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PRIMARY RESEARCH PAPER

Environmental influences on the phenology of immigrating juvenile eels over weirs at the tidal limit of regulated rivers

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Abstract Recruitment of the catadromous and critically endangered European eel *Anguilla anguilla* in Europe has declined substantially since the 1980s, with considerable knowledge gaps remaining in many aspects of their life cycle. The aim was to assess eel migration phenology in three regulated rivers in England between 2009 and 2019 through analyses of eel numbers using passes at their tidal limits, with calculation of the annual timings of migration initiation (10% of all eels passed, T_{10}), peak (50%, T_{50}) and conclusion (90%, T_{90}). Across the three rivers, T_{10} varied between Julian Day ('Day') 94 and 173. Years of earlier T_{10} had significantly earlier T_{50}, where T_{50} varied between Day 105 and 200. The considerable inter-annual variability in migration timings was associated with environmental variables; earlier T_{10} and T_{50} occurred in years of warmer river temperatures (RTs) and cooler sea surface temperatures (SST), and in years where RTs were higher than SSTs. No environmental variables were significant predictors of T_{90}. These results indicate that whilst there is annual variability in the timing of eel migration initiation and peak into freshwaters, this variability is predictable according to differences in environmental conditions. As many of these conditions associated with annual variability in temperature and precipitation then climate change has the potential to shift these migration timings.

Keywords Anguillid · Phenology · Migration · Red list species

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Introduction

Migration is an important component of the life history of many species, with movements between different habitats as a response to food availability, predation risk, and reproduction success (Brönmark et al., 2014). The timing of key life-history events (i.e. phenology) is often influenced by environmental triggers, where migratory fish species rely on a combination of factors (e.g. water temperature, light, and discharge) to initiate migratory behaviours (Tylianakis et al., 2008; Nagelkerken & Munday, 2015). Environmental changes can alter the initiation or duration of life-history events and in turn impact recruitment success (Botkin et al., 2007), population dynamics (Lowerre-Barbieri et al., 2019) and, ultimately, large-scale patterns of biodiversity (Tamario et al., 2019). In some species, high temperatures have been associated with shorter and earlier spawning periods as seen in, North Sea sole *Solea solea* (Fincham et al., 2013) and silver carp *Hypophthalmichthys molitrix* (Xia et al., 2021), whilst in cooler years, the winter spawning migrations of flounder *Platichthys flesus* were up to 2 months earlier (Sims et al., 2004).

Migration phenology is of critical importance for diadromous fishes for ensuring their arrival times in new habitats coincide with optimal conditions (Otero et al., 2014). Following the spawning of the catadromous European eel, *Anguilla anguilla* ("eel" hereafter) in the Sargasso Sea (Wright et al., 2022), the leptocephalus larvae drift in oceanic currents towards their growing habitats in European coastal and freshwaters (Lagarde et al., 2022). As these larvae enter coastal waters, they transform into elongated glass (non-pigmented) eel, and in more northern latitudes, enter estuaries from November to February (O'Leary et al., 2022). As temperatures start to rise, they develop pigmentation (Briand et al., 2005), and as temperatures increase to 9–11 °C many start actively migrating into freshwaters as glass/pigmented eels (< 80 mm) or elvers (> 80 mm) (Harrison et al., 2014). Following growth and maturity in freshwaters (for up to 50 years) (O'Leary et al., 2022), they migrate back to the Sargasso Sea to complete their life cycle (Van Ginneken & Maes, 2005). Due to substantial declines in their recruitment to European waters in recent decades, eel was listed as 'critically endangered' on the IUCN Red List of Threatened Species (Pike et al., 2020).

The complex life cycle of eel means that multiple factors can impact their populations, including barriers to migration (Moriarty & Dekker, 1997), overfishing (ICES, 2016) and novel parasite infection (Kirk, 2003). Their population declines may also be due to an alteration in the timing of their European arrival, which may determine the success of the transition from oceanic to estuarine and freshwater habitats (Tzeng et al., 2000). Factors that have been found to influence this transition include oceanic factors, such as the position of the North Atlantic Oscillation (NAO), inshore and estuarine temperatures (Martin, 1995; Edeline et al., 2006), river flow (Bolliet & Labonne, 2008), river temperature (Monteiro et al., 2023), and moon phase (O'Leary et al., 2022). In rivers in Southern Spain, short-term changes in glass eel density were partially driven by local environmental variables including rainfall, temperature, and turbidity (Arribas et al., 2012). Whilst in the River Shannon estuary in western Ireland, water temperature and moon phase were important drivers of glass eel immigration (O'Leary et al., 2022).

The importance of these environmental factors for the estuarine and freshwater entry of glass and pigmented eel suggests that there will be inter-annual variation in migration phenology that is associated with temporal differences in the key abiotic drivers. Understanding annual differences requires temporal phenological data to enable the assessment of influencing factors, yet many studies lack both spatial and temporal replication. For example, O'Leary et al. (2022) studied eel immigration in one estuary over two years, Lagarde et al. (2022) continuously assessed one lagoon over approximately 650 days, and Monteiro et al. (2023) assessed eel upstream movements in the Mondego River between 2017 and 2019. Conversely, here we use datasets collated over an 11-year period (2009–2019), where glass eel and pigmented eels were sampled at weirs representing the tidal limit of three regulated lowland rivers in England. These rivers are regulated due to the presence of weirs, which are principally constructed for water level management purposes. The objectives were to quantify the extent of inter-annual variability in eel migration phenology into these rivers, including the timing of both onset and peak arrival and to test the influence of abiotic factors including river temperature (RT hereafter), sea surface temperature (SST hereafter), river level and moon phase on these migration timings.

Methods

Study sites and sampling

Timing of eel immigration were analysed from the River Cary in Southwest England and the River

Chelmer and River Stour located in the East of England (Fig. 1). The River Cary (51.161, -2.990) is located in Somerset, southwest England and passes through King's Sedgemoor Drain, an artificial drainage channel. In mid-2008, two eel passes each consisting of an open-topped metal channel with bristle climbing substrate were installed at Greylake Sluice (51.133, -2.921) on King's Sedgemoor Drain ('Greylake' hereafter), located upstream of the tidal limit. Eels were recorded migrating upstream via remote monitoring (where cameras were installed on the eel pass and were operated between 8 pm and 6am from February to November. Migrating eels (primarily as non-pigmented glass eel) were then manually counted from recordings, with a total overnight number recorded.

