



Upstream movement of juvenile eels (*Anguilla anguilla* L.) in a southwestern European river

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Abstract The upstream movement of juvenile eels (median total length (TL)=138 mm) in the Mondego River, Portugal, was analysed between January 2017 and August 2019. A total of 12,019 individuals (TL ranging from 60 to 287 mm) were counted and measured on an eel ladder at Coimbra weir, 44 km upstream from the river mouth, during their upstream movements. Although eels were counted throughout the year, a clear seasonal peak was detected in spring and late summer, with 93% of total movements occurring between April and September. No differences were found in the total length of individuals moving upstream between years. Generalised additive models, with an explained deviance of 83% and an adjusted R^2 of 0.88, identified minimum water temperature as the main environmental variable explaining these movements, with a threshold of 13 °C triggering

the onset of movements, and a peak between 15 and 19 °C, which corresponds to the spring and summer periods. Other predictors such as photoperiod, precipitation and river flow also contributed as explanatory variables in the model but less importantly. The present results may contribute to the management of this endangered species in the southern region of its distribution range by defining adequate temporal windows to monitor and promote the movement of juvenile European eels through obstacles to migration.

Keywords European eel · River basin colonisation · Freshwater migration · Water temperature · Mondego River · Portugal

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Introduction

The catadromous life cycle of the European eel, *Anguilla anguilla* (Linnaeus, 1758), begins when eggs hatch into leptocephali larvae in the Sargasso Sea (Schmidt 1923). Oceanic currents transport these larvae until they reach their continental distribution range, between the Barents Sea and North Africa, including the Mediterranean basin (Schmidt 1923). After reaching continental waters, some eels remain in estuaries, while others move upstream in river basins (Daverat et al. 2006) where they grow up to 20 years (Vøllestad 1992) until they migrate back to the Sargasso Sea as silver eels.

Recruitment of the panmictic population of European eel (Als et al. 2011) suffered a sharp decline across its distribution range in the 1980s (ICES 2021), remaining low in subsequent years. This led to the adoption of Council Regulation (EC) No. 1100/2007 that establishes measures for the recovery of the stock. The causes for this decline are multiple and occur in both oceanic and continental environments, affecting all life stages. Climate change can modify oceanographic conditions, impairing larval survival and migration (Hanel et al. 2014; Miller et al. 2016). During the continental life phase, eels are also exposed to several pressures that include overfishing (ICES 2021), as well as parasites and pathogens, chemical contaminants and habitat loss (Belpaire et al. 2016; Miller et al. 2016; Righton et al. 2021). Some authors point to contamination and habitat loss as the causes with the greatest impact, but there is no consensus on their relative importance (Miller et al. 2016). Non-fishery anthropogenic impacts including the parasite *Anguillicola crassus*, and the environmental pollution by chemicals, which can cause direct mortality or have sublethal effects at several biological organisation levels (Bourillon et al. 2022; Geeraerts and Belpaire 2010), may have detrimental effects on the quality of spawners and their reproductive migration (Belpaire et al. 2016; Palstra et al. 2007). Habitat loss due to the construction of obstacles that impede upstream colonisation of river basins has been considered one of the most impacting threats by some authors (e.g. Clavero and Hermoso 2015; Righton et al. 2021). It is known that juvenile eels can colonise freshwater habitats up to 1000 km from the river mouth (Tesch 2003), depending on latitude and altitude (Moriarty and Dekker 1997). However, due to the interruption of river connectivity caused by the construction of

dams and weirs, their natural distribution in continental waters is currently restricted to a small fraction of their historical habitats (e.g. <20% in the Iberian Peninsula according to Clavero and Hermoso (2015)), despite the remarkable ability of small eels to climb vertical walls (Porcher 2002), as long as their surface is wet and irregular (Kerr et al. 2015). Regardless of this climbing ability, only a small proportion manages to overcome obstacles (White and Knights 1997a), with most individuals remaining in the downstream area (Domingos et al. 2006) contributing to a sex-ratio shifting towards males (Leo and Gatto 1996; Costa et al. 2008).

Despite not considered migratory in the yellow phase (ICES 2020), eels exhibit seasonal peaks of activity (Baras et al. 1998; Tesch 2003). These peaks include upstream movements to colonise the river basin, which usually occur in spring and summer (Moriarty 1986; Naismith and Knights 1988; Vøllestad and Jonsson 1988; White and Knights 1997a; Acou et al. 2009; ICES 2020). As the minimum body length increases with distance from the river mouth (Knights and White 1998; Domingos et al. 2006; Tamario et al. 2019), when conducting these studies in upstream areas, there is a risk of considering larger and older animals (Ibbotson et al. 2002; Santos et al. 2002; 2016; Matondo and Ovidio 2016) that are exhibiting daily home range movements, rather than an upstream directional movement of juveniles to colonise the river. These different behaviours, with different goals, should be analysed separately to avoid biased conclusions in both cases (ICES 2020).

