, L.) at a watershed scale. *Bulletin Français de la Pêche et de la Pisciculture*, 378-379, 67–86. https://doi.org/10.1051/kmae:2005004

Carle, F.L. & Strub, M.R. (1978). A new method of estimating population size from removal data. *Biometrics*, 34(4), 621–630. https://doi.org/10.2307/2530381

Carss, D.N., Elston, D.A., Nelson, K.C. & Kruuk, H. (1999). Spatial and temporal trends in unexploited yellow eel stocks in two shallow lakes and associated streams. *Journal of Fish Biology*, 55(3), 636-654. https://doi.org/10.1111/j.1095-8649.1999.tb00704.x

Champkin, J.D., Copp, G.H., Sayer, C.D., Clilverd, H.M., George, L., Bilizzi, L. et al. (2017). Responses of fishes and lampreys to the re-creation of meanders in a small English chalk stream. *River Research and Applications*, 34(1), 34-43. https://doi.org/10.1002/rra.3216

Christoffersen, M., Svendsen, J.C., Kuhn, J.A., Nielsen, A., Martjanova, A., Stottrup, J.G. (2018). Benthic habitat selection in juvenile European eel *Anguilla anguilla*: implications for coastal habitat management and restoration. *Journal of Fish Biology*, 93(5), 996–999. https://doi.org/10.1111/jfb.13807

Convention on International Trade in Endangered Species of Wild Fauna and Flora. (2021). Appendices I, II and III. Available at: https://cites.org/eng/app/appendices.php. [Accessed 12 October 2021]

Clilverd, H.M., Thompson, J.R., Heppell, C.M., Sayer, C.D. & Axmacher, J.C. (2013). River–floodplain hydrology of an embanked lowland Chalk River and initial response to embankment removal. *Hydrological Sciences Journal*, 58(3), 1-24. https://doi.org/10.1080/02626667.2013.774089

Convention on Migratory Species. (2020). Appendix I & II of CMS. Available at: https://www.cms.int/en/page/appendix-i-ii-cms. [Accessed 12 October 2021]

Copp, G.H. & Peňáz, M. (1988). Ecology of fish spawning and nursery zones in the flood plain, using a new sampling approach. *Hydrobiologia*, 169, 209-224. https://doi.org/10.1007/BF00007312

Copp, G.H., Daverat, F. & Bašić, T. (2020). The potential contribution of small coastal streams to the conservation of declining and threatened diadromous fishes, especially the European eel. *River Research and Applications*, 37(6), 111-115. https://doi.org/10.1002/rra.3746

Daverat, F., Limburg, K.E., Thibault, I., Shiao, J.C., Dodson, J.J., Caron, F. et al. (2006). Phenotypic plasticity of habitat use by three temperate eel species, *Anguilla anguilla*, *A. japonica* and *A. rostrata*. *Marine Ecology Progress Series*, 308, 231-241. https://doi.org/10.3354/meps308231

Davey, A.J.H. & Jellyman, D.J. (2005). Sex determination in freshwater eels and management options for manipulation of sex. *Reviews in Fish Biology and Fisheries*, 15(1), 37-52. https://doi.org/10.1007/s11160-005-7431-x

Department for Environment, Food and Rural Affairs. (2010). *Eel management plans for the United Kingdom; Anglian River Basin District*. Available at: https://www.broads-authority.gov.uk/looking-after/managing-land-and-water/conservation-publications-and-reports/water-conservation-reports/42.-Eel-management-plan-Anglian.pdf [Accessed 15 December 2021]

Degerman, E., Fogelgren, J.E., Tengelin, B. & Thörnelöf, E. (1986). Occurrence of salmonid parr and eel in relation to water quality in small streams on the west coast of Sweden. *Water, Air, and Soil Pollution*, 30, 665-671. https://doi.org/10.1007/BF00303330

Degerman, E., Tamario, C., Watz, J., Nilsson, P.A. & Calles, O. (2019). Occurrence and habitat use of European eel (*Anguilla anguilla*) in running waters: Lessons for improved monitoring, habitat restoration and stocking. *Aquatic Ecology*, 53, 639-650. https://doi.org/10.1007/s10452-019-09714-3

Dekker, W. (2003). On the distribution of the European eel (*Anguilla anguilla*) and its fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*, 60(7), 787–799. https://doi.org/10.1139/f03-066

Dekker, W. (2008). Coming to Grips with the Eel Stock Slip-Sliding Away. In: Schlechter, M.G., Leonard, N.J. & Taylor, W.W. (Eds.) *International Governance of Fisheries Eco-systems: Learning from the Past, Finding Solutions for the Future, American Fisheries Society, Symposium 58*. Maryland, USA: Bethesda, pp. 335–355. https://doi.org/10.47886/9781888569995

Dekker, W. & Beaulaton, L. (2015). Climbing back up what slippery slope? Dynamics of the European eel stock and its management in historical perspective. *ICES Journal of Marine Science*, 73(1), 5–13. https://doi.org/10.1093/icesjms/fsv132

Domingos, I., Costa, J.L. & Costa, M.J. (2006). Factors determining length distribution and abundance of the European eel, *Anguilla anguilla*, in the River Mondego (Portugal). *Freshwater Biology*, 51(12), 2265-2281. https://doi.org/10.1111/j.1365-2427.2006.01656.x

Durif, C., Dufour, S. & Elie, P. (2005). The silvering process of *Anguilla anguilla*: A new classification from the yellow resident to the silver migrating stage. *Journal of Fish Biology*, 66(4), 1025-1043. https://doi.org/10.1111/j.0022-1112.2005.00662.x

