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RESEARCH ARTICLE

# Variability in the duration and timing of the estuarine to freshwater transition of critically endangered European eel *Anguilla anguilla*

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**Abstract**
The European eel (*Anguilla anguilla* L.) is a critically endangered catadromous fish. Their inshore and in-river arrival as glass eel and elvers is an important stage of their life cycle, marking the transition from marine to freshwater habitats. Considerable knowledge gaps remain on the temporal and spatial patterns of this transition period to freshwater residency. Stable isotope (SI) analysis ($\delta^{13}C$, $\delta^{15}N$) was used to assess the timing and duration of the marine to freshwater transition among glass eels and elvers migrating upstream of the weirs at, or just upstream of, the tidal limit of four English rivers. (Parrett, Frome, Piddle, Chelmer). Variability in SI was low in the Parrett and Frome, resulting in narrow isotopic niches, but was high in the Piddle and Chelmer, resulting in wider niches. The Parrett and Frome data were then used to train a discriminant function analysis (DFA) model to classify eels as 'marine', 'freshwater-established' and 'transitioning'. When applied to the Piddle and Chelmer eel SI data, only a small proportion of eels were classified as marine and transitioning, with most being freshwater established. These results suggest that most eels present in the lower reaches rivers have been present for sufficient time for their SI values to represent feeding on local prey resources, with relatively few eels being newly arrived from the marine environment. The transition of eels from marine to freshwater in this species can therefore be prolonged, with many ascending rivers at least one winter after their initial arrival.

**Keywords** Anguillid · Stable isotope analysis · Critically endangered · Glass eel · Elver · Freshwater · Estuary

## Introduction

Species with complex life histories often exhibit ontogenetic distribution shifts and exploit a wide range of habitats across their lifecycle (Hobbs et al. 2019). For many fish species, the ability to select environments that provide the functional habitats necessary at each life stage is important to maximise their fitness (Kristensen et al. 2019). This is particularly important for diadromous species, whose movements between marine and freshwater environments involve trade-offs between their ability to gain greater body mass via accessing new and profitable feeding grounds versus the elevated predation risks and energetic costs of moving to these areas (e.g. Jensen et al. 2019). These risks and costs might be elevated in situations where accessing the new feeding grounds requires movements across complex environments over extended time periods (Arai 2020, 2022).

The European eel (*Anguilla anguilla* L.) is a facultative catadromous fish with a complex life history involving oceanic migration to continental habitats as larvae, continental migration as juveniles and oceanic migration back to spawning grounds as adults (Arai 2022). Following adult spawning in the Sargasso Sea, leptocephalus larvae migrate to European coastlines where they metamorphose into post-larval, non-pigmented eels, referred to as 'glass eels' (< 80 mm) (Tesch 1980; Cresci 2020; ICES 2022). To commence their continental migration, glass eels must cross the continental

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shelf into coastal waters, where there is high variability in their habitat use as individuals use marine, brackish and/or freshwater (Arai 2022). As individuals move into brackish and then freshwater, they begin to develop a pigmentation and are often referred to as pigmented glass eels (< 80 mm) before developing into elvers (81–120 mm) and then yellow eels (Tesch 1980; Cresci 2020; ICES 2022). They remain as yellow eels until the commencement of their oceanic migration back to the spawning grounds as silver eels (Schmidt 1923; Righton et al. 2016).

Glass eels use currents and passive tidal transport to move upstream into brackish and freshwater environments (Gascuel 1986; Laffaille et al. 2007). The duration of this transition period between saline and freshwater can be variable, as some glass eels move into freshwater relatively quickly, while others remain in estuarine or coastal waters for extended periods (Bardonnet and Riera 2005). Although the feeding ecology and habitat preferences of elver and yellow eel have received a great deal of attention (e.g. Harrod et al. 2005; Yokouchi et al. 2012; Denis et al. 2022), there remains uncertainty in the extent of their movements as they transition between brackish and freshwater environments (Elise et al. 2014). This is made more complex by the lack of available methods to track the movements of these early life stages, with the relatively small size of these life stages inhibiting the use of external or internal tags. However, natural chemical tags, especially stable isotopes (SI), have successfully been applied to eel trophic ecology, where the isotopic values of the eel tissues reflect the isotopic signature of their recent foraging areas, providing temporally integrated information on their resource and habitat use (e.g. Harrod et al. 2005). When bulk stable isotope analysis is used, the $^{13}C$ isotope is useful for discriminating between marine (enriched values, e.g. –19‰, –20‰) and freshwater habitats (depleted values, e.g. < 27‰) (Nolan et al. 2019). Stable isotope data are also influenced by the tissues analysed, with different tissues having contrasting isotopic turnover rates with, for example, dorsal muscle having a considerably longer isotopic turnover rate than blood and mucus (Vander Zanden et al. 2015; Hobson 2023).

With European eel assessed as critically endangered on the IUCN Red List (Jacoby and Gollock 2014; Pike et al. 2020), understanding their habitat use, feeding ecology and foraging behaviour throughout all life stages and distributions is crucial for their conservation and management (Feunteun 2002). The aim of this study was to assess the timing and duration of the marine to freshwater transition of non-pigmented (glass eel hereafter) and pigmented glass eels/pigmented eels (elver hereafter) in four rivers in England through an approach based on bulk stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$).

Using eel traps located on structures either at or just upstream of the tidal limit of each river, individuals migrating upstream of the structures in 2021 and 2022 were sampled, with $\delta^{13}C$ and $\delta^{15}N$ used to determine and predict their recent habitat use (i.e. marine versus freshwater), including the extent of variation within and between rivers.