This study aims to characterise the upstream movement of juvenile eels in a freshwater stretch of a regulated river (16 km upstream of the tidal limit) in the southwest of the Iberian Peninsula, by counting individuals at an eel ladder and identifying the environmental variables that explain these movements. Information on upstream movements of juvenile eels is considered crucial for the management of this critically endangered species because it contributes to improving the mitigation of obstacles in general.

Materials and methods

Study site

The Mondego River, with a total length of 234 km, is the longest river flowing exclusively in Portuguese

territory. It rises on the highest mountain in continental Portugal (Serra da Estrela) at 1425 m of altitude and flows into the Atlantic Ocean, at Figueira da Foz. The Formoselha weir, located 29 km from the river mouth and 16 km downstream of the Coimbra weir, is a low-head stone weir that marks the limit of tidal influence on the Mondego River (Fig. 1), but it is not considered an insurmountable obstacle for the eel (Domingos et al. 2006).

As most European rivers, Mondego is highly impacted by a series of weirs and dams. The river flow is artificially regulated by a hydroelectric scheme comprising three large dams, two of them located in the mainstem (Raiva and Aguieira dams, 77 and 86 km upstream from the river mouth, respectively) and another one, the Fronhas dam, located on an

important tributary, the Alva River, 22 km upstream from the confluence with the Mondego River. Still in the Mondego mainstem, at 44 km from the river mouth, the Coimbra weir, with a height of 6.2 m and equipped with 9 sluice gates to control the river flow, was built in the early 1980s for flood control, public and industrial water supply, and irrigation. Although this weir was not the upstream limit for the colonisation of European eel, an accumulation of small individuals downstream of this obstacle and a substantial reduction in their abundance in the upstream sections was observed (Domingos et al. 2006), despite the existence of an obsolete fish pass. Thus, to improve connectivity, a new multi-specific vertical-slot fish pass was installed at this weir in 2011, but with very limited efficiency for European eel. The Raiva dam is