Feunteun, E., Rigaud, C., Elie, P. & Lefeuvre, J.-C. (1999). Les peuplements piscicoles des marais littoraux endigués atlantiques: un patrimoine à gérer? Le cas du marais de Bourgneuf-Machecoul (Loire-Atlantique, France). *Bulletin Français de la Pêche et de la Pisciculture*, 352, 63–79. https://doi.org/10.1051/KMAE:1999021

Feunteun, E. (2002). Management and restoration of European eel population (*Anguilla anguilla*): An impossible bargain. *Ecological engineering*, 18(5): 575-591. https://doi.org/10.1016/S0925-8574(02)00021-6

Feunteun, E., Laffaille, P., Robinet, T., Briand, C., Baisez, A., Olivier, J-M. et al. (2003). A review of upstream migration and movements in inland waters by Anguillid Eels:

Toward a general theory. In: Aida K., Tsukamoto K., Yamauchi K. (Eds.) *Eel Biology*. Tokyo: Springer, pp 191-213.

Geffroy, B. & Bardonnet, A. (2016). Sex differentiation and sex determination in eels: Consequences for management. *Fish and Fisheries*, 17(2), 375-398. https://doi.org/10.1111/faf.12113

Herrera, M., Moreno-Valcárcel, R., de Miguel Rubio, R. & Fernández-Delgado, C. (2019). From transient to sedentary? Changes in the home range size and environmental patterns of movements of European eels (*Anguilla anguilla*) in a Mediterranean river. *Fishes*, 4(3), 43. https://doi.org/10.3390/fishes4030043

Hervé, M. (2020). RVAideMemoire: Testing and plotting procedures for biostatistics. R package version 0.9-75. Available at: https://CRAN.R-project.org/package=RVAideMemoire [Accessed 15 December 2021]

Hood, G. A. & Larson, D. G. (2015). Ecological engineering and aquatic connectivity: A new perspective from beaver-modified wetlands. *Freshwater Biology*, 60(1), 198-208. https://doi.org/10.1111/fwb.12487

Ibbotson, A., Smith, J., Scarlett, P. & Aprhamian, M. (2002). Colonisation of freshwater habitats by the European eel *Anguilla anguilla*. *Freshwater Biology*, 47(9), 1696-1706. https://doi.org/10.1046/j.1365-2427.2002.00930.x

ICES (2018). Report of the Joint EIFAAC/ICES/GFCM Working Group on Eels (WGEEL), 5–12 September 2018, Gdańsk, Poland. ICES CM 2018/ACOM:15.

Jacoby, D. & Gollock, M. (2014). *Anguilla anguilla*. The IUCN Red List of Threatened Species 2014: e.T60344A45833138. Available at: http://dx.doi.org/10.2305/IUCN.UK.2014-1.RLTS.T60344A45833138.en. [Accessed 26 August 2021]

Jacoby, D.M.P., Casselman, J.M., Crook, V., DeLucia, M-B., Ahn, H., Kaifu,K. et al. (2015). Synergistic patterns of threat and the challenges facing global anguillid eel conservation. *Global Ecology and Conservation*, 4, 321-333. https://doi.org/10.1016/j.gecco.2015.07.009

Jellyman, D.J. & Arai, T. (2016). Juvenile eels: Upstream migration and habitat use. In: Arai, T. (Ed.) *Biology and ecology of anguillid eels*. Boco Raton, FL: CRC Press, pp 143–170.

Jessop, B.M. (2000). Estimates of population size and instream mortality rate of American eel elvers in a Nova Scotia river. *Transactions of the American Fisheries Society,* 129(2), 514–526. https://doi.org/10.1577/1548-8659(2000)129<0514:EOPSAI>2.0.CO;2

Knights, B., Bark, A.W., Ball, M., Williams, F., Winter, E. & Dunn, S. (2001). *Eel and elver stocks in England and Wales: Status and management options*. R & D Technical Report W248, Environment Agency, Bristol, UK.

Kruskal, W.H. & Wallis, A. (1952). Use of ranks in one-criterion variance analysis. *Journal of the American Statistical Association,* 47(260), 583–621. https://doi.org/10.2307/2280779

Laffaille, P., Feunteun, E., Baisez, A., Robinet, T., Acou, A., Legault, A. et al. (2003). Spatial organisation of European eel (*Anguilla anguilla* L.) in a small catchment. *Ecology of Freshwater Fish*, 12(4), 254-264. https://doi.org/10.1046/j.1600-0633.2003.00021.x

Laffaille, P., Baisez, A., Rigaud, C. & Feunteun, E. (2004). Habitat preferences of different European eel size classes in a reclaimed marsh: A contribution to species and ecosystem conservation. *Wetlands*, 24, 642-651. https://doi.org/10.1672/0277-5212(2004)024[0642:HPODEE]2.0.CO;2

Laffaille, P., Acou, A. & Guillouët, J. (2005). The yellow European eel (*Anguilla anguilla* L.) may adopt a sedentary lifestyle in inland freshwaters. *Ecology of Freshwater Fish*, 14(2), 191-196. https://doi.org/10.1111/j.1600-0633.2005.00092.x

Laffaille, P., Briand, C., Fatin, D., Lafae, D. & Lasne, E. (2005a). Point sampling the abundance of European eel (*Anguilla anguilla*) in freshwater areas. *Archiv fur Hydrobiologie*, 162(1), 91-98. https://doi.org/10.1127/0003-9136/2005/0162-0091