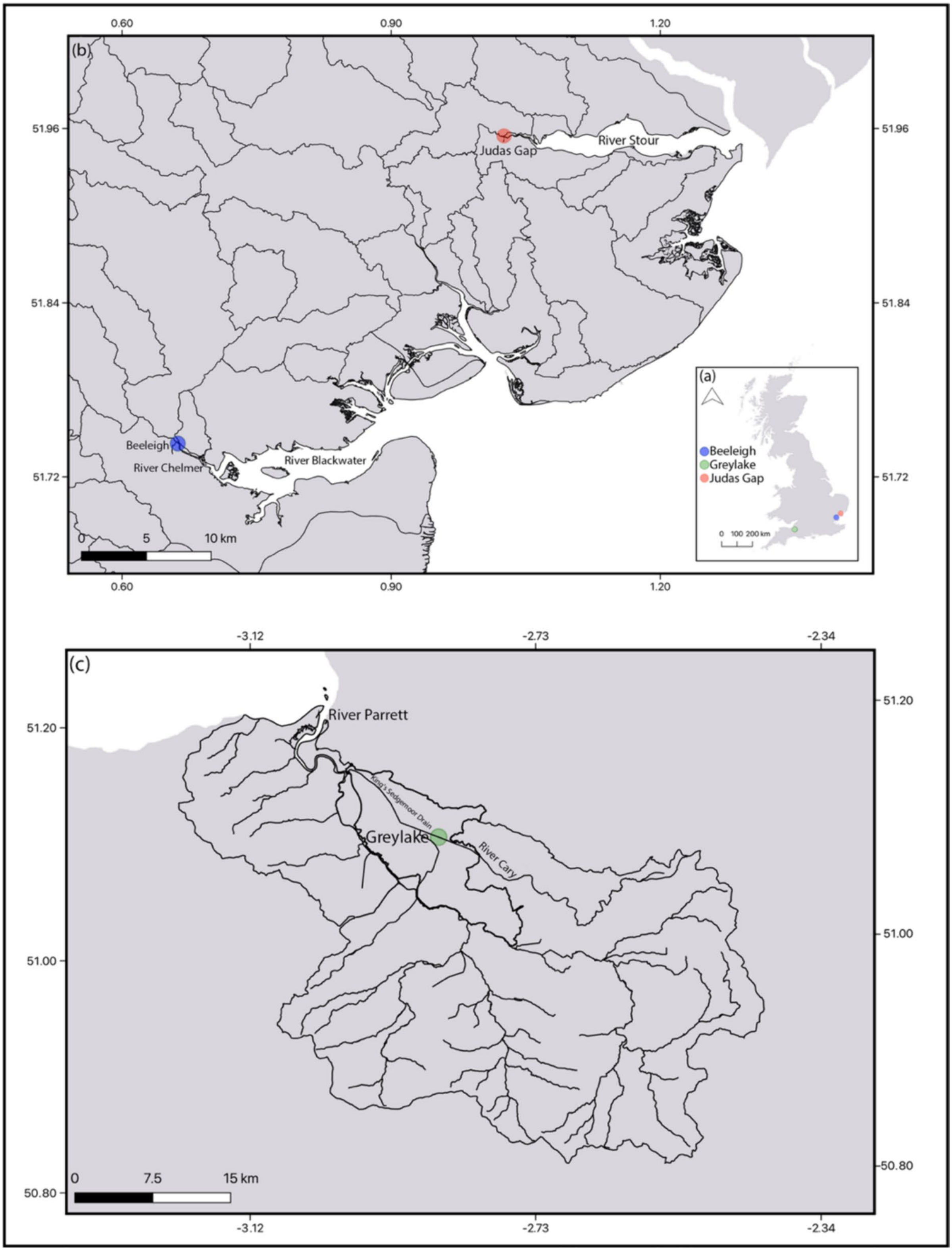
The River Chelmer (51.753, 0.594) is located in East Anglia, and combines with Blackwater at Beeleigh weir, near Maldon, discharging into the North Sea via the Blackwater Estuary. Eel sampling was carried out here each year between March and November. Eels (a mix of non-pigmented and pigmented) were captured by installing eel traps at Beeleigh Weir (51.744, 0.662), which represents the lower freshwater/saltwater limit ('Beeleigh' hereafter). The period between operating the monitoring box was up to 48 h, with additional checks within a 24 h period during spring tides and the peak migration season (May–June). Upon capture, individuals were counted (total count) and released to continue their upstream migration.

The River Stour (51.955, 1.160) a lowland river also located in East Anglia, flows eastwards for approximately 98 km from its source north of Haverhill, becoming tidal at Manningtree where it enters the estuary and joins the North Sea at Harwich. Upon arriving at the estuary, eels can pass over Judas Gap (51.954, 1.025), a 20.8 m wide, 1.8 m above ordnance datum Newlyn (AODN) concrete broad-crest weir, which represents the freshwater/saltwater limit. Monitoring was generally conducted at Judas Gap between April and November, employing the same method as at Beeleigh. In all rivers, the dataset was available for the period from 2009 to 2019 although no data were available for 2010 at Judas Gap. Due to logistical constraints, the eel surveys did not commence at the same time every year, with sampling at Judas Gap often not starting until May. Only a sub-sample of individuals were measured (total length), although most eels moving upstream at Greylake were non-pigmented (glass eel), whereas, at Beeleigh and Judas Gap, catches were a mixture of non-pigmented and pigmented eels.

Analyses on the temporal patterns of eel arrival into each river

Daily eel count data were used to determine the annual onset of migration (represented as the Julian day, when 10% of the eels have migrated T_{10}), the migration peak (represented as the Julian day, when 50% of the eels have migrated T_{50}), and the end of migration (represented as the Julian day, when 90% of the eels have migrated T_{90}). This was initially done on all of the data from each site per year, with these referred to as the unstandardised dataset (Supplementary Information: Table S1). However, at each site, the timing of the start and end of the sampling varied annually (Table S3). To enable valid comparisons of migration timings between years, a standardised annual dataset was developed (Table S2). This was to provide consistent start and end dates each year per site while accepting that some early and late migrating eels would be omitted from the dataset in some years.

The standardised datasets were developed by setting the start dates for the analysed data to be the latest start date across all years at each specific weir. For end dates, most sites stopped sampling and very few individuals were captured after September. The standardised end dates for all sites were the 30th of September and start dates were the 7th of April at Greylake, 3rd of April at Beeleigh and 20th of May at Judas Gap. Standardisation resulted in 0.12% of all sampled eels being removed from the Greylake dataset, 0.02% from Beeleigh, and 0.14% from Judas Gap (Figure S1). Following comparisons of unstandardised versus standardised values of T_{10}, T_{50} and T_{90}, the standardised datasets were used exclusively for the remainder of the analyses. For the number of eels recorded per day, the camera had some brief periods of downtime (Greylake), and the traps were not always emptied daily (Beeleigh and Judas Gap). This resulted in some periods having zero daily observations followed by large catches the following day.


(b)
Judas Gap
River Stour
Beeleigh
River Chelmer
River Blackwater
0 5 10 km
(a)
Beeleigh
Greylake
Judas Gap
0 100 200 km
(c)
River Parrett
King's Sedgemoor Drain
Greylake
River Cary
0 7.5 15 km

◂**Fig. 1** Location map of study sites with General location (**a**), Essex Catchment with the location of Beeleigh (blue circle) and Judas Gap weirs (red circle), (**b**) River Parrett Catchment with the location of Greylake weir (green circle) (**c**)

Environmental data

To test the influence of environmental factors on eel migration timings, daily river level data were obtained from the Environment Agency, from the monitoring stations closest to each weir. At Judas Gap, for water to flow over the weir to provide an attraction flow for eels to migrate, the river level has to be above the height of the weir crest (1.8 m above Ordnance Datum Newlyn (AODN). Accordingly, the height of the weir was subtracted from the daily recorded river level, which was input into the model as a categorial factor where "0" represented no flow (river level was below 1.8 m) and "1" represented flow (i.e. river level was above 1.8 m). For Greylake, SST was taken at Burnham-on-Sea, located 17 km from the River Cary, for Beeleigh, it was taken at Brightlingsea 30 km from the River Chelmer mouth and for Judas Gap, it was taken at Manningtree located 7 km from the River Stour mouth (www.seatemperature.info). These SST datasets were used to calculate daily mean SST across the study period. Moon phase for each day of the migration period was determined using the 'getMoonIllumination' function from the R package suncalc (Thieurmel & Elmarhraoui, 2019), where it was calculated as a as a fraction from 0.0 (new moon) to 1.0 (full moon).

The RT at Greylake was recorded daily using temperature loggers (TinyTag©) during 2013–2017. Temperature at Beeleigh and Judas Gap was recorded manually at the site when the trap was emptied, resulting in periods of missing temperature data. Local air temperature data taken from nearby weather stations (station 3853 located 24.67km from Greylake, 3683 located 13.44 km from Beeleigh and 3590 located 18.79 km from Judas Gap) were used to replace the days with missing temperature data (https://meteostat.net). A linear regression model tested the relationship between daily air and water temperature, with the `lag` function within the `dyn R package` incorporated into the model to test for any time delay; the Pearson correlation coefficient (r) evaluated the strength of the linear relationship as significant and defined the optimal time lag (Table S4). Because no water temperature was recorded throughout 2009–2012 and 2017–2019 at Greylake, optimal time lags could not be determined for each year, therefore the average time lag was calculated from years with available data. In total, 694 and 514 days of water temperature was missing and replaced with lagged local air temperatures at Beeleigh and Judas Gap, respectively, while 7 years of water temperature at Greylake was replaced with air temperature with a 1-day time-lag.

Data and statistical analyses

Differences in the number of migrating eels were tested between sites using ANOVA, with inter-annual variations in the timing of eel migration (as T_{10}, T_{50} and T_{90}) within each site then tested by linear regression (DoY as the response variable, year as the fixed effect). Linear regression then tested whether T_{10} could predict the timings of T_{50} and T_{90}. To test for the influence of environmental factors on T_{10}, T_{50} and T_{90}. Generalised additive models (GAMs; *gam* function in the *mgcv*) (Wood, 2017), with a Gaussian identity link distribution were fitted, where DoY was the response variable, and the explanatory variables were the environmental data outlined above. Prior to analyses, all variables were tested for normality and homoscedasticity (Shapiro–Wilk and Levene tests, respectively), and collinearity (Pearson's correlation). All variable combinations had $r < 0.70$ and were included in the model together (Figure S2, S3). As the number of eels migrating on any particular day could have been influenced by events before that day, RT for the 5-day period, SST, for the 10-day period and moon phase and river level for the 5-day period preceding the onset, peak and end were included in the final models. RT, river level, moon phase and year were included as smooth terms (s) (excluding Judas Gap where level was a factor) with a maximum of 4 knots, which was considered reasonable to avoid overfitting the models based on the amount of available data. Initial analysis found the relationship between the dependent variable and SST was linear, so this was included in the model as a parametric term. To investigate the potential effect of the difference between RT and SST on the onset of migration, a separate GAM model was constructed. This model included DoY as the response variable and the thermal difference (Temp_diff) as a smooth term.