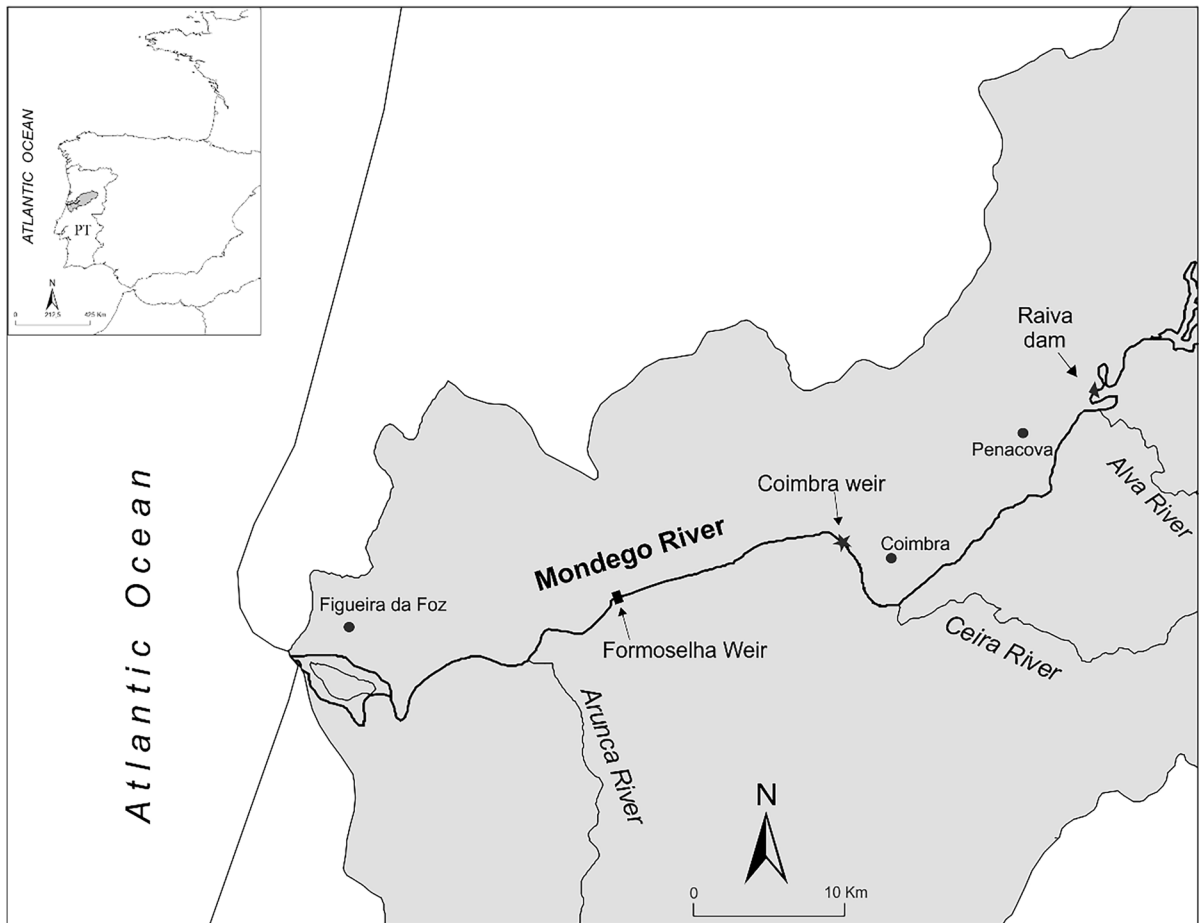


Fig. 1 Map of Mondego River and main tributaries. The study site (black star) Coimbra weir, the limit of the tidal influence—Formoselha weir (black rectangle)—and the upstream limit for

the species in the mainstem—Raiva dam (black triangle)—are also represented

currently the upstream distribution limit for most diadromous species that still occur in this basin, namely European eel, sea lamprey (*Petromyzon marinus* L.), allis shad (*Alosa alosa* L.) and twaite shad (*Alosa fallax*) (Lacépède, 1803) (Pereira et al. 2017). To improve eel access to habitats upstream of the Coimbra weir, an eel ladder was installed in 2016.

Data collection

Eels were trapped and counted regularly between January 2017 and August 2019 at the Coimbra weir eel ladder. This eel ladder is located on the left side of the Coimbra weir and the entrance to this pass is located next to the entrance to the vertical-slot fish pass. The eel ladder may be divided into three sections. The first, the entrance zone, consists of five brush ramps (35–51° angle), and four resting pools covering a 6-m height difference. The progression zone is a 60-m horizontal tube with two pools at both ends. In the upstream area, the third zone comprises a brush ramp and a holding tank where the eels can be trapped for monitoring. Constant water supply is provided by two pumps. At each sampling observation (ideally, but not always secured, on a weekly basis), all eels collected in the trap were anaesthetised with a 0.4 ml/L of a solution of 2-phenoxyethanol and their total length (TL, mm) was

recorded (except on 30 May 2019 when due to the large number of specimens observed only a subset of 33.5% was measured). After measurement, the individuals were placed in a 25-L tank with river water until fully recovered and then released in an area upstream of the obstacle.

Fourteen environmental variables (Table 1) that were shown to potentially influence upstream movements of anguillid species (e.g. Sloane 1984; Moriarty 1986; White and Knights 1997b; Acou et al. 2009; Kume et al. 2022) were considered predictors for modelling the upstream movement. Water temperature was continuously measured with an EXO2 water probe deployed at the Coimbra weir. River flow was measured at the Coimbra weir gauging station by the Portuguese Environment Agency (APA). Precipitation data, collected at the Tentúgal meteorological station (40°14'33.5"N; 8°35'37.0"W), were obtained from the National Water Resources Information System from APA, while data on photoperiod (number of daylight minutes) were obtained from the Lisbon Astronomical Observatory. Except for mean river flow, cumulative precipitation and mean precipitation, which were also estimated for 5 and 10 days prior to sampling, all the other variables were obtained for the interval between two consecutive sampling occasions.

Table 1 Environmental variables initially considered for modelling the upstream movements of eels, their unit of measurement, range between brackets and the period when the variables were measured. Water temperature was measured every

30 min, river flow every hour and both photoperiod and precipitation daily. All data were collected between January 2017 and August 2019. (*) indicates variables used for model fitting