Laffaille, P., Acou, A., Guillouët, J. & Legault, A. (2005b). Temporal changes in European eel, *Anguilla anguilla*, stocks in a small catchment after installation of fish passes. *Fisheries Management and Ecology*, 12(2), 123-129. https://doi.org/10.1111/j.1365-2400.2004.00433.x

Laffaille, P., Lasne, E. & Baisez, A. (2009). Effects of improving longitudinal connectivity on colonization and distribution of European eel in the Loire catchment, France. *Ecology of Freshwater Fish*, 18(4), 610-619. https://doi.org/10.1111/j.1600-0633.2009.00378.x

Lamouroux, N., Capra, H., Pouilly, M. & Souchon, Y. (1999). Fish habitat preferences in large streams of southern France. *Freshwater Biology*, 42(4), 673-687. https://doi.org/10.1046/j.1365-2427.1999.00521.x

Lasne, E. & Laffaille, P. (2008). Analysis of distribution patterns of yellow European eels in the Loire catchment using logistic models based on presence–absence of different size-classes. *Ecology of Freshwater Fish*, 17(1), 30-37. https://doi.org/10.1111/j.1600-0633.2007.00253.x

Lyche Solheim, A., Globevnik, L., Austnes, K., Kristensen, P., Moe, S.J., Persson, J. et al. (2019). A new broad typology for rivers and lakes in Europe: Development and application for large-scale environmental assessments. *Science of The Total Environment*, 697, 134043. https://doi.org/10.1016/j.scitotenv.2019.134043

Meulenbroek, P., Hammerschmied, U., Schmutz, S., Weiss, S., Schabuss, M., Zornig, H. et al. (2020). Conservation Requirements of European Eel (*Anquilla anquilla*) in a Balkan Catchment. *Sustainability*, 12(20), 8535. https://doi.org/10.3390/su12208535

Moriarty, C. (1972). Studies of the eel *Anguilla anguilla* in Ireland. 1. In the lakes of the Corrib system. *Irish Fisheries Investigations A*, 10, 1-13.

Moriarty, C. & Dekker, W. (1997). Management of the European eel. *Irish Fisheries Bulletin*, 15, 1-125.

Naismith, I.A. & Knights, B. (1990). Studies of sampling methods and of techniques for estimating populations of eels, *Anguilla anguilla* L. *Aquaculture and Fisheries Management*, 21(3), 357–367. https://doi.org/10.1111/j.1365-2109.1990.tb00473.x

Nzau Matondo, B., Benitez, J-P., Dierckx, A., Rollin, X. & Ovidio, M. (2020). An evaluation of restocking practice and demographic stock assessment methods for cryptic juvenile European eel in upland rivers. *Sustainability*, 12, 1124. https://doi.org/10.3390/su12031124

Ovidio, M., Seredynski, A.L., Philippart, J-C. & Nzau Matondon, B. (2013). A bit of quiet between the migrations: The resting life of the European eel during their freshwater growth phase in a small stream. *Aquatic Ecology*, 47(3), 291-301. https://doi.org/10.1007/s10452-013-9444-1

Perrow, M.R., Jowitt, A.J.D. & Zambrano González, L. (1996). Sampling fish communities in shallow lowland lakes: Point-sample electric fishing vs. electric fishing within stop-nets. *Fisheries Management & Ecology*, 3(4), 303-313. https://doi.org/10.1046/j.1365-2400.1996.d01-152.x

Perrow, M.R., Winfield, I.J., Tomlinson, M.L. & Harwood, A.J.P. (2017). *Designing a methodology for surveying fish populations in freshwater lakes*. Natural England Commissioned Report NECR230. Available at: http://publications.naturalengland.org.uk/file/4749528681414656 [Accessed 12th October 2021]

Piper, A.T., Wright, R.M. & Kemp, P.S. (2012). The influence of attraction flow on upstream passage of European eel (*Anguilla anguilla*) at intertidal barriers. *Ecological Engineering*, 44, 329-336. https://doi.org/10.1016/j.ecoleng.2012.04.019

QGIS Development Team (2021). QGIS Geographic Information System. Open Source Geospatial Foundation Project. Available at: http://qgis.osgeo.org [Accessed 15 December 2021]

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.R-project.org/ [Accessed 15 December 2021]

Rideout, N.K., Wegscheider, B., Kattilakoski, M., McGee, K.M., Monk, W.A. & Baird, D.J. (2021). Rewilding watersheds: Using nature's algorithms to fix our broken rivers. *Marine and Freshwater Research*, 72(8), 1118-1124. https://doi.org/10.1071/MF20335

Rohtla, M., Silm, M., Tulonen, J., Paiste, P., Wickström, H., Kielman-Schmitt, M. et al. (2021). Conservation restocking of the imperilled European eel does not necessarily equal conservation, *ICES Journal of Marine Science*, 78(1), 101-111. https://doi.org/10.1093/icesjms/fsaa196

Royle, J.A., Nichols, J.D. & Kery, M. (2005). Modelling occurrence and abundance of species when detection is imperfect. *Oikos*, 110(2), 353–359. http://www.jstor.org/stable/3548476.