To examine the factors affecting the daily number of migrating eels, GAM models with a Tweedie distribution because of the multiple zeros in the dataset (Wood, 2018). The response variable was the daily count of individuals, and the explanatory variables were the environmental data outlined above. The influence of SST, RT, river level, and moon phase were included as smooth terms (s) (excluding Judas Gap where level was a factor) with a maximum of 4 knots. To address year-to-year variations, a random effect was incorporated using a penalised regression term, specified as "bs = re" (Wood, 2004, 2017). Models were examined for the effects of autocorrelation in residuals by plotting the autocorrelation function (acf) (Venables & Ripley, 2002) from the R Stats package. Autocorrelation was detected in the initial model therefore a residual correlation structure (ar1) was added, improving the model fit (Figure S4). During the fitting of the GAMs for T_{10}, T_{50} and T_{90} and the daily number of migrating eels, model selection was performed automatically. This involved adding an additional penalty term to each smooth term, allowing penalisation to zero and enabling selection out of the model. The 'mgcv' package facilitates this process by utilising the argument select = TRUE in the gam () function (Wood, 2008). Any terms from the full model with estimated degrees of freedom less than 1 were subsequently dropped from the final model, as were any retained terms with *P* values > 0.05. To investigate the effect of the difference between RT and SST on the daily number of migrating eels a separate GAM model (Tweedie distribution) was constructed. This model included DoY as the response variable and the thermal difference (Temp_diff) between the two environments as a smooth term and year as a random effect.

Results

Environmental data

Over the study period, the average SST at Greylake was 15.08 °C, with the highest recorded in 2014 (15.87 °C) and the lowest in 2012 (14.16 °C). The average RT at Greylake was 15.49 °C, with the warmest year being 2014 (17.78 °C) and the coolest in 2012 (13.28 °C) (Figure S5–S7). At Beeleigh the average SST at Beeleigh was 15.55 °C, with 2018 being the warmest year (16.56 °C) and 2010 the coolest (14.61 °C) years. RT averaged 15.40 °C at Beeleigh, rising in 2018 (16.61 °C) and reaching its lowest in 2012 (14.46 °C) (Figure S5–S7). Whilst the average SST at Judas Gap was 17.01 °C, with the warmest year in 2019 (17.58 °C) and the coolest in 2013 (16.26 °C). The average RT was 17.99 °C and was highest in 2018 (18.76 °C) and lowest in 2012 (17.21 °C) (Figure S5-S7).

Unstandardised versus standardised datasets

Across all years in the unstandardised dataset, there were 256,272 eels recorded across Greylake Weir, 113,765 eels recorded as moving upstream over Beeleigh and 79,671 across Judas Gap Weir, with the annual numbers differing significantly between the rivers (ANOVA: $F_{2,28} = 5.10$, $P < 0.01$). The annual number of eels was highest in 2016 at Greylake ($n = 45{,}804$, 18%), 2013 at Beeleigh ($n = 33{,}382$, 30%), and 2012 at Judas Gap ($n = 17{,}174$, 22%).

Comparisons between the unstandardised and standardised datasets (Fig. 2) revealed a significant relationship ($R^2 = 0.89$). Differences in migration timings were relatively minor at T_{10}, where across the 32 years of data over the three sites, 21 years had no change and, in years where standardisation resulted in a shift in T_{10}, the mean change was 8 ± 4 days. For T_{50}, changes in migration timings occurred in 11 of 32 years, where altered timings were for a mean of 9 ± 3 days. For T_{90}, changes in the migration timings between the datasets were more substantial and although there were 24 of 32 years with no change, in years with altered timings, the mean change was 34 ± 7 days, where the primary change was the loss of very late migrating eels from the standardised dataset at Greylake Weir in 2013–2015.

Timing and numbers of migrating eel

Across the standardised datasets, T_{10} varied between DoY 94 and 176, T_{50} between 114 and 200, and T_{90} between 152 and 243 (Fig. 3). The timing of T_{10} was a significant predictor of T_{50}, where years of earlier T_{10} resulted in earlier T_{50} (linear regression: $R^2 = 0.55$, $F_{1,30} = 37.57$, $P < 0.001$), but with T_{10} not being a significant predictor of T_{90} ($R^2 = 0.07$, $F_{1,29} = 2.47$, $P = 0.12$). The timings of T_{10}, T_{50} and T_{90} were relatively consistent between years

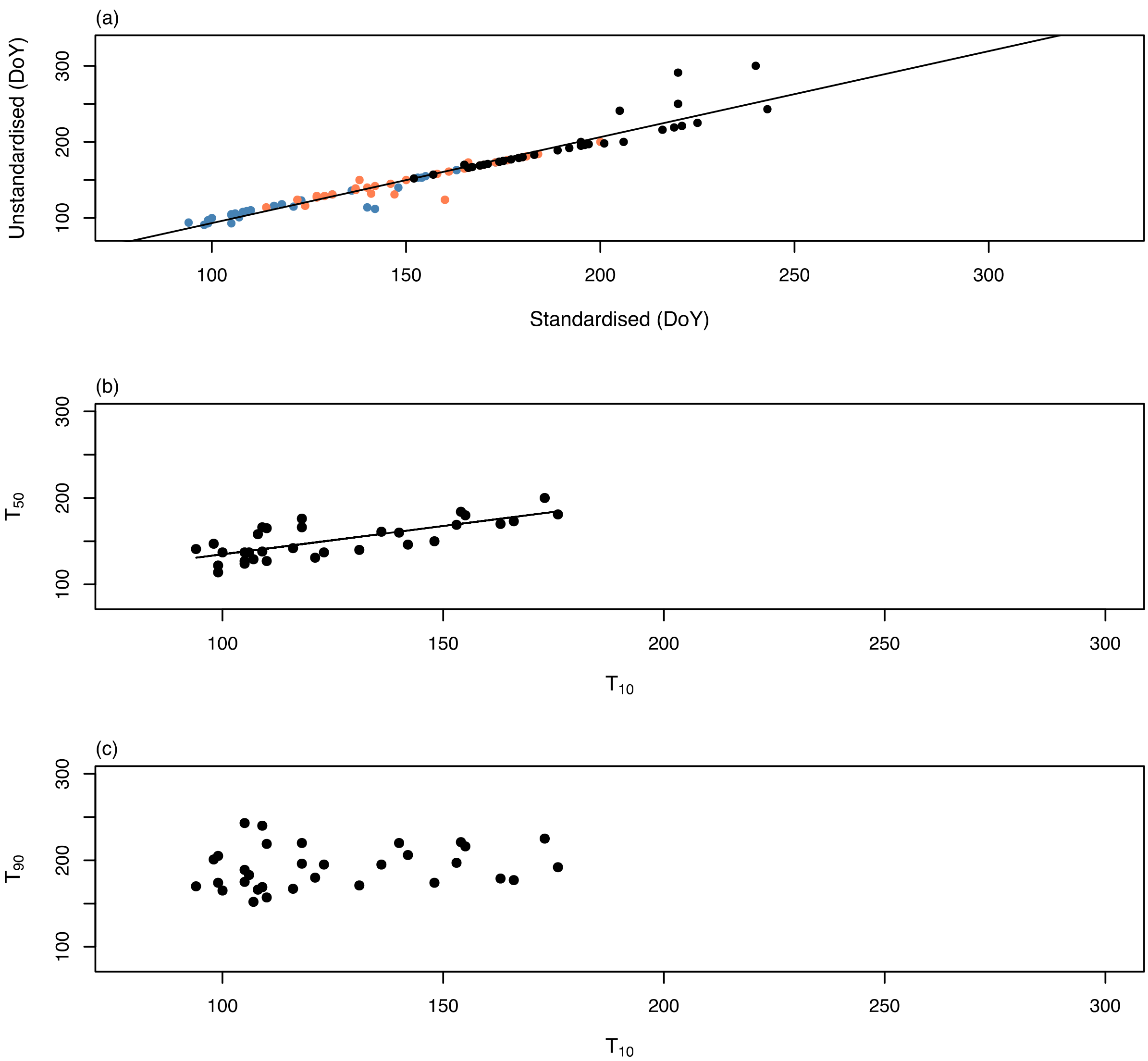


Fig. 2 **(a)** Comparison of T_{10} (blue circle), T_{50} (orange circle) and T_{90} (black circle) for combined data across the three weirs between the unstandardised and standardised datasets, where the solid line represents equality. **(b)** T_{10} versus T_{50} and **c** T_{90} across the datasets, where the bold line represents the significant relationships according to linear regression (cf. Results)