## Materials and methods

### Sample sites

The movements of glass eels and elvers were assessed in four rivers located in eastern, southern and southwest England (Fig. 1). The River Frome (50.688533, –2.081004) is a lowland chalk stream located in southern England, which rises in central Dorset near Evershot and flows for approximately 70 km (Fig. 1). Eels were collected at a side-stream at East Stoke (50.679936, –2.185172), about 8 km upstream from the tidal limit at Wareham, where this tidal limit is 'soft' (i.e. there is not a hard barrier between the saltwater—freshwater zones, which vary according to tidal state and river flow). The River Piddle (50.688096, –2.124328) flows south-eastwards, roughly parallel to the Frome, before emptying into Poole Harbour, through which both rivers reach the English Channel (Fig. 1). As with the Frome, there is no hard structure marking the tidal limit. Eels were captured monthly from May to September 2021 by back-mounted electric fishing (LR-24, Smith-Root, Vancouver, WA, USA) in the River Frome and weekly by using a trap operated over 24 h periods on an existing elver pass on the River Piddle.

The River Parrett (51.047146, –2.883918) is located in southwest England and flows northwest through Somerset, before reaching its confluence with the Bristol Channel at Burnham-on-Sea, where it flows into Bridgwater Bay. Eels (Fig. 1) were captured once a month by installing monitoring traps over 24 h periods from March to June throughout 2021 and 2022 at Oath Lock (51.047094, –2.881561) and Huntspill Sluice (51.204015, –2.988507) (located on different channels), which are approximately 30 km and 5 km, respectively, from the Bristol Channel confluence. In both channels, the sluices represented a hard barrier between the upstream freshwater habitat and the tidal, brackish habitat downstream.

The River Chelmer (51.736099, 0.479800) is located in eastern England and flows for approximately 48 km from its source near Thaxted to Springfield Basin in Chelmsford, where it joins a number of other significant tributaries and rivers (Fig. 1). The Chelmer combines with Blackwater at Beeleigh Weir, near Maldon, discharging into the North Sea via the Blackwater Estuary (Fig. 1). Eels were captured once a month between March and September in 2021 and 2022 using monitoring traps over 24 h periods at Beeleigh Weir (51.743006, 0.662116), which is the tidal limit, with the weir separating the lower freshwater river from the upper estuary.

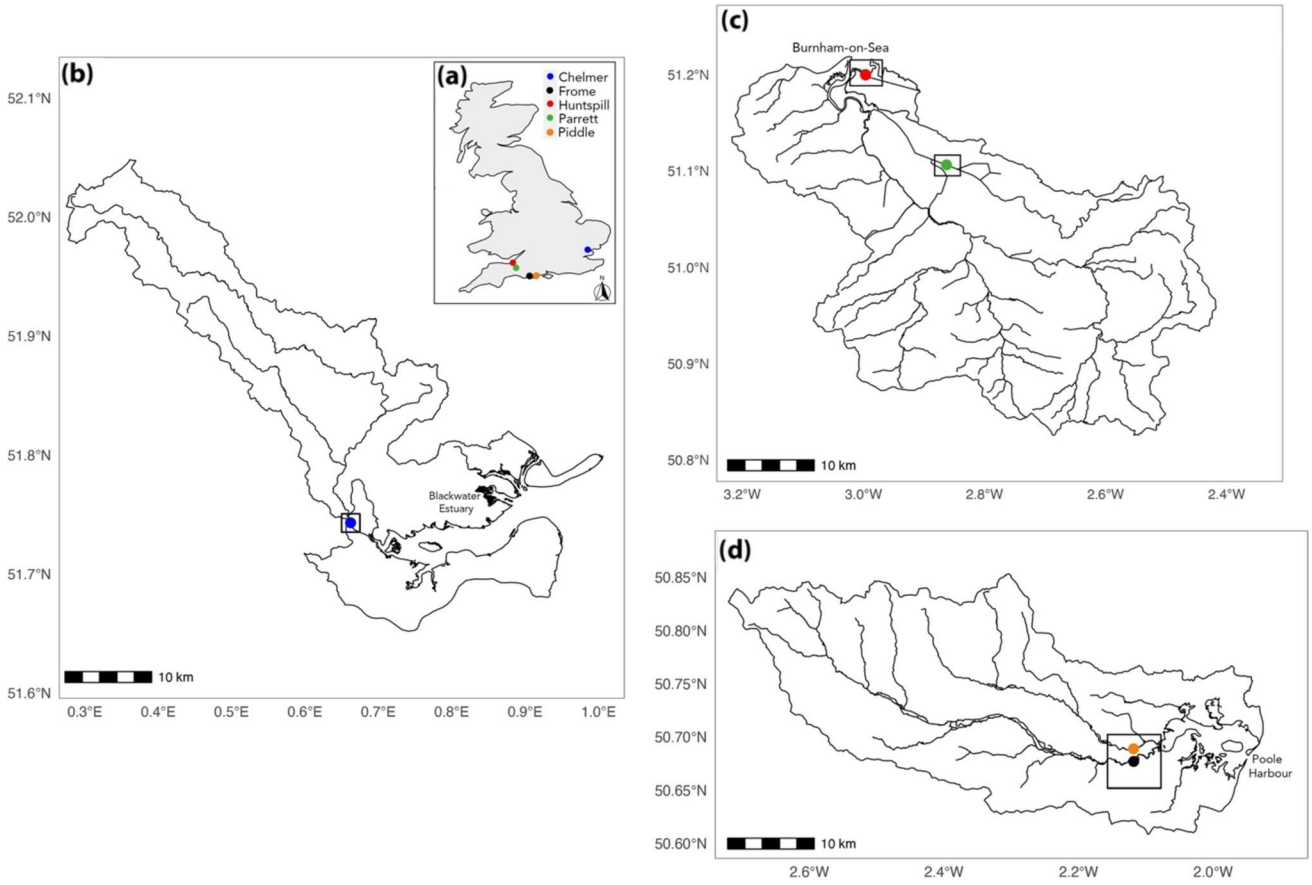


**Fig. 1** Location map of study sites with general location (**a**), the River Chelmer catchment (**b**) with the points representing the location of Beeleigh Weir (purple dot), the River Parrett catchment (**c**) with the points representing the location of Huntspill Sluice (red dot) and Oath Weir (green dot) and Poole Harbour catchment (**d**) with the points representing the location of Frome (black dot) and Piddle (orange dot)