Variables (unit)	Abbreviation	[Minimum–maximum]	Period of measurement
Mean water temperature (°C)	<i>MeanTemp</i>	[8.8–23.3]	Between two samplings
Maximum water temperature (°C)	<i>MaxTemp</i>	[9.8–26.4]	Between two samplings
(*) minimum water temperature (°C)	<i>MinTemp</i>	[7.5–22.4]	Between two samplings
Mean maximum water temperature (°C)	<i>MeanMaxTemp</i>	[9.1–24.1]	Between two samplings
Mean minimum water temperature (°C)	<i>MeanMinTemp</i>	[8.4–22.7]	Between two samplings
Mean river flow (m ³ s ⁻¹)	<i>Rf</i>	[3.2–309.8]	Between two samplings
Mean river flow 5 days (m ³ s ⁻¹)	<i>RfMean5</i>	[3.0–425.0]	Five days prior to sampling
(*) Mean river flow 10 days (m ³ s ⁻¹)	<i>RfMean10</i>	[3.3–344.3]	Ten days prior to sampling
(*) photoperiod (min)	<i>Photop</i>	[560–904]	Between two samplings
(*) Mean precipitation (mm)	<i>Precip</i>	[0.0–14.1]	Between two samplings
Cumulative precipitation 5 days (mm)	<i>PrecSum5</i>	[0.0–77.5]	Five days prior to sampling
(*) Cumulative precipitation 10 days (mm)	<i>PrecSum10</i>	[0.0–140.7]	Ten days prior to sampling
Mean precipitation 5 days (mm)	<i>PrecMean5</i>	[0.0–15.5]	Five days prior to sampling
Mean precipitation 10 days (mm)	<i>PrecMean10</i>	[0.0–14.0]	Ten days prior to sampling

Data analyses and modelling

Differences in the length distribution of individuals counted at the eel ladder between years and seasons were assessed using a permutational multivariate analysis of variance (PERMANOVA) conducted with the add-on package PERMANOVA for PRIMER+v6.0 (Anderson et al. 2008), with a two-way fixed-effect crossed design (factors: year with two levels, 2017 and 2018 and season (with four levels—winter, spring, summer and autumn) in which the months corresponds to the four seasons: winter (January–March); spring (April–June); summer (July–September); and autumn (October–December)). As 2019 was only partially monitored (until the end of August), this analysis was performed considering just the complete years, i.e. 2017 and 2018. Data were square root transformed and Bray–Curtis similarity coefficient was used as a resemblance matrix. Pairwise tests were used when significant differences were found.

The upstream movement of juvenile eels and the influence of environmental variables considered relevant (Table 1) were modelled by generalised additive models (GAM) (Hastie and Tibshirani 1986; 1990). The number of eels was used as a proxy for upstream movement intensity, and so, the dependent variable ($Y\text{-Mean}_{ind}$) is the mean number of individuals per day, between two sampling occasions (i.e. counts at the Coimbra weir eel ladder). GAMs are extensions of generalised linear models that also use a link function to establish the relationship between the mean of the response variable and, in GAM, the smooth function of the predictor variables. The smooth function is the effect of each input variable (predictor) that is specified by a non-parametric smooth function, determining the shape of the response curve based on the observed data.

Following preliminary tests on the data distribution and the evaluation of the model's performance using different distributions, the relationship between these movements and environmental variables was modelled by fitting a Quasi-Poisson distribution family with a "log" link function. Prior to modelling, Spearman's correlation analysis was performed to assess the correlation between the 14 environmental variables considered (Table 1). When two variables had a high correlation coefficient, i.e. $\rho > 0.7$ (Dormann et al. 2013), the variable used to fit the model was the one with the highest deviance explained in univariate GAM models (the results of

Spearman's correlation tests and univariate models are presented in Supplemental Table 1). To fit the model, several GAM models were generated to compare environmental data with upstream movements. The best fitted model was chosen after a stepwise backwards selection of the significant variables ($p\text{-value} < 0.05$). The lower global cross-validation with the highest total deviance explained and R^2 was considered the best model. The model was validated based on the independence, homogeneity and normality of the residuals. Differences in the environmental predictors affecting the upstream movement of eels may exist depending on the size structure of individuals, particularly when considering individuals of 0+ age (e.g. Moriarty 1986; Naismith and Knights 1988). Thus, given that no glass eel was caught in the eel ladder trap, two previous GAM models were conducted according to two groups based on their potential age, a first model considering eels < 150 mm as 0+ (thus in the first year of their continental life), and a second model considering eels ≥ 150 mm as eels after their first year of continental life. As these models showed no differences in the environmental predictors ruling upstream movements (Supplemental Table 2 and Supplemental Fig. 1), all individuals were used in the final GAM model.

All statistical analyses, except for PERMANOVA, were performed using R software (R Core Team 2022), and the packages "ggplot2" (Wickham 2016), "dplyr" (Wickham et al. 2019), and "mgcv" (Wood 2017) were selected to conduct these analyses. A significance level of 0.05 was considered for all test procedures.