at Greylake and Beeleigh (Table 1, Fig. 3), with no significant annual differences (linear regression: Greylake, T_{10}: $R^2 = -0.10$; $F_{1,9} = 0.04$; $P = 0.82$; Greylake, T_{50}: $R^2 = 0.08$; $F_{1,9} = 0.85$; $P = 0.37$; Greylake, T_{90}: $R^2 = 0.04$; $F_{1,9} = 0.42$; $P = 0.53$; Beeleigh, T_{10}: $R^2 = 0.09$; $F_{1,9} = 0.95$; $P = 0.35$; Beeleigh, T_{50}: $R^2 = 0.13$; $F_{1,9} = 1.39$; $P = 0.26$; Beeleigh, T_{90}: $R^2 = 0.04$; $F_{1,9} = 0.40$; $P = 0.53$).

In contrast, at Judas Gap, there were significant differences in the annual timing in both T_{10} ($R^2 = 0.45$; $F_{1,7} = 5.82$; $P = 0.01$) and T_{50} ($R^2 = 0.57$; $F_{1,7} = 9.38$; $P < 0.001$), with a general pattern of individuals arriving earlier every year, with no significant difference in T_{90} ($R^2 = 0.19$; $F_{1,7} = 1.73$; $P = 0.22$) (Table 1, Fig. 3). At all sites, standardised T_{90} was rarely after DoY 200 (latest DoY 243). The migration period lasted 82 ± 20 days at Greylake, 67 ± 26 days at Beeleigh and 40 ± 23 days at Judas Gap.

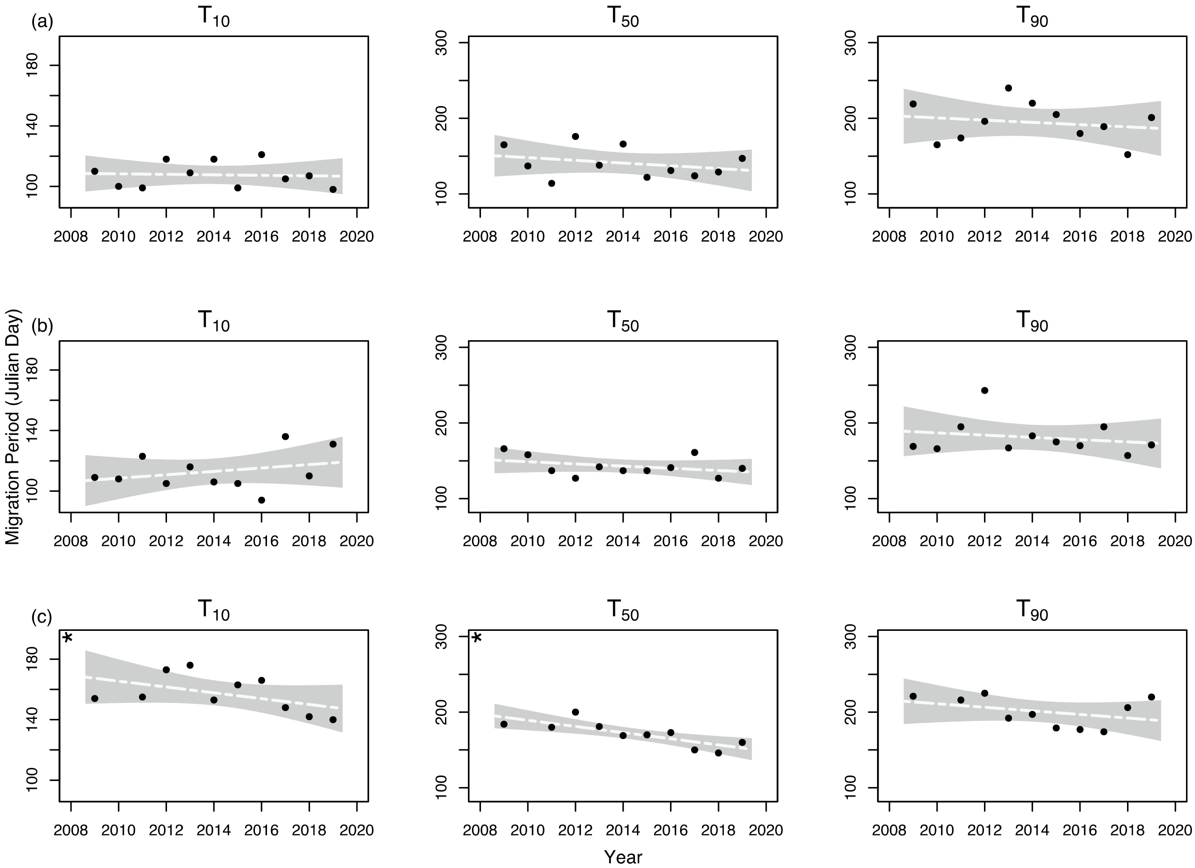


Fig. 3 The timing (Julian day) of eel migration at **a** Greylake (2009–2019), **b** Beeleigh (2009–2019) and **c** Judas Gap (2011–2019) described by the onset (T_{10}), peak (T_{50}) and end (T_{90}) of migration. May 21st is DoY 141. Data points are Julian days, shaded areas indicate the 95% confidence interval, and panels marked with an asterisk (*) represent a significant relationship between year and DoY

Table 1 Median (and range) arrival period, 10-day mean SST (± 95% confidence interval), 5-day mean RT (± 95% CI) and 5-day mean (± 95% CI) river level, on the T_{10}-T_{90} arrival period of eels at each site

Site/migration stage	Julian day	SST(°C)	RT (°C)	River level (m)
Greylake, T_{10}	108 (98–121)	12.25 ± 1.73 (9.60–16.01)	12.66 ± 0.73 (10.99–15.22)	3.44 ± 0.05 (3.29–3.50)
Greylake, T_{50}	140 (114–176)	12.47 ± 2.05 (9.30–15.20)	14.67 ± 3.07 (12.0–19.20)	3.54 ± 0.24 (3.42–3.49)
Greylake, T_{90}	190 (152–240)	17.48 ± 2.01 (12.00–20.40)	17.89 ± 3.01 (15.50–20.70)	3.46 ± 0.36 (3.26–3.52)
Beeleigh, T_{10}	113 (94–136)	9.54 ± 1.81 (6.91–13.01)	14.2 ± 1.77 (10.01–16.58)	0.13 ± 0.08 (0.01–0.20)
Beeleigh, T_{50}	143 (127–166)	13.35 ± 1.49 (9.89–16.81)	13.69 ± 3.15 (10.10–18.09)	0.10 ± 0.09 (0.03–0.37)
Beeleigh, T_{90}	195 (157–243)	17.27 ± 2.27 (15.97–20.35)	17.20 ± 2.49 (14.45–22.01)	0.10 ± 0.12 (0.01– 0.44)
Judas gap, T_{10}	157 (140–176)	15.20 ± 2.29 (12.60–15.70)	15.46 ± 1.29 (10.90–18.20)	1.83 ± 0.12 (1.55–1.91)
Judas gap, T_{50}	170 (146–200)	14.29 ± 1.07 (11.80–14.99)	16.74 ± 3.49 (12.50–21.10)	1.78 ± 0.12 (1.60–2.03)
Judas gap, T_{90}	200 (174–225)	18.29 ± 2.58 (16.07–21.41)	19.12 ± 3.07 (15.10–23.93)	1.80 ± 0.08 (1.57–1.90)

Influences on eel migration onset (T_{10}) and peak (T_{50})

The best fitting GAM testing environmental influences on the timing of T_{10} included RT as a significant effect (Table 2, Fig. 4), with eels arriving earlier when RTs were warmer at all sites. SST had a significant influence on T_{10} at Greylake and Beeleigh, where T_{10} occurred earlier when SSTs were cooler, but had no influence at Judas Gap. River level had a significant influence on T_{10} at Beeleigh and Judas Gap with eels arriving earlier when river levels were higher but had no influence at Greylake (Table 2, Fig. 4).