## Data collection

After capture, the eels were counted and a subsample taken (maximum 30 per sampling occasion), which were euthanised (overdose of anaesthetic; MS-222). Individuals were transferred to small sample bags and transported to the laboratory on ice (except the River Chelmer, where samples were preserved in ethanol). Ethanol preservation does not significantly alter the $\delta^{13}C$ and $\delta^{15}N$ values of eel dorsal muscle (Boardman et al. 2022), and so no corrections to the SI data were required. Sampling permissions were through the Environment Agency (permit reference EP/EW027-C-042/19919/01), with eel sampling and euthanasia completed after an ethical review by the UK Home Office Project licence (P47216841).

In the laboratory, each eel was defrosted individually and measured [total length (TL), nearest mm], before a sample was taken for stable isotope analysis (SIA). For all eels except those from the River Chelmer, SIA was completed using epidermal mucus. The rationale for using mucus was that it generally provides insight into shorter-term dietary changes than dorsal muscle and fin (Church et al. 2009; Winter et al. 2019b), so is appropriate for assessing whether there have been recent changes in habitat use (i.e. marine to freshwater). As the River Chelmer samples had been preserved in ethanol, mucus samples were unable to be taken effectively, so dorsal muscle had to be used instead. Epidermal mucus was collected from individual eels by running a sterile coverslip along the length of one side of the eel before being transferred to a sample tube with no further treatment (Winter et al. 2019a; Winter and Britton 2021). For muscle, a sample of tissue was excised from the dorsal area. All samples were then dried to constant weight (60 °C for 48 h), before being bulk analysed for $\delta^{13}C$ and $\delta^{15}N$ in a Thermo Delta V isotope ratio mass spectrometer (Thermo Scientific, Waltham, MA, USA) interfaced to an NC2500 elemental analyser (CE Elantach Inc, Lake-wood, NJ, USA). Analytical precision of the $\delta^{13}C$ and $\delta^{15}N$ sample runs was estimated against an internal standard sample of animal material every ten samples, with the overall standard

deviation estimated at 0.08 and 0.04‰, respectively. With some C:N ratios exceeding 4.0, mathematical lipid correction was required (Post 2002), using the equation of Kiljunen et al. (2006). Non-normalised SI data summary statistics are provided in Supplementary Information: Table S1.

### Data and statistical analyses

Eel length and SI data were similar between years (2021–2022) at each site, with no significant differences in $\delta^{13}C$. Although $\delta^{15}N$ was significantly different this was likely due to the size of individual eel and not a reflection of temporal differences and so were combined for all subsequent analyses (Table S2). Inter-site differences in $\delta^{13}C$ and $\delta^{15}N$ of eels were evaluated using ANOVA, with Tukey post hoc tests identifying the site differences. The effect of sampling month and eel length on $\delta^{13}C$ and $\delta^{15}N$ were tested using generalised linear models (GLM; Gaussian distribution). Initially, the full model included the intercept, eel length and sampling month, with a backward stepwise approach used to select the best fitting model based on the lowest Akaike Information Criterion (AICc) value (corrected for small sample size), with model fit also assessed through visual examination of Pearson residuals plotted against fitted values and model covariates. To then assess the spatial and temporal variability in eel $\delta^{13}C$ and $\delta^{15}N$, site-specific data were grouped by month and the isotopic niche size estimated using standard ellipse areas (SEA) in the R package SIBER (Jackson et al. 2011), where each ellipse enclosed the core 90% of the SI data (Jackson et al. 2011). A Bayesian estimate of SEA ($SEA_B$) tested the differences in niche size between each site and month.

Predictions of the recent migration history were made for the rivers Piddle and Chelmer (which had the most extensive monthly sampling and where the eel samples were highly variable in their stable isotope values; cf. Results). These predictions were developed from the SI data and eel length data from the rivers Parrett and Frome. The glass eel life stage indicates a relatively recent metamorphosis from leptocephali and arrival into inshore areas (Miller et al. 2015), with only glass eels sampled from the River Parrett. Thus, $\delta^{13}C$ data from these eels were considered as representative of eels newly arrived from the marine environment ('marine'; –19.00 to –21.00‰; Table 1). The $\delta^{13}C$ data of some Parrett eels were also considered to represent eels transitioning from marine to freshwater (–21.00 to –24.00‰; Table 1). These values are typical of European eel in estuarine habitats, i.e. eels transitioning between the marine and freshwater environment (Bardonnet and Riera 2005). Conversely, all eels sampled from the River Frome were elvers, and compared with the other sites, relatively large (Table 1), plus were sampled in freshwater approximately 8 km from the tidal limit. Thus, their $\delta^{13}C$ data were considered as representing eels that had established in freshwater (< –25.00‰; Table 1). These $\delta^{13}C$ data were used as the basis of a discriminant function analysis model (DFA) developed in the MASS and klaR R package, where the DFA was trained using the rivers Parrett and Frome $\delta^{13}C$, $\delta^{15}N$ and eel length data to classify between newly arrived (i.e. marine), transitioning and freshwater-established eels. The model was then applied to classifying the individual eels from the Piddle and Chelmer into these three groups. The performance of the classification groups was assessed through cross-validation in which one individual is removed from the original matrix (jack-knife classification). All data analyses were conducted in R (2023) and prior to analyses, data were tested for normality (Shapiro–Wilks) and homogeneity of variance (Levene's test).