Results

Over the study period, a total of 12 019 juvenile eels were counted in the Coimbra weir eel ladder. The TL of eels ranged from 60 to 287 mm, with a mean and median length of 142 mm and 138 mm, respectively. No glass eels were caught in the trap.

The upstream movement took place throughout the year, with the lowest catches occurring consistently between January and March over the 3-year monitored (Fig. 2). In contrast, the highest catches were obtained in May and June. Overall, 95% of eels measured were smaller than 200 mm in TL. Eels with less than 150 mm in TL represented 63.5% of total catches and were the dominant class in all months.

The PERMANOVA analysis revealed that there were no significant differences in length distribution

between years (PERMANOVA, Year, pseudo $F=0.79$, $P_{\text{perm}}>0.05$), but there were differences between seasons (PERMANOVA, Season, pseudo $F=31.17$, $P_{\text{perm}}<0.05$), with Summer being identified as the only statistical difference in the pairwise tests. A significant interaction was also observed (PERMANOVA, Year \times Season, pseudo $F=5.78$, $P_{\text{perm}}<0.05$), indicating that differences between years occurred only in summer (PERMANOVA pairwise tests, $P_{\text{perm}}<0.05$), whereas differences between seasons occurred in 2017 between summer and both spring and winter (PERMANOVA pairwise tests, $P_{\text{perm}}<0.05$), and in 2018 with summer being significantly different than the remaining seasons, but also with a difference between spring and autumn

seasons (PERMANOVA pairwise tests, $P_{\text{perm}}<0.05$). This difference is mainly explained by the summer of 2018, the period with the lowest average total length (128 mm), followed by the summer of 2017 and spring 2018 (total length of 137 mm and 143 mm, respectively). The variation in TL over the study period is shown in Fig. 3, with the smallest individuals occurring during the summer, especially in 2018, which is identified in the PERMANOVA analysis.

After running several GAM models (Supplemental Table 3), the model (Eq. 1) that best explained the upstream movements of juvenile eels accounted for 83% of the deviance (Global Cross Validation: 14.17; adjusted R^2 : 0.88).

$$\text{Mean}_{\text{ind}} \sim s(\text{MinTemp}, k = 20) + s(\text{RfMean10}, k = 7) + s(\text{Photop}, k = 15) + \text{Precip} \quad (1)$$