For T_{50}, RT was retained in the best fitting GAM at Judas Gap and Beeleigh, with earlier T_{50} in warmer years (Table 2, Fig. 5). Cooler SSTs coincident with earlier T_{50} at Greylake and Beeleigh but had no influence at Judas Gap (Table S5). Moon phase did not have any influence on the timing of eel migration and was not retained in the final model at any of the sites (Table S5). In contrast to T_{10} and T_{50}, no significant models were found for T_{90}, indicating that the environmental variables examined did not have a significant effect on this aspect of the migration period.

The temperature difference between RT and SST had no significant influence at Judas Gap but did have a significant influence on T_{10} at Greylake and Beeleigh, where migration generally occurred earlier when the RT was warmer than the SST (Table 2, Fig. 6).

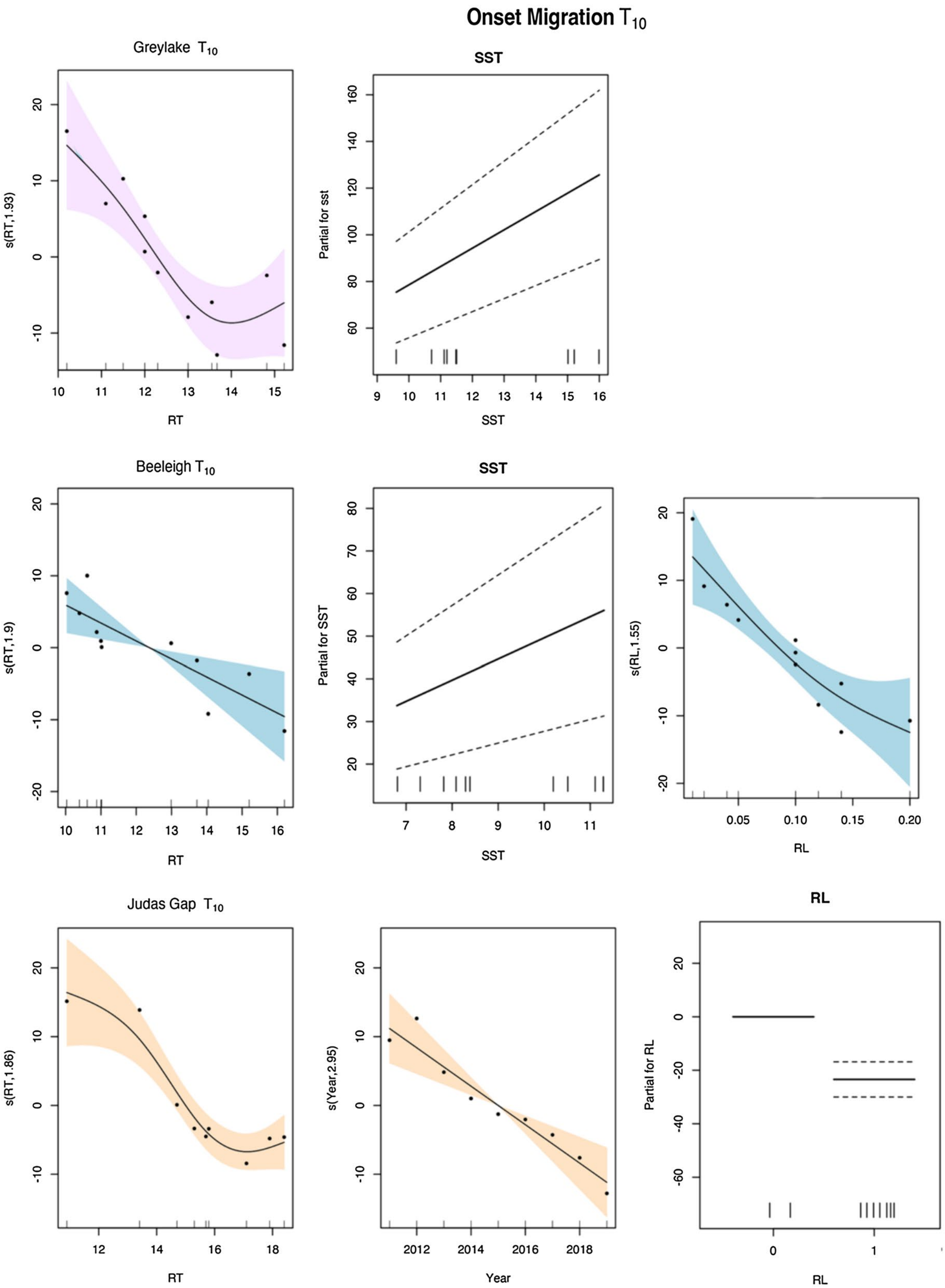
Influence of environmental parameters on daily eel arrivals

The best fitting GAM testing environmental parameters on daily eel arrivals, included RT as a significant effect at all sites (Table 3, Fig. 7). Increasing temperatures between (10–20 °C), had a significant, positive influence on the number of eels passing the

Table 2 Summary of the retained parametric coefficients and smooth terms in the Generalised additive model (GAM) (Gaussian identity link function), assessing the influence of environmental parameters (RT, SST, River Level, Moon Phase and temperature difference (Temp_diff) between SST and RT on the onset (T_{10}) and peak (T_{50}) migration of eels for each site

Site/migration stage	Predictors	Estimate ± SE	t value	edf	*F*	*P*	Deviance explained (%)
Greylake, T_{10}	Intercept	40.64 ± 13.96	2.91			< 0.02	92.2
	SST	7.85 ± 1.13	6.94			< 0.001	
	RT			2.94	6.11	< 0.01	
	Intercept	136.90 ± 1.83	74.3			< 0.001	78.7
	Temp_diff			1.52	43.27	< 0.001	
Greylake, T_{50}	Intercept	11.32 ± 12.26	0.93			0.38	94.1
	SST	10.19 ± 0.97	10.50			< 0.001	
Beeleigh, T_{10}	Intercept	4.24 ± 0.02	147.22			< 0.001	92.2
	SST	0.04 ± 0.02	16.93			< 0.001	
	RT			9.96	133.23	< 0.001	
	Level			9.20	6.73	< 0.001	
	Intercept	113.90 ± 2.56	44.98			< 0.001	65.7
	Temp_diff			1.42	9.55	< 0.01	
Beeleigh, T_{50}	Intercept	4.35 ± 0.23	78.54			< 0.001	98.9
	SST	0.05 ± 0.03	14.52			< 0.001	
Judas Gap, T_{10}	Intercept	191.62 ± 22.75	8.42			< 0.001	93.2
	RT			2.85	15.36	< 0.01	
	Level	− 24.41 ± 3.40	− 7.18			< 0.001	
	Year			9.53	13.44	< 0.01	
	Intercept	156.88 ± 3.97	39.43			< 0.001	31.3
	Temp_diff			0.78	0.73	0.11	
Judas Gap, T_{50}	Intercept	119.45 ± 7.88	15.14			< 0.01	98.2
	RT			9.84	21.27	< 0.01	
	Year			2.60	86.46	< 0.001	

Note that EDF values are only given for smooth terms in the model. See Table S5 for full model


Onset Migration T10
Greylake T10
s(RT,1.93)
RT
SST
Partial for sst
SST
Beeleigh T10
s(RT,1.9)
RT
SST
Partial for SST
SST
s(RL,1.55)
RL
Judas Gap T10
s(RT,1.86)
RT
s(Year,2.95)
Year
RL
Partial for RL
RL

◂**Fig. 4** Partial effects of environmental variables of the retained coefficients in the Generalised additive model (GAM) (Gaussian identity link function), assessing the influence of environmental parameters on the onset (T_{10}) migration of eels for Greylake, Beeleigh and Judas Gap. Black dots represent the partial residuals for each term. The y-axis indicates the estimated partial effect size, with shaded areas representing the 95% confidence intervals

weirs (Figure S8). In contrast more eels passed the weirs when SST were cooler at Beeleigh and Greylake (Table 2, Fig. 7). Moon phase had a significant effect on the number of eels with more eels passing the weir on darker nights. River level had a significant influence with more eels passing the weir when river levels were high (Table 3, Fig. 7). The temperature difference between RT and SST had a significant influence across all sites, where more individuals passed the weir when RT was warmer than SST although when the temperature difference exceeded 5 °C the number of eels passing declined (Table 3, Fig. 8).