Sayer, C.D. (2014). Conservation of aquatic landscapes: ponds, lakes, and rivers as integrated systems. *Wiley Interdisciplinary Reviews – Water*, 1(6), 573-585. https://doi.org/10.1002/wat2.1045

Sayer, C.D. & Greaves, H. (2020). Making an impact on UK farmland pond conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(9), 1821-1828. https://doi.org/10.1002/aqc.3375

Schmidt, J. (1923). Breeding places and migrations of the eel. *Nature*, 111, 51–54. https://doi.org/10.1038/111051a0

Silberschneider, V., Pease, B.C. & Booth, D.J. (2001). A novel artificial habitat collection device for studying resettlement patterns in anguillid glass eels. *Journal of Fish Biology*, 58(5), 1359-1370. https://doi.org/10.1111/j.1095-8649.2001.tb02292.x

Steele, K., Chadwick, S., Debney, A. & Gollock, M. (2018). Variation between European eel *Anguilla anguilla* (L.) stocks in five marshes of the Thames Estuary (United Kingdom). *Wetlands Ecology and Management*, 26(6), 1181-1188. https://doi.org/10.1007/s11273-018-9628-5

Tamario, C., Degerman, E., Donadi, S., Spjut, D., & Sandin, S. (2018). Nature-like fishways as compensatory lotic habitats. *River Research and Applications*, 34(3), 253–261. https://doi.org/10.1002/rra.3246

Tamario, C., Calles, O., Watz, J., Anders Nilsson, P. & Degerman, E. (2019). Coastal river connectivity and the distribution of ascending juvenile European eel (*Anguilla anguilla* L.): Implications for conservation strategies regarding fish-passage solutions. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29(4), 612-622. https://doi.org/10.1002/aqc.3064

Tesch, F.W. (2003). The eel, 5th Edition. Oxford, UK: Blackwell Publishing.

Thompson, M.S.A., Brooks, S.J., Sayer, C.D., Woodward, G., Axmacher, J.C., Perkins, D.M. et al. (2018). Large woody debris "rewilding" rapidly restores biodiversity in riverine food webs. *Journal of Applied Ecology*, 55(2), 895-904. https://doi.org/10.1111/1365-2664.13013

Verhelst, P., Reubens, J., Pauwels, I., Buysse, D., Aelterman, B., Van Hoey, S. et al. (2018). Movement behaviour of large female yellow European eel (*Anguilla anguilla* L.) in a freshwater polder area. *Ecology of Freshwater Fish*, 27(1), 471-480. https://doi.org/10.1111/eff.12362

Walker, A.M., Godard, M.J. & Davison, P. (2014). The home range and behaviour of yellow-stage European eel *Anguilla anguilla* in an estuarine environment. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24(2), 155–165. https://doi.org/10.1002/aqc.2380

Warry, F.Y., Reich, P., Hindell, J.S., McKenzie, J. & Pickworth, A. (2013). Using new electrofishing technology to amp-up fish sampling in estuarine habitats. *Journal of Fish Biology*, 82(4), 1119-1137. https://doi.org/10.1111/jfb.12044

Wood, S. (2017). Mixed GAM computation vehicle with automatic smoothness estimation. Vienna, Austria: R Foundation for Statistical Computing. Accessed at: https://cran.r-project.org/web/packages/mgcv/mgcv.pdf [15 December 2021]

Zalewski, M., Cowx, I., (1989). Factors affecting the efficiency of electric fishing. In: Cowx, I.G., Lamarque, P. (Eds.) *Fishing with Electricity Applications in Freshwater Fisheries Management*. Oxford, UK: Blackwell Scientific Publications, pp. 89–111.

Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3-14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

Tables:

Table 1. Summary of total length (mm) and weight (g) of European eels, from three habitat types in the River Glaven catchment, tagged with acoustic or Passive Integrated Transponder (PIT) tags during the period 21 May to 20 September 2018. Standard errors associated with mean measurements are provided in parentheses.

		Acoustic & PIT-tagged					PIT-tagged only				
Habitat type	**No. sites**	***n***	**Mean length (mm)**	**Length range (mm)**	**Mean weight (g)**	**Weight range (g)**	***n***	**Mean length (mm)**	**Length range (mm)**	**Mean weight (g)**	**Weight range (g)**
Paludal	5	28	377.8 (13.6)	310–549	113.6 (15.6)	45–307	47	291.6 (9.1)	163–523	79.8 (25.0)	7–327
Lotic	6	25	372.9 (16.5)	263–563	93.7 (13.4)	22–262	66	224.5 (6.5)	123–366	19.6 (1.8)	3–59
Lacustrine	3	23	592.8 (20.6)	368–804	418.4 (45.5)	84–1101	26	401.3 (24.4)	206–661	169.6 (38.5)	14–612
Overall	**14**	**76**	**441.3 (15.0)**	**263–804**	**204.3 (23.6)**	**22–1101**	**139**	**280.3 (8.4)**	**123–661**	**55.6 (9.9)**	**3–612**

Table 2. Summary of survey effort, total catch data and derived density and Catch-Per-Unit-Effort (CPUE) estimates (standard errors in parentheses) of European eels caught in contemporary point abundance sampling (PAS), continuous electric fishing runs along the littoral margin and fyke net surveys of different habitats.