## Results

### Variation in $\delta^{13}C$ and $\delta^{15}N$ by site

Across both sampling years, the River Parrett eels were strongly and significantly enriched in $^{13}C$ and depleted in $^{15}N$ compared with other sites ($^{13}C$ ANOVA: $F_{3,625} = 318.21$, $P < 0.001$; $^{13}N$ ANOVA: $F_{3,625} = 93.17$, $P < 0.001$) (Table 1; Fig. 2). The most depleted $^{13}C$ values were in elvers from the River Frome, where the maximum value was –27.71‰. The highest $\delta^{13}C$ range was in the River Piddle (12.16‰) but was also relatively high for the River Chelmer (9.01‰) (Table 1). For $^{15}N$, the most depleted mean values were in River Parrett eels (6.91‰). Although mean $\delta^{15}N$ values

**Table 1** Sample size, stage (GE: glass eel; EL: elver) mean (±95% CI) and range (as minimum ('min') and maximum ('max') of total length ('length'), $\delta^{13}C$ (lipid corrected) and $\delta^{15}N$ for each site, where data are combined for 2021 and 2022

| River | *n* | Stage | Mean length ±95% CI (min, max) (mm) | Mean $\delta^{13}C$ ±95% CI (min, max) (‰) | Mean $\delta^{15}N$ ±95% CI (min, max) (‰) |
|---|---|---|---|---|---|
| Parrett | 73 | GE | 68 ± 0.93 (59–78) | –20.78 ± 0.21 (–25.65, –19.71) | 6.91 ± 0.40 (4.65, 12.29) |
| Chelmer | 199 | EL | 73 ± 0.79 (62–93) | –23.44 ± 0.30 (–28.44, –19.43) | 10.88 ± 0.38 (5.63, 16.30) |
| Piddle | 317 | EL | 78 ± 1.02 (61–129) | –29.24 ± 0.25 (–32.44, –20.28) | 10.66 ± 0.16 (5.01, 16.87) |
| Frome | 39 | EL | 98 ± 5.34 (68–124) | –28.82 ± 0.21 (–30.43, –27.71) | 11.98 ± 0.21 (10.17, 13.46) |

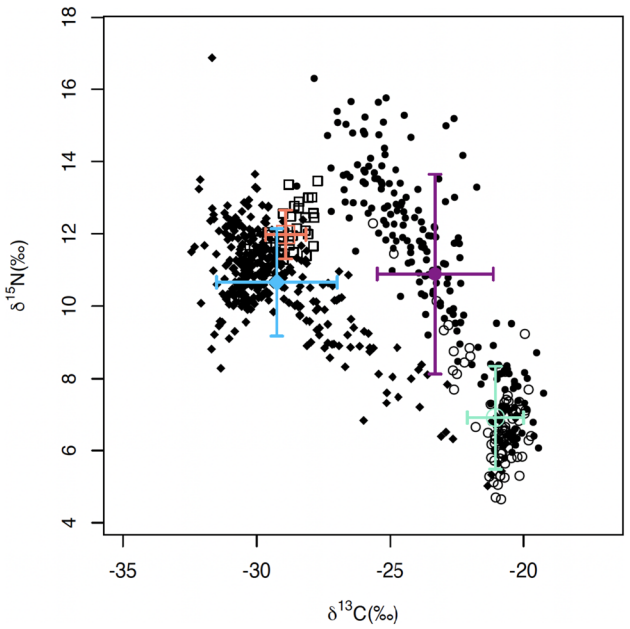


**Fig. 2** Stable isotope biplots for European eel for Parrett (clear circle), Chelmer (filled circle), Piddle (diamond) and Frome (clear square). Group means (coloured shape) and error bars represent the standard deviation for Parrett (green), Chelmer (purple), Piddle (blue) and Frome (orange)

were similar between the other three rivers, a proportion of the Piddle and Chelmer eels had $\delta^{15}N$ values similar to Parrett eels, but this was not evident in the Frome (Table 1; Fig. 2).

## Eel lengths versus temporal SI data

Eel TL ranged from 59 to 129 mm (mean $77 \pm 0.83$ mm) and differed significantly across all sites (ANOVA: $F_{3,625} = 120.01$, $P < 0.001$; Fig. 3). The smallest TLs were glass eels in the Parrett and largest for elvers in the Frome (Table 1). The best-fitting GLMs indicated that $\delta^{13}C$ and $\delta^{15}N$ values were significantly influenced by eel TL and sample month in the River Piddle (Table 2). Month and TL had no significant influence on $\delta^{13}C$ at the rivers Frome and Parrett, while $\delta^{15}N$ values were significantly influenced by TL in the River Frome, and month in the Parrett (Table 2, Table S3). For the River Chelmer, $\delta^{13}C$ values were influenced by TL and $\delta^{15}N$ by month (Table 2, S3).

## Temporal patterns in eel isotopic niche

Stable isotope biplots of eels from the rivers Piddle and Chelmer indicated distinct temporal patterns. Across both