Discussion

Understanding the relationship between environmental conditions during the early life stages of eel as they transition from marine to freshwater environments is important to derive better understandings of how climate variability may impact this species recruitment. Here, the timing and duration of eel passage across the tidal weirs in the three rivers showed considerable variation, but generally occurred from April to September, with peak movements in June, and with few eels sampled after September. These findings are consistent with previous studies on the seasonality of eel migration in Northern Europe, such as the River Thames in Southern England, where eel migration occurred between April and October, with most arriving in May and June (Naismith & Knights, 1988), the River Shannon in Ireland where upstream migration begins in May and peaks in June to July (Moriarty, 1986), and Den Oever (The Netherlands), where eels arrive from March to May (Dekker, 2003). In contrast, eel inshore migration starts earlier in Southern European rivers, such as Spain where migration peaks in December and January (Aranburu et al., 2016), while along the French Atlantic coast, migration peaks during January and February (Gascuel et al., 1995) and between February and March in Portugal (Stratoudakis et al., 2018). Across the three weirs here, eels continued to arrive into freshwater over extended periods, particularly at Greylake, where small numbers of eels continued to pass the weir until late Autumn.

While the timing of the migration period remained fairly stable over the study, eels tended to arrive earlier at Greylake and then Beeleigh. Conversely, at Judas Gap, eels tended to arrive later in the year, with the onset and peak period of the eel run occurring earlier across the study period. Differences in the migration timing at each site could be associated with spatial variations in environmental conditions between the sites, given Greylake is western England and the other two sites in eastern England. Furthermore, factors such as the distance from the river mouth to the weir, estuary characteristics and the physiological condition of eel could contribute to the observed differences (Elie & Rochard, 1994; Zompola et al., 2008). There is, also some complexity at the sites relating to their regulation of river flow that relates to land drainage and flood management. For example, Greylake Weir is situated on an artificial drainage channel that redirects the flow of the River Cary and discharges it into the tidal River Parrett, which then flows into the Bristol Channel, and so this route might result in some slight delay in the eel arriving at the weir.

Numerous studies have found that various environmental factors, including lunar phase, tidal cycle, diurnal rhythm, water temperature, salinity, turbidity, olfactory cues, and rainfall, influence the recruitment dynamics of eels (e.g. Jellyman, 1979; Bardonnet & Riera, 2005; Sullivan et al., 2009). Among these factors, water temperature plays a crucial role in the inshore migration of eels. Increased water temperatures have been linked to higher levels of active swimming, upstream migration, growth, metabolism, and pigmentation along Atlantic and Mediterranean coasts (Boëtius & Boëtius, 1989; Edeline et al., 2006). Here, the timing of eel migration was significantly influenced by RT, with an optimal range that facilitates migration across all three sites. Individuals arrived earlier when RTs were warmer, with the onset of arrival generally occurring when mean temperatures exceeded 10 °C at Greylake and Beeleigh and 11 °C at Judas Gap. Similar temperature thresholds have been observed in other regions, such as the

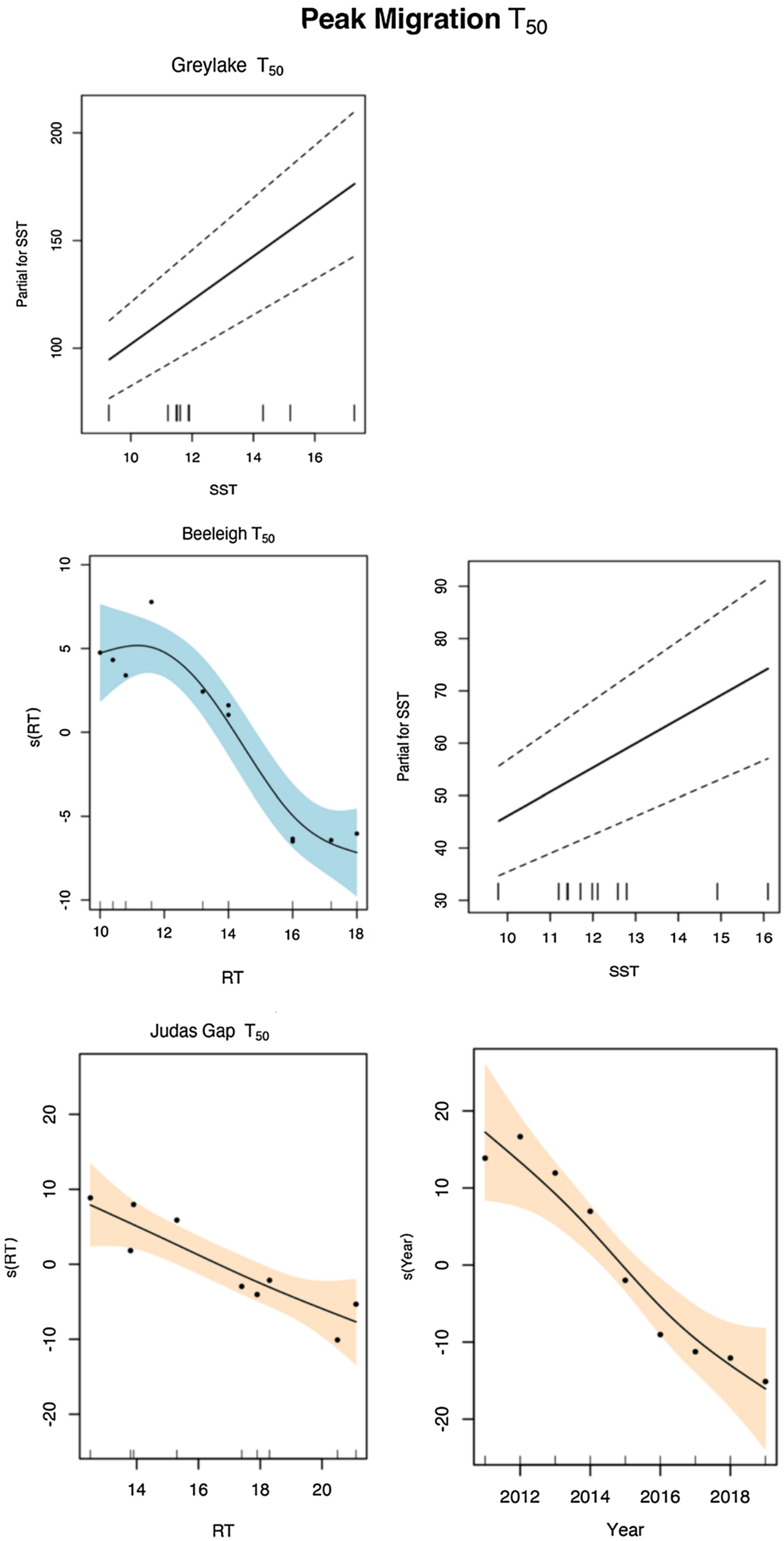


Fig. 5 Partial effects of environmental variables on the retained coefficients in the Generalised additive model (GAM) (Gaussian identity link function), assessing the influence of environmental parameters on the onset (T_{50}) migration of eels for Greylake, Beeleigh and Judas Gap. Black dots represent the partial residuals for each term. The y-axis indicates the estimated partial effect size, with shaded areas representing the 95% confidence intervals

Fig. 6 Partial effect plots assessing the influence of the temperature difference between RT and SST (Temp_diff) on T_{10} for Greylake, Beeleigh and Judas Gap. Black dots represent the partial residuals for each term. The y-axis indicates the estimated partial effect size, with shaded areas representing the 95% confidence intervals