Habitat type	Electric fishing								Standard fyke nets			
	n surveys	PAS				Continuous littoral runs						
		Total *n* points	*n* eels	Mean density (ind. m^{-2})	Mean biomass (g m^{-2})	Total run length (km)	*n* eels	Mean CPUE (per m margin)	*n* surveys	Total net ends	*n* eels	Mean CPUE (per net end)
Paludal	4	216	2	0.008 (0.001)	0.343 (0.029)	0.42	9	0.021 (0.006)	25	218	94	0.418 (0.088)
Lotic	40	1,951	53	0.020 (0.001)	0.462 (0.022)	4.81	114	0.023 (0.004)	7	120	7	0.124 (0.069)
Lacustrine	16	1,491	20	0.005 (0.0003)	0.695 (0.036)	5.71	57	0.007 (0.003)	37	437	41	0.155 (0.049)
Total	60	3,663	75	0.015 (0.001)	0.516 (0.018)	10.93	180	0.019 (0.003)	69	775	142	0.247 (0.044)

Table 3. Indicative relative abundance estimates (and 95% confidence intervals) of European eel for the three catchment habitat types surveyed. Estimates were derived from mean densities (ind. m^{-2}) and associated confidence intervals (CIs) derived from the latest point abundance sampling (PAS) at each independent site, multiplied by the estimated surface area of each habitat. Coefficients of variation (CVs) associated with the mean estimates are provided for reference. A total catchment population size was calculated by combining density estimates for individual habitats weighted according to the area contributed to the total available habitat.

Habitat type	Estimated area (m^2)	*n* surveys	Mean density (ind. m^{-2})	CV (%)	Relative population (ind.)
Paludal	681,488	4	0.008 (0.009)	57.8	5,452 (±5,983)
Lotic	151,274	30	0.020 (0.014)	35.3	3,025 (±2,143)
Lacustrine	325,525	16	0.005 (0.006)	57.6	1,628 (±2,858)
All habitats	1,158,287	50	0.015 (0.009)	31.1	16,886 (±10,307)
Weighted estimate	1,158,287		0.009		10,425

Table 4. Summary of the top four ranked Generalised Additive Models (GAMs) used to investigate the effects of covariates on the probability of eel presence at a site. The covariates considered were sample method, point abundance sampling (PAS), continuous marginal electric fishing runs or catch-depletion electric fishing, site size, distance to the estuary (km) and distance to the main river (km). Model estimates, β coefficients (standard errors in parentheses) for parametric and estimated degrees of freedom (*edf*) for smooth splines, are presented with associated levels of significance.

Model rank	Parametric coefficients			Smooth terms (*edf*)			Weight	df	AIC	ΔAIC	UBRE
	Intercept	Fyke nets	PAS and marginal runs	s(log[site area])	s(dist. to estuary)	s(dist. to river)					
1	0.420 (0.227)			2.084***	2.681**		0.406	5	138.9	0.00	0.055
2	-0.464 (0.228)			2.413**	1.000***	1.707	0.314	6	139.4	0.52	0.059
3	1.157 (0.553)*	-1.134 (0.691)	-0.536 (0.711)	1.895**	1.000***		0.173	5	140.6	1.71	0.068
4 (Full)	0.988 (0.701)*	-1.032 (0.704)	-0.704 (0.751)	1.899**	1.000***	1.419	0106	7	141.6	2.69	0.073
Null	0.418 (0.179)*						0.000	1	178.0	39.16	0.055

Note. Abbreviations: AIC: Akaike's information criteria; UBRE: unbiased risk estimator.

Significance levels *P* <0.05 *, *P* <0.01**, *P* <0.001***

Table 5. Results of Fisher's exact tests of independence (*P*-values) based on occurrence of eels (of all sizes or divided into length classes of ≤ 160 or > 160 mm) in point abundance sampling (PAS) points with varying habitat characteristics in lotic and marginal lacustrine habitats. Significant *P*-values (*P* < 0.05 threshold) are highlighted in bold.

	Lotic			Lacustrine margins
Habitat characteristic	**All eels**	**Eels ≤160 mm**	**Eels >160 mm**	**All eels**
Large substrate dominant	0.211	0.378	0.067	**0.004**
Coarse substrate dominant	0.065	0.096	0.527	0.711
Fine substrate dominant	0.220	0.066	1.000	0.374
Solid substrate dominant	1.000	1.000	0.417	1.000
Water depth	**0.004**	**0.012**	0.122	0.844
Flow (surface velocity)	0.280	0.234	0.638	NA
Submerged plant	**0.003**	**<0.001**	0.723	0.720
Emergent plant	0.263	0.579	0.528	0.618
Floating plant	0.214	0.673	0.215	1.000
Filamentous algae	0.512	0.396	0.180	0.873
Benthic litter	0.148	0.671	0.053	0.587
Large woody material	**0.008**	1.000	**<0.001**	0.124
Overhanging vegetation	0.051	0.980	**<0.001**	**0.005**
Canopy cover	0.203	0.140	0.872	0.428

Table 6. Summary of eel detection rates associated with different tags and across different habitats including numbers of eels detected exhibiting characteristic net downstream (D/S) movements, movements into the estuary or no recorded movements (only subsequently detected at the tagging location). Note that three lotic and one lacustrine eel showed net downstream movement and were subsequently recorded moving into the estuary.

Tag location	Tag type (number of eels tagged)	Detection rate (ind.)	Length range (mm)	Percentage of detected eels showing different types of movement (ind.)		
				No detected movement	Net D/S freshwater movement	Moved into estuary
Lotic	PIT only (66)	12.1% (8)	163–366	0% (0)	100% (8)	
	Acoustic & PIT (25)	32.0% (8)	308–482	12.5% (1)	50% (4)	37.5% (3)
Lacustrine	PIT only (26)	15.4% (4)	425–547	0% (0)	100% (4)	
	Acoustic & PIT (23)	82.6% (19)	368–804	94.7% (18)	NA	15.8% (1)
Paludal	PIT only (47)	2.1% (1)	324	100% (1)	NA	
	Acoustic & PIT (28)	57.1% (16)	310–549	56.3% (9)	NA	43.8% (7)
Combined	PIT only (139)	9.4% (13)	163–547	7.7% (1)	92.3% (12)	
	Acoustic & PIT (76)	56.6% (43)	308–804	65.1% (28)	9.3% (4)	25.6% (11)
Overall	All tags (215)	26.0% (56)	163–804	51.8% (29)	28.6% (16)	19.6% (11)
Length range (mm)				123–804	163–649	322–649