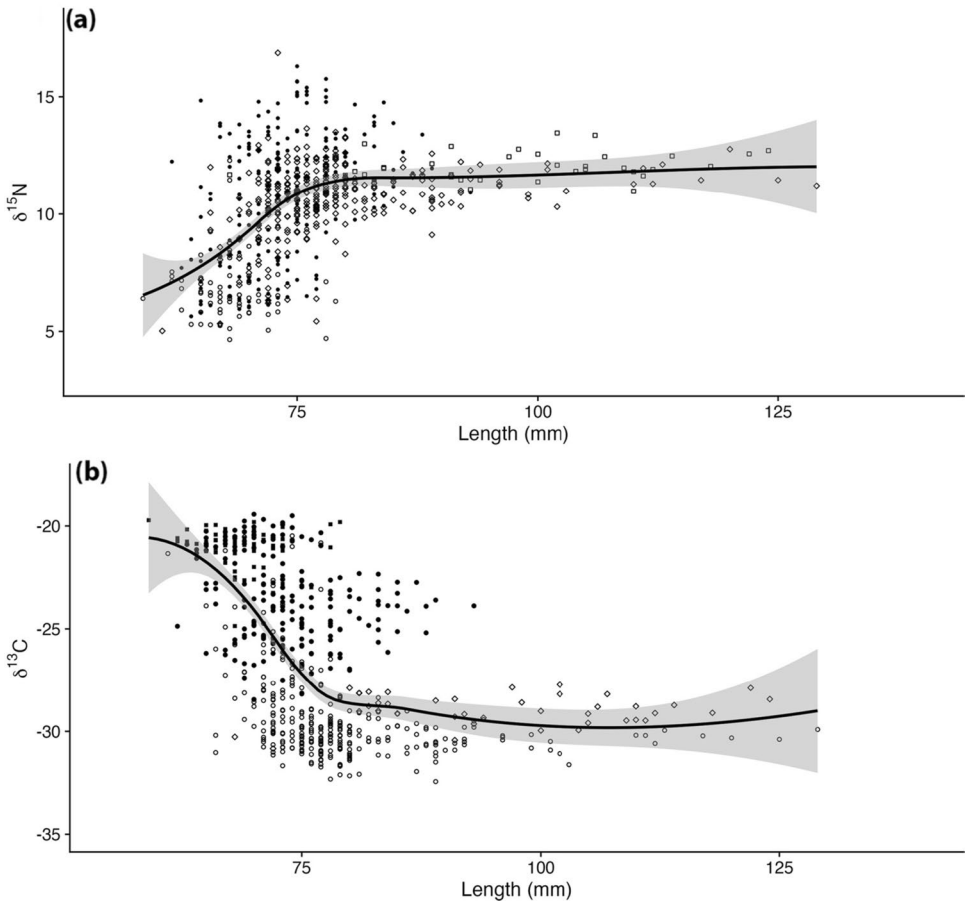


**Fig. 3** Non-linear relationships between eel length (mm) with $\delta^{15}N$ (**a**) and $\delta^{13}C$ (**b**) for Parrett (filled square), Chelmer (filled circle), Piddle (clear circle) and Frome (clear diamond), with 95% confidence intervals around the fitted values. The grey shading represents 95% confidence intervals

**Table 2** Summary of the retained coefficients in the most parsimonious generalised linear model (GLM), (with lowest AICc) predicting variation in **a** $\delta^{13}C$ and **b** $\delta^{15}N$ for each site

| River | Predictors | Estimate ± SE | *t* | *P*-value |
|---|---|---|---|---|
| (a) $\delta^{13}C$ | | | | |
| Parrett | (Intercept) | –8.58 ± 1.47 | –8.26 | < 0.001 |
| | ~Month | –0.13 ± 0.03 | –1.09 | < 0.29 |
| Chelmer | (Intercept) | –17.58 ± 0.44 | 39.68 | < 0.001 |
| | ~Length | –0.90 ± 0.06 | –13.66 | < 0.001 |
| Piddle | (Intercept) | –19.15 ± 1.38 | –13.82 | < 0.001 |
| | ~Length | –0.09 ± 0.01 | –7.52 | < 0.001 |
| | ~Month | –0.35 ± 0.11 | –3.16 | < 0.001 |
| Frome | (Intercept) | –29.96 ± 0.70 | 42.41 | < 0.001 |
| | ~Length | 0.10 ± 0.01 | 1.50 | 0.14 |
| (b) $\delta^{15}N$ | | | | |
| Parrett | (Intercept) | 4.95 ± 2.50 | 1.97 | < 0.05 |
| | ~Month | 0.72 ± 0.11 | 6.21 | < 0.001 |
| Chelmer | (Intercept) | 2.51 ± 0.46 | 5.36 | < 0.001 |
| | ~Length | 1.28 ± 0.06 | 18.45 | < 0.001 |
| Piddle | (Intercept) | 3.64 ± 0.90 | 4.01 | < 0.001 |
| | ~Length | 0.05 ± 0.01 | 6.81 | < 0.001 |
| | ~Month | 0.36 ± 0.07 | 5.08 | < 0.001 |
| Frome | (Intercept) | 10.18 ± 0.58 | 17.56 | < 0.001 |
| | ~Length | 0.18 ± 0.05 | 3.13 | < 0.001 |

sampling years, Piddle eels had a wide range of $\delta^{15}N$ and $\delta^{13}C$ values in May but with the isotope range narrowing by month up to September, whereas the opposite pattern was generally apparent in the Chelmer (Fig. S1). The overall isotopic niche size (as $SEA_B$) was largest for the River Chelmer, followed by the Piddle and was smallest for the River Frome (Fig. 4; Table 3), with the 95% posterior draws of $SEA_B$ indicating that the isotopic niches by month differ significantly for each river (Fig. 4; Table S4). River Piddle eels had a relatively large isotopic niche early on in the sampling season (May), with this niche then becoming significantly smaller in samples collected by September. Conversely, the smallest isotopic niche in the River Chelmer was in samples collected in May, with niche size being significantly larger in other months (Figs. 4; S4). The reduction in isotopic niche size over time in the Piddle was through the loss of $^{13}C$-enriched fish from samples collected throughout the summer, whereas in the Chelmer, the increase in isotopic niche size over time was through an increase in $^{13}C$-depleted fish (Fig. 4).

## Predicting recent eel movements

In the trained DFA based on Parrett (marine, transitioning) and Frome (freshwater established) eels, the first discriminant function ($\delta^{13}C$) explained most of the variation between the groups (98%) (Wilk's lambda $\lambda = 0.21$, $P < 0.001$) (Fig.