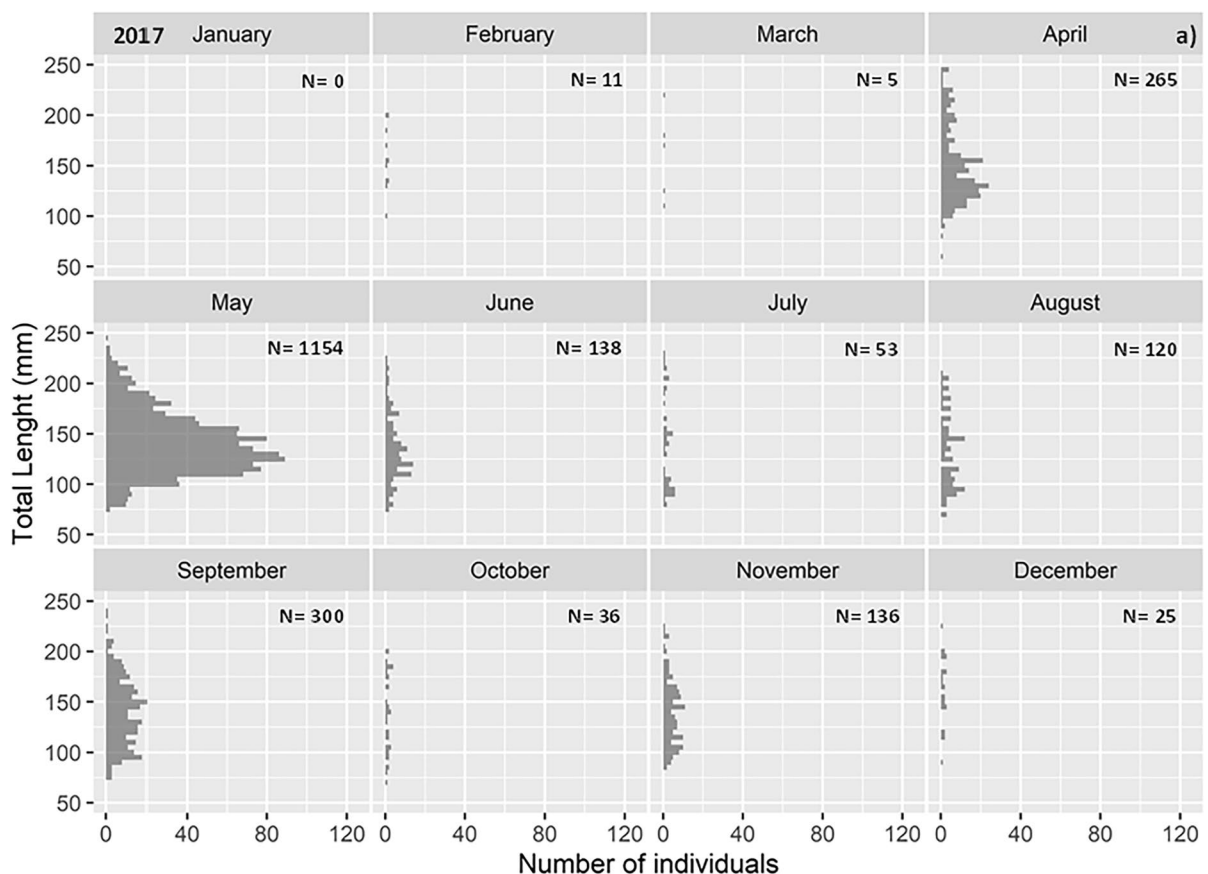


Fig. 2 Monthly variation in the number of yellow eels that used the eel ladder over the study period **a** 2017; **b** 2018; **c** 2019). “N” represents the total number of individuals measured in each month

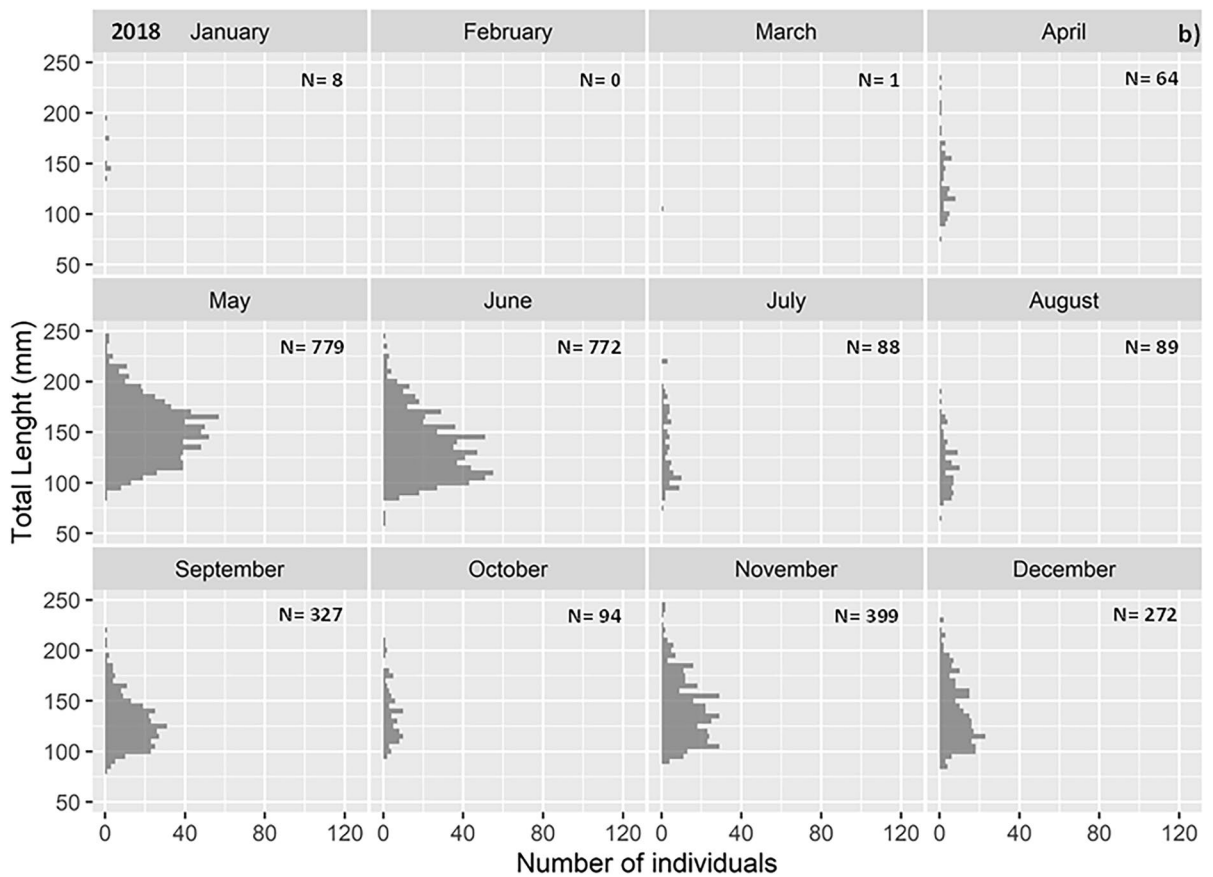


Fig. 2 (continued)