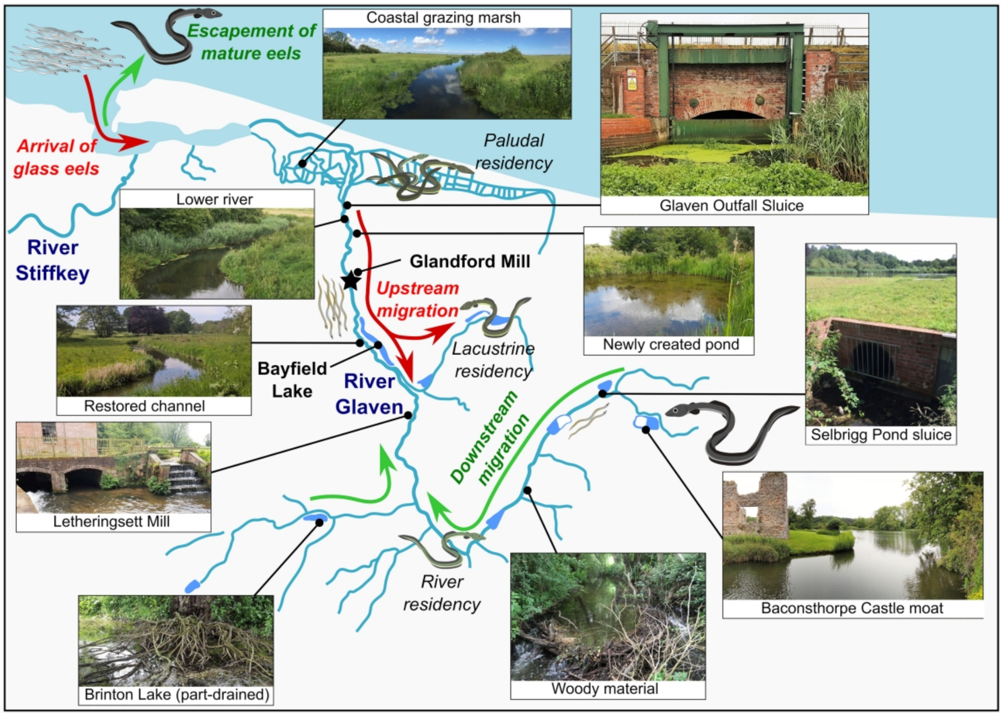

Figure 1. Stylised representation of the River Glaven catchment, illustrating some of the key processes and issues influencing European eels from arrival as glass eels, through upstream migration as elvers, general residency as yellow eels and escapement as mature silver eels.

249x177mm (300 x 300 DPI)

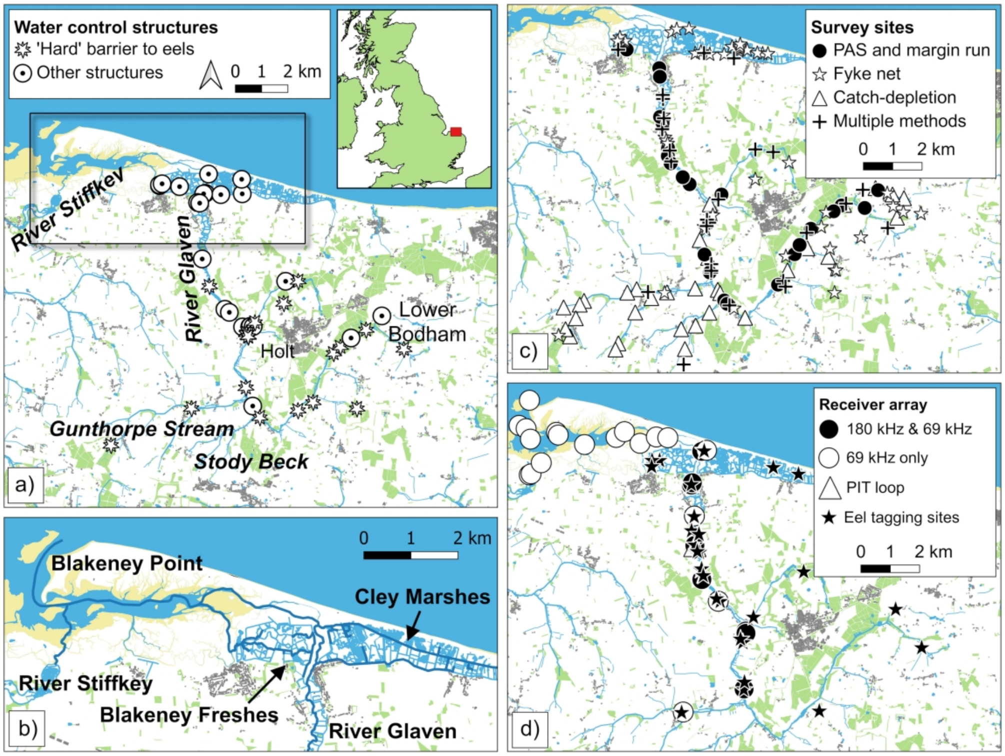

Figure 2. Overview of the study area, showing a) the River Glaven catchment, locations of water control structures and potential barriers to eel movements, b) the approach to the river and associated coastal marshes, c) independent sites sampled by point abundance sampling (PAS) and continuous electric fishing run of a littoral margin (n = 50), fyke netting (n = 69) and UK Environment Agency single run or catch-depletion electric fishing (n = 35), with n = 27 of the sites surveyed by multiple methods, and d) the telemetry array and eel tagging locations. Contains Ordnance Survey data © Crown copyright and database right 2021.