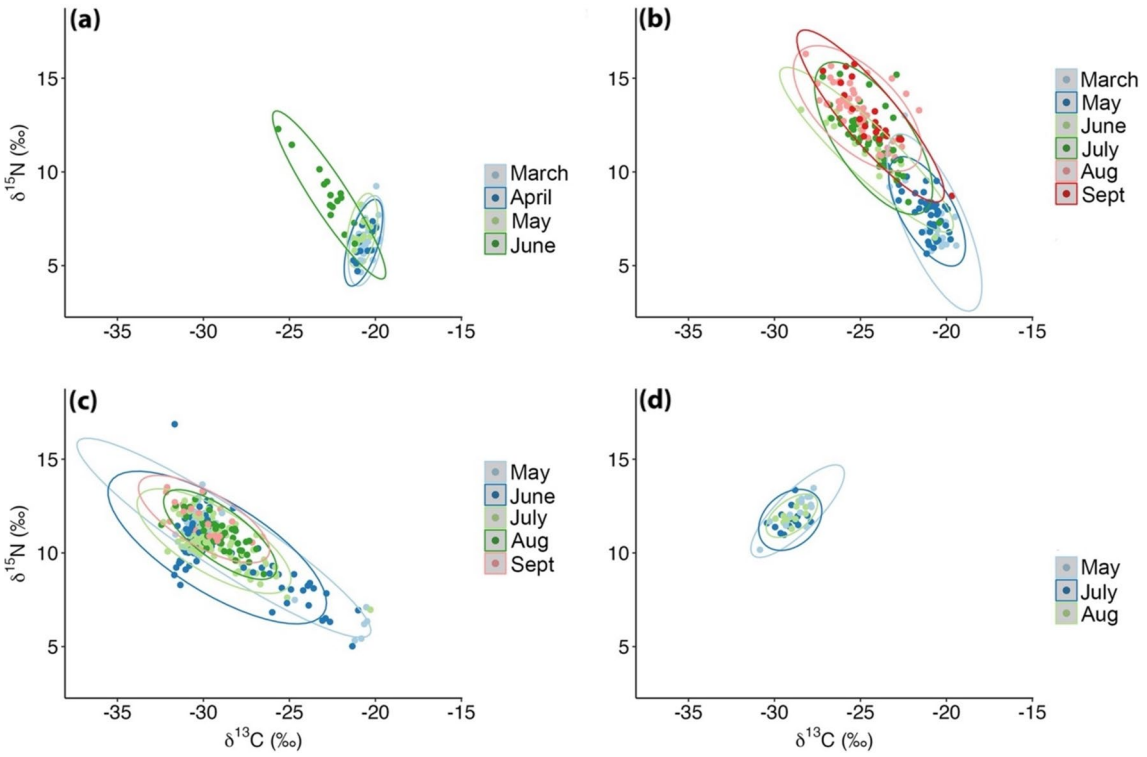


**Fig. 4** Stable isotope biplots for European eel by sites and month, where the standard ellipse areas (90% SEAc) are shown by sample month. **a** River Parrett, **b** River Chelmer, **c** River Piddle, **d** River Frome

**Table 3** Isotopic niche metrics for eel by site and groups (month). TA: the total area of the convex hull encompassing the data points; SEA: the standard ellipse area containing 90% of the data; $SEA_C$: correction applied to SEA to account for small sample sizes; Bayesian estimate for SEA ($SEA_B$) with 95% credible intervals

| Site | TA | SEA | $SEA_C$ | $SEA_B$ | 95% CI | Overlap with Parrett (%) |
|---|---|---|---|---|---|---|
| Parrett | 47.56 | 8.55 | 8.60 | 8.70 | 7.55, 10.00 | – |
| Chelmer | 63.47 | 6.71 | 6.73 | 6.69 | 6.01, 7.49 | 29% |
| Piddle | 17.13 | 3.41 | 3.46 | 3.44 | 2.72, 4.33 | 5% |
| Frome | 4.13 | 1.06 | 1.09 | 1.06 | 0.76, 1.47 | 0% |

**Table 4** Results of discrimination function analysis (DFA), where: (a) the results of the trained discriminant function model, showing the number and proportion (%) of eels in the River Parrett and Frome that were classified as marine, transitioning and freshwater established, where observed data were allocated by authors (according to SI data and eel length), and predicted and cross-validated (CV) allocated by the model; and (b) the number and proportion of eels sampled from the rivers Piddle and Chelmer predicted as marine, transitioning and freshwater established

| | Marine | Transitioning | Freshwater |
|---|---|---|---|
| (a) | | | |
| Parrett | | | |
| Observed *n* (%) | 49 (67%) | 23 (32%) | 1 (1%) |
| Predicted *n* (%) | 57 (78%) | 15 (21%) | 1 (1%) |
| CV *n* (%) | 55 (79%) | 15 (21%) | 0 (0%) |
| Frome | | | |
| Observed *n* (%) | 0% | 0% | 39 (100%) |
| Predicted *n* (%) | 0% | 0% | 39 (100%) |
| CV *n* (%) | 0% | 0% | 38 (100%) |
| (b) | | | |
| River | | | |
| Piddle predicted *n* (%) | 8 (3%) | 19 (6%) | 290 (91%) |
| Chelmer predicted *n* (%) | 50 (25%) | 102 (51%) | 47 (24%) |

S7). The observed versus predicted group classification of these eels had 79% agreement for the Parrett and 100% in the Frome (cross-validated) (Table 4). When the trained model was applied to the Piddle and Chelmer eels, a total of 65% were classified as freshwater established, 23% were in transition and only 11% were recently arrived from the marine environment (Table 4). The proportion of eels classified as from the marine environment and transitioning was higher in the Chelmer than the Piddle (Table 4).