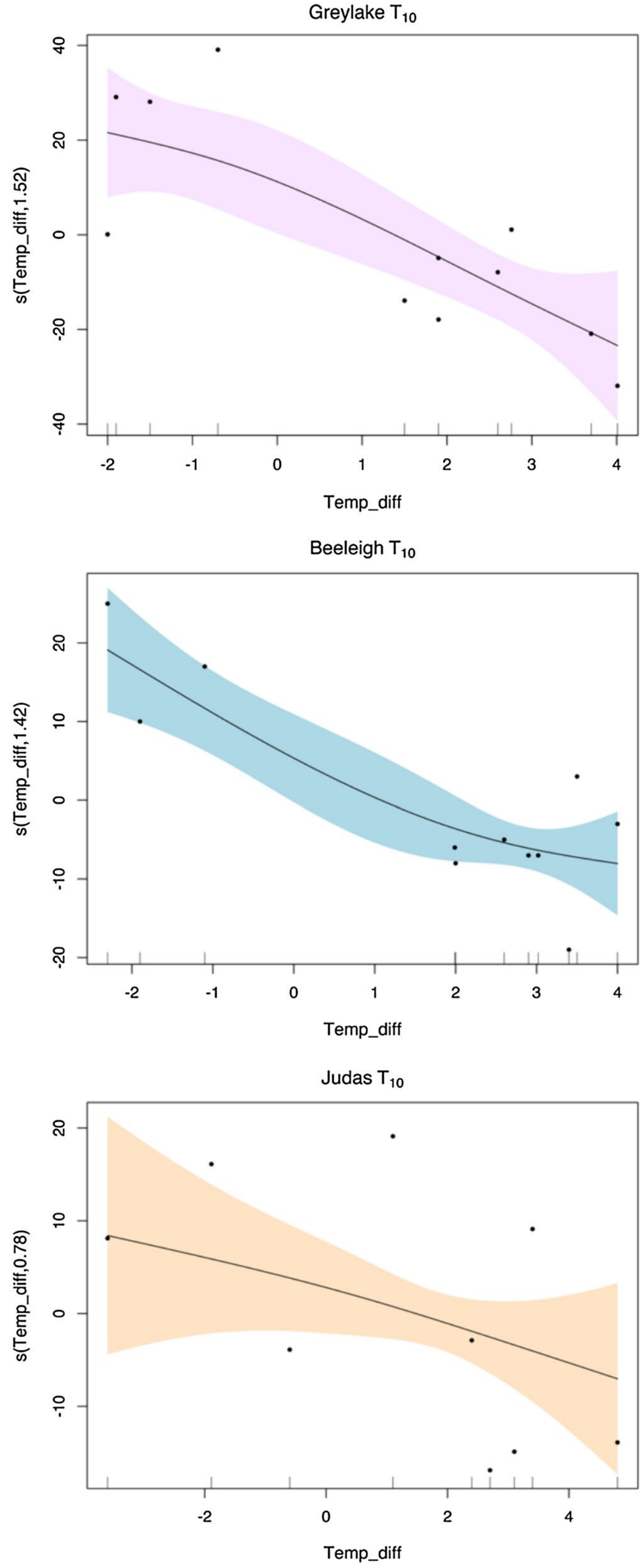


Table 3 Summary of the retained parametric coefficients and smooth terms in the Generalised additive model (GAM) (Tweedie distribution), assessing the influence of environmental parameters (SST, RT, River Level, Moon and Temperature difference (Temp_diff) between RT and SST) on the number of migrating eels for Greylake, Beeleigh and Judas Gap

Site/migration stage	Predictors	Estimate ± SE	*t* value	edf	*F*	*P*	Deviance Explained (%)
Greylake	(Intercept)	3.88 ± 0.37	10.46			< 0.001	69.1
	SST			2.54	467.03	< 0.001	
	RT			1.92	391.66	< 0.001	
	River level			1.73	96.04	< 0.01	
	Moon phase			2.37	83.66	< 0.001	
	Year (random effect)			9.76	49.32	< 0.001	
	(Intercept)	2.14 ± 0.42	4.99				
	Temp_diff			2.84	24.52	< 0.001	46.6
	Year			9.74	36.26		
Beeleigh	(Intercept)	3.51 ± 0.11	11.42			< 0.001	67.1
	SST			1.68	738.03	< 0.001	
	RT			1.96	753.98	< 0.001	
	River level			2.01	41.33	< 0.01	
	Moon phase			1.98	128.52	< 0.001	
	Year (random effect)			9.69	52.75	< 0.001	
	(Intercept)	4.51 ± 0.22	21.39			< 0.001	37.6
	Temp_diff			1.99	87.04	< 0.001	
	Year			9.69	34.17	< 0.001	
Judas gap	(Intercept)	2.01 ± 0.57	3.50			< 0.001	65.9
	RT			1.90	109.89	< 0.001	
	River level (factor)	0.44 ± 0.17	2.80			< 0.01	
	Moon phase			2.36	42.94	< 0.001	
	Year (random effect)			7.73	26.38	< 0.001	
	(Intercept)	3.22 ± 0.55	5.82			< 0.001	22.3
	Temp_diff			1.96	114.62	< 0.001	
	Year			7.76	21.36	< 0.001	

Note that year was included as a random effect and EDF values are only given for smooth terms in the model. See Table S6 for full model

northern region of Nova Scotia (Jessop, 2003), where American eel *Anguilla rostrata* began actively swimming upstream when temperatures reached 10–12 °C, while upstream migration commenced in a southern USA coastal watershed when water temperatures exceeded a threshold range of 10–15 °C (Overton & Rulifson, 2008).

RT was also found to influence the abundance of eels, with higher abundances being observed at temperatures from 10 to 20 °C, with minimal eel migration observed above 21 °C and below 8 °C. Exposure to low temperatures could result in extended periods of starvation and weight loss in eels, that in combination, might affect their ability to move upstream (Han, 2011). These findings align with observations elsewhere, such as reduced recruitment of shortfin eel (*Anguilla australis*) when water temperatures exceeded 22 °C (August & Hicks, 2007). Additionally, in Sardinia, Italy, Podda et al. (2020) found that the abundance of glass eels was primarily influenced by water temperatures ranging from 12.3 to 14.5 °C, while the abundance of elvers was associated with temperatures between 14 and 21 °C.

Conversely individuals arrived earlier when SSTs were cooler (between 6.8 and 9 °C). at Greylake and Beeleigh, with individuals arriving later when SSTs

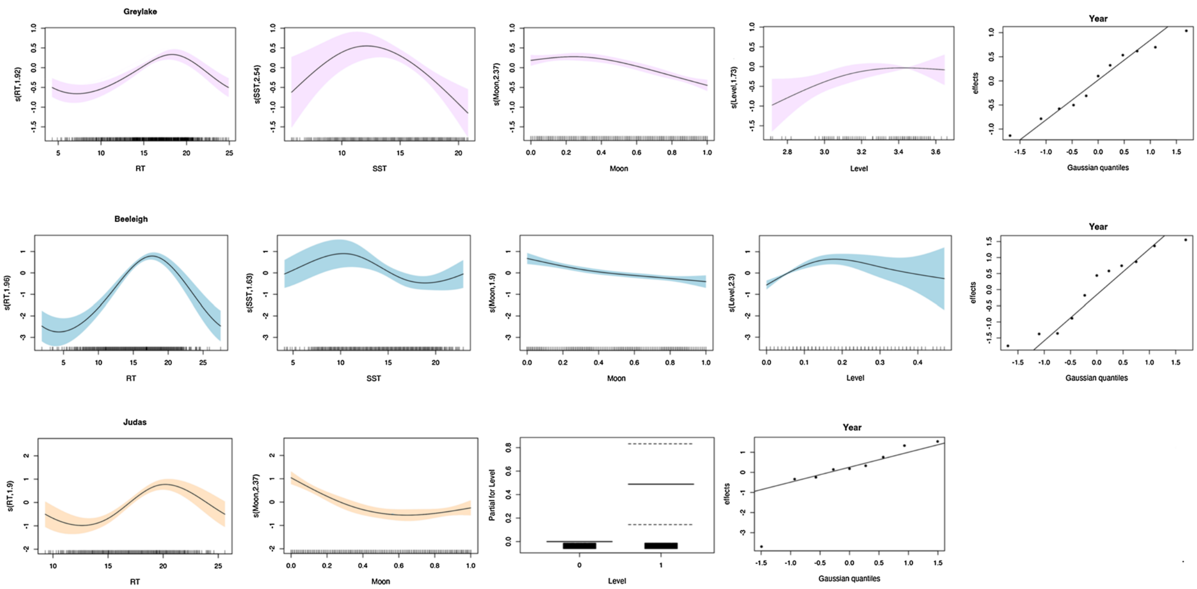


Fig. 7 Partial effects of environmental variables on the retained coefficients in the Generalised additive model (GAM) (Tweedie distribution), assessing environmental parameters on the number of eels arriving at Greylake, Beeleigh and Judas Gap. The y-axis indicates the estimated partial effect size, with shaded areas representing the 95% confidence interval. Black lines indicate the value of GAMs coefficient

were around 14 °C. Similar migration timings have been found in other species, such as European flounder *Platichthys flesus*, where individuals settled in estuaries later when SSTs were high (Vaz et al., 2023) and in Atlantic salmon, *Salmo salar* where later migrants were associated with higher SSTs (Otero et al., 2014). SST was also found to influence the abundance of eels, with more eels passing the weir when SSTs were cooler (between 5.5 and 10 °C), with fewer eels ascending the weir when SST were around 15 °C. However, SST did not influence the migration period or the number of eels passing the weir at Judas Gap, which could be related to eels arriving later on in the season (May and June) when SSTs were generally warmer (< 3 °C). In contrast an increase in the recruitment of *A. rostrata* in Nova Scotia, Canada was significantly correlated with elevated coastal and continental shelf SSTs (Jessop, 2021). Further to this, earlier start dates of the elver fishery were associated with higher SSTs, whereas later start dates were associated with cooler SSTs (Jessop, 2021).