where $Mean_{md}$ is the dependent variable of mean number of individuals per day; $s(MinTemp, k=20)$ denotes the thin plate regression spline function applied to the covariate minimum water temperature, with a “ k ” dimension of 20; $s(RfMean10, k=7)$ the thin plate regression spline function applied to the covariate mean 10-day river flow, with a “ k ” dimension of 7; $s(Photop, k=15)$ the thin plate regression spline function applied to the covariate photoperiod, with a “ k ” dimension of 15 and $Precip$ the covariate precipitation.

Among the four environmental variables retained in the final GAM model, minimum water temperature and photoperiod were the most relevant (p -value < 0.001) variables explaining the upstream movement of juvenile eels. Precipitation and mean 10-day river flow although less relevant (p -value < 0.01 and p -value < 0.05, respectively) were also retained by the model.

The response curves showing the effects of significant variables on upstream movements, where positive and negative values indicate increasing and decreasing influence on these movements, are represented in Fig. 4.

The minimum water temperature plot shows that upstream movements occurred over the temperature range 7.5–22.4 °C (see Table 1), but the intensity of these movements varied (Fig. 4a). Minimum water temperature below 13.5 °C had a negative effect on movements, with values below 9.0 °C accounting for less than 1% of total movements. Movements are clearly favoured when the minimum temperature rises above 15.0 °C, with 51% of movements occurring between 15.0 and 19.0 °C, and a peak at around 16.0 °C although, 21% of the movements occurred with temperatures above 20.0 °C.

Regarding the photoperiod, upstream movements are more likely to occur when the daylight hours