249x187mm (300 x 300 DPI)

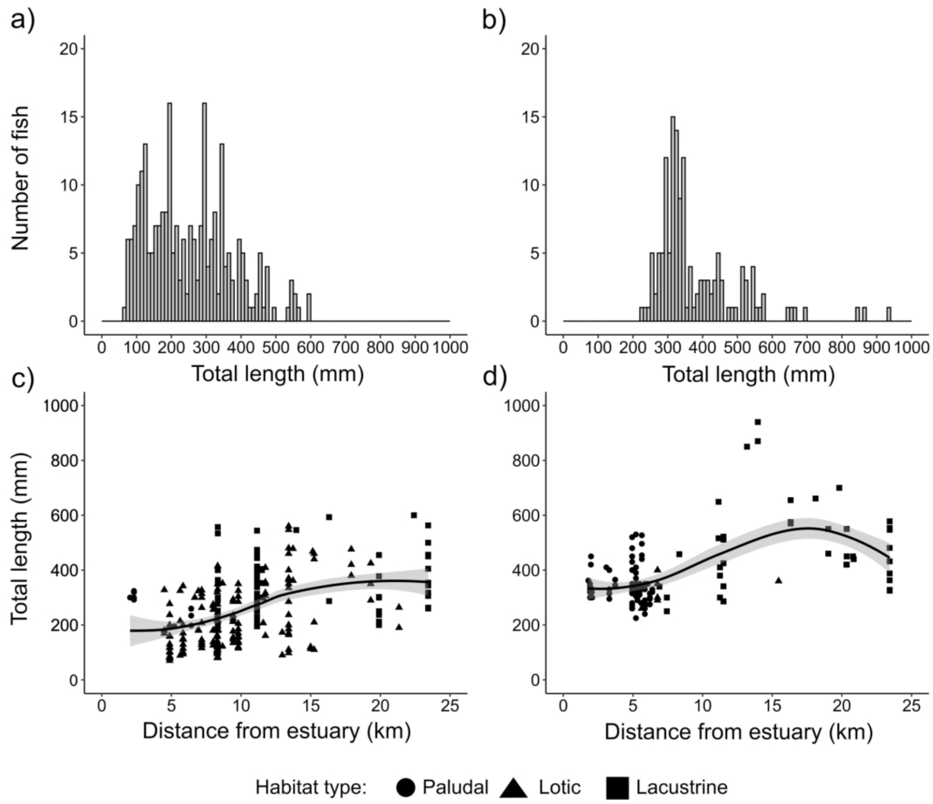

Figure 3. Variation in total length of eels captured during the study shown as the length frequency distributions (10 mm bins) derived from a) point abundance sampling (PAS) and continuous littoral margin electric fishing runs (*n* = 255), and b) fyke net sampling (*n* = 142); and according to distance from the estuary for eels in different habitat types sampled using c) PAS and continuous littoral electric fishing, and d) fyke nets. Smooth local regression (loess) lines have been fitted (span = 1) to highlight trends in length with distance from the estuary (shaded areas represent associated 95% confidence intervals).

199x163mm (300 x 300 DPI)

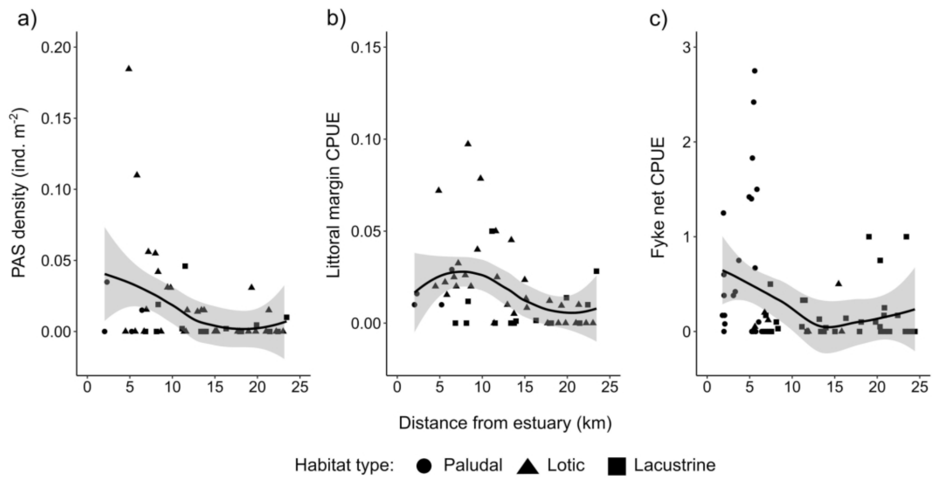

Figure 4. Variations in density (ind. m^{-2}) and Catch-Per-Unit-Effort (CPUE) estimates derived from a) point abundance sampling (PAS) (*n* = 50 sites), b) continuous littoral margin electric fishing runs (*n* = 50 sites), and c) fyke netting (*n* = 69 sites) with distance from the estuary and habitat type. Smooth local regression (loess) lines have been fitted (span = 1) to all data, with shaded areas representing associated 95% confidence intervals.