In the River Piddle, eels classified as marine ranged from 61 to 76 mm (mean: 70 ± 4.19 mm) and were only present in samples between May and July (Table 5). The lengths of classified Piddle eels differed significantly between marine, transitioning, and freshwater established (ANOVA: $F_{2,314} = 11.19$, $P < 0.001$), with marine and transitioning eels being smaller than freshwater established (Tukey's post hoc tests: $P < 0.01$) but were not different between the marine and transitioning eels ($P = 0.99$) (Table 5). In the River Chelmer, eels classified as marine were 63–77 mm (mean: 70 ± 0.98 mm) and although these fish were present in samples collected between March and September, the majority were sampled in May (67%) (Table 5). Length also differed between the classified groups (ANOVA: $F_{2,196} = 15.78$, $P < 0.001$), with marine classified being significantly smaller than transitioning and freshwater established ($P < 0.01$), but

**Table 5** Mean total lengths ± 95% CI and length range, and the month when the highest proportion of eels arrived ('Main month') and range of month for eels predicted by the discriminant function analysis model as marine, transitioning and freshwater in each river

| River | Metric | Marine | Transitioning | Freshwater |
|---|---|---|---|---|
| Parrett | Mean length (range) (mm) | 68 ± 1.90 (59–79) | 69 ± 0.93 (65–76) | 68 mm[a] |
| | Main month (range) | April (March–May) | June (April–June) | June[a] |
| Frome | Mean length (range) (mm) | – | – | 98 ± 1.02 (68–124) |
| | Main month (range) | – | – | July (March–August) |
| Chelmer | Mean length (range) (mm) | 70 ± 0.98 (63–77) | 75 ± 1.65 (67–84) | 75 ± 1.10 (68–93) |
| | Main month (range) | May (March–September) | July (March–September) | July (March–September) |
| Piddle | Mean length (range) (mm) | 70 ± 4.19 (61–76) | 71 ± 3.93 (65–77) | 80 ± 1.06 (66–129) |
| | Main month (range) | June (March–July) | June (June–July) | July (May–September) |

[a]Only one individual so no variation to report

with no difference between transitioning and freshwater ($P = 0.93$).

## Discussion

Our study revealed significant differences in the $\delta^{13}C$ and $\delta^{15}N$ values of the eels both within and between sites, suggesting considerable individual variability in the timing and duration of their transition into freshwater. The DFA based on eel length, $\delta^{13}C$ and $\delta^{15}N$ accurately classified eels between the rivers Parrett (marine, transitioning) and Frome (freshwater established), with most of this variation explained by the $\delta^{13}C$ isotope. When applied to the Piddle and Chelmer eels, the model classified the majority of eels as freshwater established, followed by transitioning and then as recently arrived from the marine environment.

Eels captured from the River Parrett were strongly enriched in $^{13}C$, indicating recent arrival from the marine environment, given their $\delta^{13}C$ values were similar to those reported for eels feeding on marine particulate organic matter (Bardonnet and Riera 2005). The Parrett eels also exhibited low isotopic variability, suggesting minimal foraging on freshwater resources. Although the $\delta^{13}C$ data suggested that 'marine' individuals were present in all collected samples, no samples were collected after June due to low catches, which is consistent with other studies that suggest the peak arrival period of glass eels into Northern Europe is during May and June (Naismith and Knights 1988; Cresci et al. 2020).

The duration of the transition period between marine and freshwater habitats of glass eels and elvers can be from a few weeks to several years (Jellyman 1979; Sorensen and Bianchini 1986; Moriarty and Dekker 1997). In the River Parrett, eel movements from the marine to freshwater environment were considered as relatively rapid, given their enriched $^{13}C$ values, which suggested most had newly arrived from the marine environment. This contrasted to the eels in the Frome, whose relatively depleted $^{13}C$ values were similar to other freshwater fishes in that reach of river (Warren et al. 2023), indicating these eels had all been in freshwater for a considerable period. Conversely, both the Chelmer and Piddle samples comprised of eels with a wider range of lengths and SI values that were predicted by DFA as comprising of some marine and transitioning eels, but with most predicted as freshwater established, especially those sampled after June.

The DFA results suggested that most eels moving upstream into the rivers Piddle and Chelmer have already spent some time at upper estuary/freshwater boundary where they foraged on local prey resources that were relatively depleted in $^{13}C$ and enriched in $^{15}N$ versus their prey in the marine environment (Bardonnet and Riera 2005). As glass eels arrive into estuarine habitats, they undergo physiological and morphological changes, including development of pigmentation, jaws and teeth, which facilitates adaptation to their new environment and enables their exploitation of the novel prey resources (Tesch 1977; Cresci et al. 2020). Our data support the suggestion that the freshwater areas of tidal rivers are important foraging areas during this continental settlement period in the eel lifecycle (Bardonnet and Riera 2005). This period of residency in the lower reaches of rivers could enable eels to increase their energy reserves through foraging on locally abundant prey resources, which might then facilitate their subsequent upstream movements (Bureau Du Colombier et al. 2007).

Larger eels (> 415 mm) in the lower River Frome and in Piddle that were implanted with acoustic transmitters moved regularly between the freshwater and tidal reaches of the two rivers via Poole Harbour, with the movements being across a considerable salinity gradient and occurring over 24 h periods (Walker et al. 2013). Eels that settled initially into coastal lagoons in the Mediterranean remained in lagoons for 1–2 years before moving into freshwater (Panfili et al. 2012). Studies based on otolith microchemistry suggest that some eels settle into estuarine environments and remain there until they metamorphose into silver eels, with no use of freshwater environments at all (Tzeng et al. 1997; Daverat et al. 2006; Jessop et al. 2008; Bureau Du Colombier et al. 2011), while others make frequent movement back and forth between freshwater and marine systems (Tsukamoto and Arai 2001). Consequently, the patterns detected in the SI data of the smaller eels in the Piddle and Chelmer, where the majority of eels had values that were already based on freshwater prey resources, could have been making frequent small-scale movements in these lower river reaches prior to their capture. However, the small-scale movement ecology of these eels must remain speculative in the absence of any data on their actual movements.