RT and SSTs have changed temporally, with both metrics generally increasing over the study period. It has been suggested that temperature differences in excess of 3–4 °C between riverine and coastal waters may inhibit eel migration (Gandolfi et al., 1984; McGovern & McCarthy, 1992). Here we found that more eels passed the weir when RTs were warmer than SSTs (approximately 2–4 °C), while fewer eels passed when these temperature differences exceeded 5 °C. Furthermore, when RTs were warmer than SSTs the onset of migration occurred earlier at Beeleigh and Greylake. If eels were to arrive during warmer SST periods, RT might surpass their tolerance levels, leading to a slight delay in their migration to avoid unfavourable thermal conditions. Consequently, it is important for eels to enter freshwater before RTs are too high. Another possibility is that glass eels, initially in the marine environment, are more tolerant of cooler temperatures. As a result, they can withstand slightly cooler SSTs. However, upon entering rivers and moving upstream, they may choose to wait downstream until RTs rise slightly before continuing their journey. However, explanations of these patterns in an eel context remain speculative.

Regarding river level, this was retained in the best fitting model predicting the number of eels with more individuals migrating over the weir when levels were high. At Judas Gap, the height of weir is 1.8 m AODN, therefore river levels must exceed this

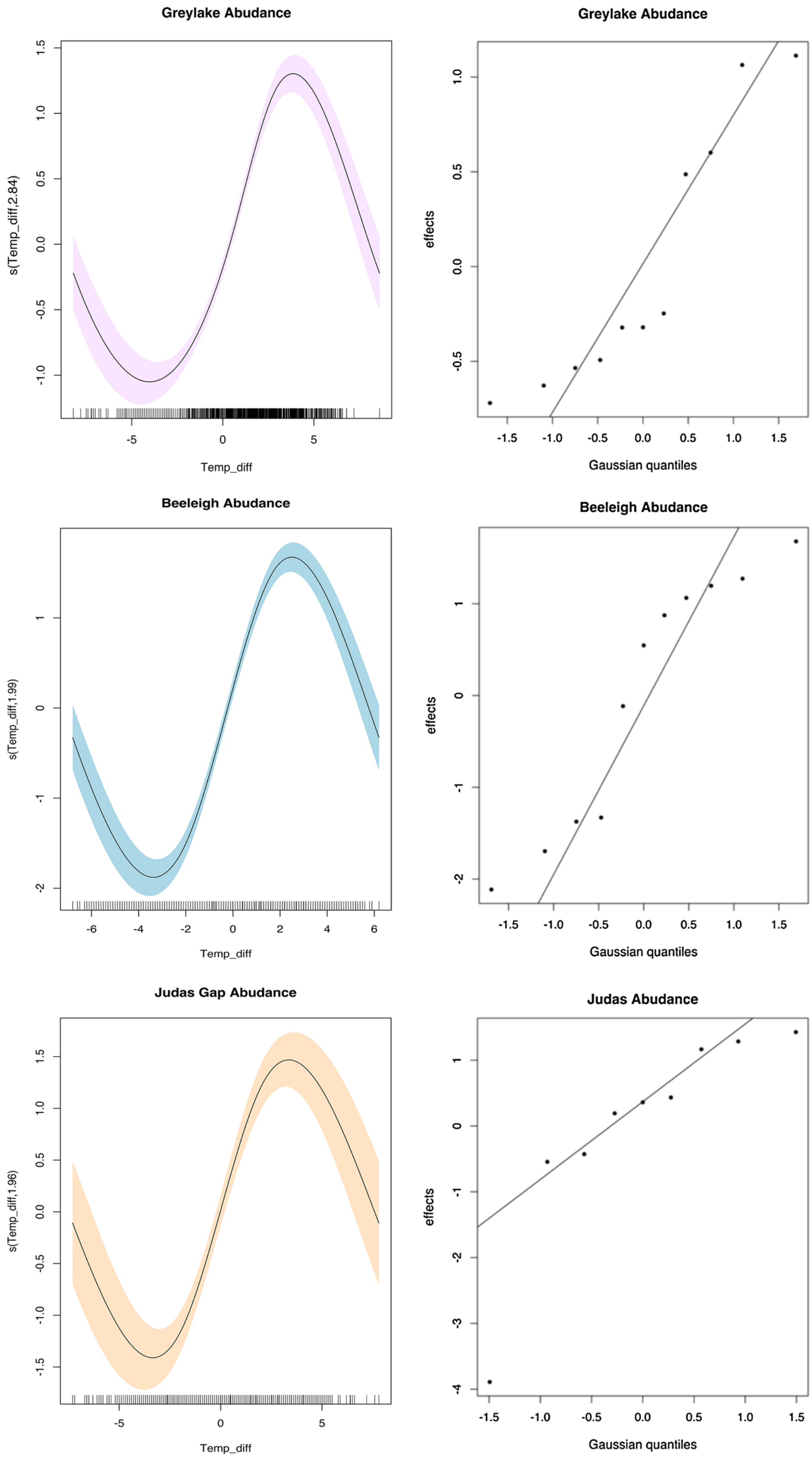


Fig. 8 Partial effect plots assessing the influence of the temperature difference between RT and SST (Temp_diff) on the number of eels arriving at Greylake, Beeleigh and Judas Gap. The y-axis indicates the estimated partial effect size, with shaded areas representing the 95% confidence interval. Black lines indicate the value of GAMs coefficient

threshold to enable flow over the weir, which forms an attraction flow for eels migrating upstream (Piper et al., 2012). Higher water levels also resulted in an earlier onset of migration at Beeleigh and Judas Gap.

The timing of eel passage over the weirs was not associated with moon phase, but higher numbers of eels passed on darker nights, when no moon or only a small fraction of the moon was illuminated. This preference for darker nights may be attributed to predator avoidance (Fukuda et al., 2016). In new moon periods, there are peaks in glass eel catches in NW Spain (Lara, 1994) and in the emigration rate of silver eels in general (Deelder, 1984; Tesch, 2003). Other studies on glass eel migration indicate that moon phase is less important and that the effect of moonlight can be obscured by cloud cover or turbid water, which causes low visibility (Cullen & McCarthy, 2003). The influence of new moon periods could also relate to the increased high tide level and thus stronger tidal current, although the influence of this would diminish with distance upstream and would be expected to also occur on a full moon, which does not correspond with the outcome of higher eel numbers passing on darker nights.

An issue inherent in the approach here was the use of long-term datasets that encompassed two different sampling techniques and had non-standardised sampling periods. The use of cameras on the pass at Greylake allowed for continuous monitoring over a longer time period (providing the equipment was working properly), whereas the manual traps on the passes at Judas Gap and Beeleigh meant there was a higher staff requirements at these sites, which meant that due to logistical reasons, the traps were not always set continuously as at Greylake. This was largely overcome by standardising the timing of the sampling periods, with a comparison of the non-standardised versus standardised datasets suggesting the process resulted in only a low proportion of eels omitted from analyses. The use of the camera at Greylake also prevented the measurement of individual eels, with catches at Judas Gap and Beeleigh also only recording numbers of eels, with only a sub-sample measured. This lack of length data thus prevented changes in the length structure of samples to be measured throughout the migration periods, a contrast to some other studies (e.g. Monteiro et al., 2023). Greylake exhibited a longer migration period and a higher number of catches compared to the other sites. This might be due to its proximity to the Bristol Channel, which serves as an important migration route for eels entering the River Severn, a recognised important glass eel fishery that is also used as a source of glass eel for stocking elsewhere (Aprahamian & Wood, 2021).

In summary, the results here on eel migration timings indicated that whilst some factors are fixed in time and space and so their influence on migration phenology will be unlikely to change in future, others were associated with annual variability in temperature. Climate change projections in the study area predict general patterns of warming temperatures and precipitation changes that result in greater extremes between low summer flows and peak winter flows (Kay et al., 2021; Lane & Kay, 2021). Consequently, such climate shifts have the ability to disrupt these eel migration timings into freshwater, with the potential for higher inter-annual variability in phenology as the temperature and precipitation patterns become even less predictable. However, whilst the timings and their variability of migration might change, as elvers have evolved to migrate upstream across a wide range of water temperatures (as observed between their immigration to rivers across a large latitudinal range), then such effects are not considered likely to have a more severe impact on eel populations.

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

Declarations

Conflict of interest The authors have not disclosed any conflict of interest.

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