199x101mm (300 x 300 DPI)

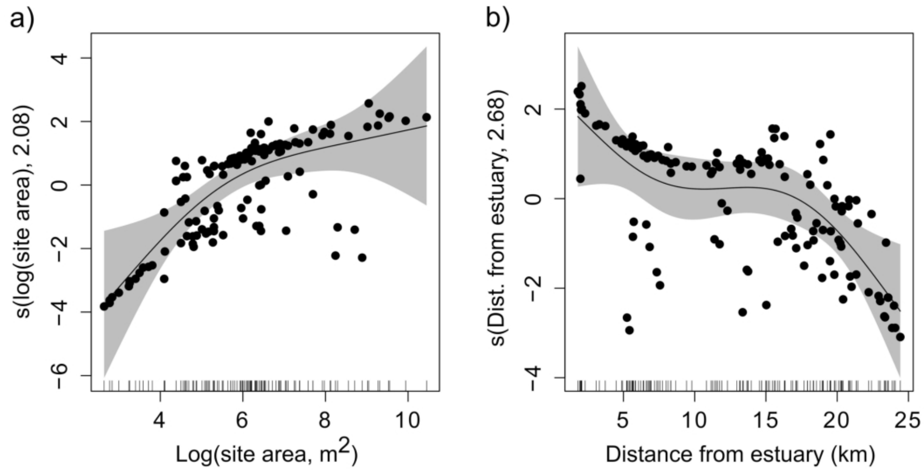

Figure 5. Results of the selected Generalised Additive Model (GAM) examining the probability of European eel presence within a site (n = 131). Figures show relationships (smooth functions) associated with a) log of site area (m^2), and b) shortest distance (km) along a watercourse to the estuary. Tick marks on the horizontal axis represent observed data. The y-axis represents log-odds centred on 0 which is equivalent to 50:50 chance of finding an eel in a survey. The solid line is the estimated smoother and the shaded areas represent 95% confidence intervals. Points represent the partial residuals for the model fits.

199x114mm (300 x 300 DPI)

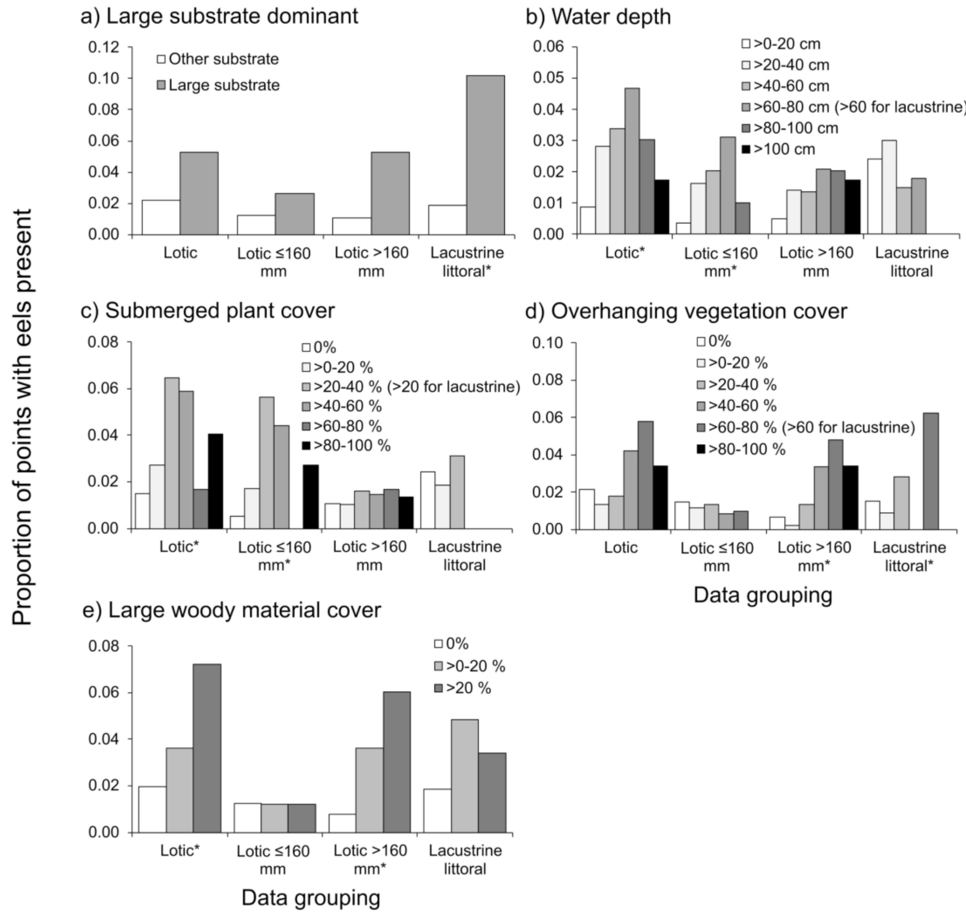

Figure 6. Variation in the proportions of point abundance sampling (PAS) points in lotic (also split for eels ≤ 160 mm and > 160 mm total length) and lacustrine (littoral margin alone) habitats recording the presence of eels according to key habitat characteristics (i.e. those that yielded at least one significant Fisher's test result): a) large substrate, b) water depth (cm), c) percentage cover of submerged plants, d) percentage cover of overhanging vegetation and e) percentage cover of large woody material. Data groupings yielding a significant Fisher's test result ($P < 0.05$ threshold) are indicated by an asterisk (*) alongside the label.

199x189mm (300 x 300 DPI)