Individuals classified as 'marine' in the River Piddle were only present in May and June, which suggests a relatively short period of eel immigration into Poole Harbour, with many of these eels considered as likely remaining in the lower, freshwater part of the River Piddle for their first winter before moving upstream during the following spring as water temperatures increase (and then being sampled). In contrast, 'marine' eels in the River Chelmer were present in samples—albeit in low proportions—throughout the summer. A range of factors have been shown to attract and direct eels to upstream freshwater habitats, including salinity gradients (Edeline et al. 2005b), tidal periodicity (Daverat and Tomás 2006), developmental stage (Crean et al. 2005) energetic status (Edeline et al. 2005a, 2006) and water temperature, with eels commencing upstream movements when water temperatures reach 15 °C (August and

Hicks 2008; Overton and Rulifson 2008). These temporal patterns highlight the dynamic nature of the habitat use of these eel life stages and suggest potential shifts in foraging strategies and resource availability throughout the season that have high context dependency on local conditions and habitat structure.

Although stable isotopes are considered a reliable tool to reconstruct animal movements at broad spatial scales (Hobson 2023), it is important to consider the issue of differences in isotopic turnover between different tissues, especially when inferring the movements of the Chelmer eels based on muscle. Tissues that exhibit a rapid response, such as mucus and blood plasma, provide insights into more recent feeding habits compared with bone and muscle, which have a slower turnover rate (Church et al. 2009; Ziegler et al. 2023). For instance, in rainbow trout (*Oncorhynchus mykiss*), the half-lives of $\delta^{13}C$ and $\delta^{15}N$ in mucus were 30 and 36 days, respectively, whereas, in muscle, they were 136 and 94 days (Church et al. 2009). In the American eel (*Anguilla rostrata*), the half-lives of $\delta^{15}N$ were 67 days in mucus and 191 days in muscle (Eberhardt 2019). Although measuring the residence times of eels was unable to be completed in our study, the mucus SI data for the Piddle, Frome and Parrett were considered to represent their diet in recent weeks, whereas for the Chelmer, the muscle SI data was likely to provide a longer temporal perspective. The use of different tissues between these two rivers is thus a study limitation, but one imposed by logistics that meant the Chelmer eels required preserving in ethanol that then prevented the effective collection of mucus samples. Nevertheless, in future studies, it is recommended that mucus is preferably used wherever possible for the SIA of eels due to its non-lethal application and ability to highlight relatively recent shifts in diet compared with dorsal muscle.

Our results provide valuable insights into the duration of eel transition from marine to freshwater environments, suggesting considerable variability between how individuals move through these habitats, with some individuals moving relatively quickly into freshwater at lengths up to 70 mm, while others at this size already have a strong freshwater SI signal. For eels that migrate up the River Piddle, they must first move through Poole Harbour, a complex environment of approximately 38 $km^2$ comprised mainly of shallow waters and extensive mud flats that are exposed during low tide, with a tidal cycle of high-water periods separated by a short period of slack water, followed by a single low-water phase (Walker et al. 2013). This complex environment might mean it take a considerable time for some newly arrived eels to move through the harbour, with them having to regularly seek refuge during low-water periods, such as in any remaining flooded sections (given adult eels tend to move into the deepest sections of tidal creek systems during daytime low tides Helfman et al. 1983). Remaining in the lower freshwater reach of the River Piddle for considerable periods before moving upstream might be thus advantageous for these eels, given there is a high diversity of habitats available that provide both refugia and foraging areas, with the tidal reaches of lower rivers often being highly productive for the foraging of juvenile fishes (Denis et al. 2022).

In contrast to the River Piddle, eels that moved into the River Parrett were entering a less complex system, where flood sluices represented the tidal limits of rivers with straightened channels, with such hard barriers known to significantly impact the migratory behaviour of fish through blocking their upstream movements (Piper et al. 2013; Wright et al. 2015). Given all Parrett eels moving upstream of the tidal sluices were glass eels and largely with marine SI values, we suggest these eels moved relatively quickly through the upper estuary, most likely using passive tidal transport given that the Bristol Channel has a relatively large tidal range, before facing a binary decision of remaining in the estuary or ascending the eel pass on the sluice to move upstream. SI values in both the Chelmer and Piddle exhibited greater heterogeneity, which suggests that the more complex environments in these rivers provided the newly arriving eels with a greater range of habitats to exploit than the Parrett, resulting in a high proportion taking advantage by settling (and foraging) there. While engineering lower rivers and regulating their tidal flows is advantageous for society, the resulting simplification of the freshwater–estuarine transitional zone reduces habitat complexity, likely resulting in the relatively swift movement of eels through what should otherwise be important habitats for settlement and early life history. Given that these tidal structures remain important for flood control, options to increase the habitat complexity of these rivers remain limited. Consequently, future management plans should ensure that barriers are fitted with eel passes to reduce the number of migrating eels that are facing delays in accessing freshwater habitats upstream that could provide higher habitat complexity and more profitable foraging areas. Estuarine habitats can provide diverse and productive foraging areas (Harrod et al. 2005) and thus many eels remain in these areas throughout their continental life stage (Arai 2022). This research highlights the significance of providing diverse and complex habitats for eels during their transition from marine to freshwater environments. Where possible, eel conservation management plans should also prioritise the protection and restoration of freshwater habitats, where the removal of migration barriers enable the free ranging of eels through the river system.

In summary, this study demonstrates considerable individual variability in the movements of glass eels and elvers into the lower reaches of four rivers in England. Where there was some habitat complexity in downstream areas, the eels migrating upstream were a mix of newly arrived, transitioning and freshwater established, whereas in the heavily

engineered River Parrett, they all had marine SI values. These results suggest that the upstream migration of eels into tidal and freshwater habitats is not uniform, highlighting the importance to provide eels with a wide range of settlement and over-wintering habitats wherever possible.

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**Data availability** Data are available from the corresponding author on reasonable request.

## Declarations

**Conflict of interest** All authors have no conflicts of interest to declare.

**Ethical statement** The study was completed following the gaining of all relevant ethical and legislative approvals (UK Home Office Project Licence P47216841; Environment Agency permit reference EP/EW027-C-042/19919/01.



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