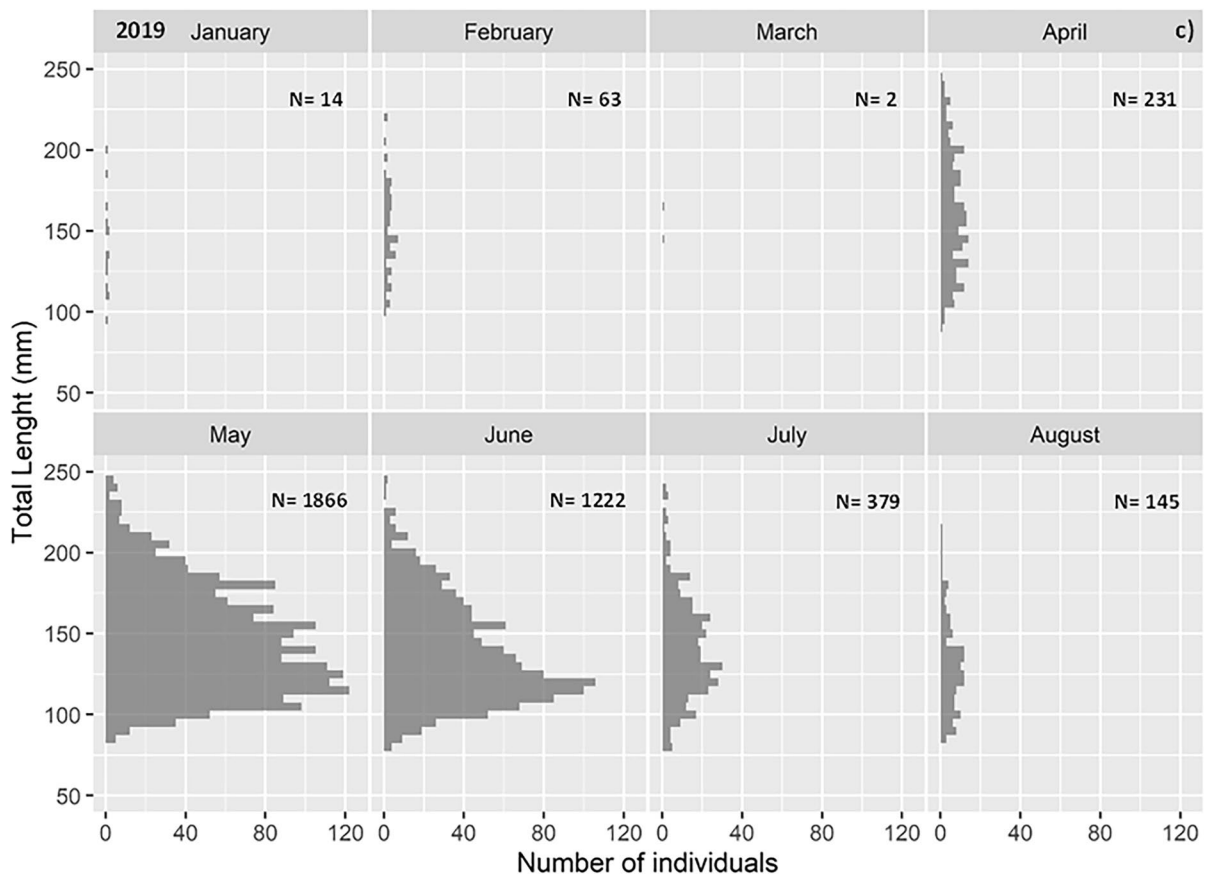


Fig. 2 (continued)

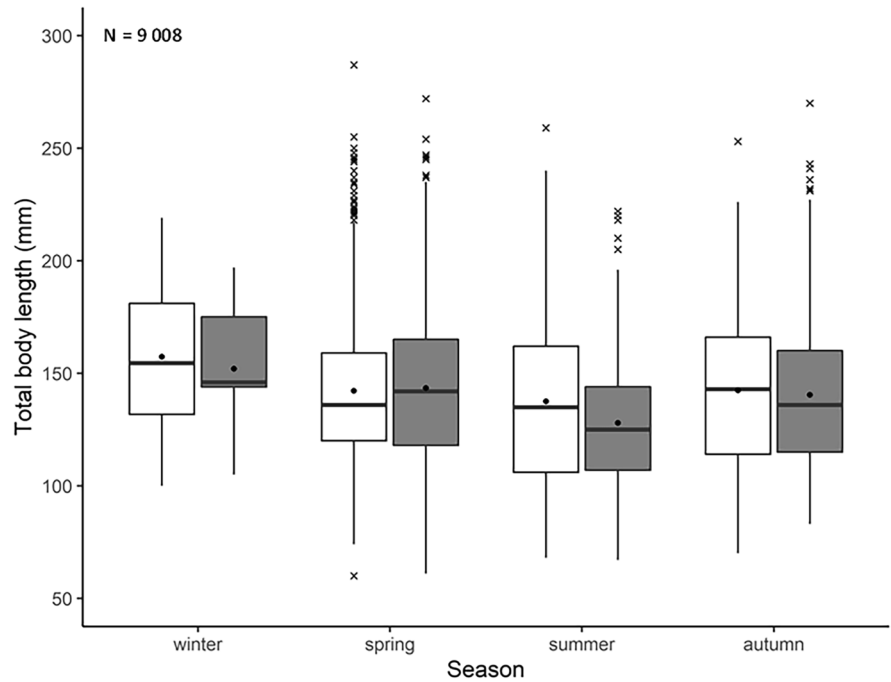
last more than 800 min, i.e. around 13 h (Fig. 4b). According to the monitoring data (Fig. 5), the peak of upstream movements occurs in May and June when the daylight hours last between 840 and 900 min, i.e. 14 h and 15 h respectively (Fig. 4b). Despite a weaker positive response, upstream movements of juvenile eels also occur during the autumn (October, November and December) when the daylight hours last between 540 and 600 min, i.e. 9 h and 10 h, respectively.

Precipitation has a positive linear response with the upstream movement of individuals (coef. = 0.09) in the entire range (0.0–14.0 mm) (Fig. 4c). The upstream movements of juvenile eels are most likely to occur with mean 10-day river flow ranging between ca. $30.0 \text{ m}^3\text{s}^{-1}$ and $160.0 \text{ m}^3\text{s}^{-1}$ (Fig. 4d).

When combining the monthly variation of the total number of individuals that used the eel ladder over the 2.5-year period and the minimum

water temperature of those months, it is possible to see that the onset of the progression starts in April, when the temperature reaches a mean minimum value ranging from 12.6 to 16.4 °C, followed by the peak observed consistently in May and June (74% of the movements) (Fig. 5). The low temperatures (<12.0 °C) observed between January and March of each year and in December 2017 appear to inhibit upstream movements, resulting in the lowest catches recorded during the study period. However, minimum water temperatures consistently above 20.0 °C (July–September) also contributed to the reduction in eel upstream movements, which is reflected in a decrease in the number of specimens caught in the trap. This reduction is clear in 2017 when temperatures reached that value earlier. In total, 93% of the movements occurred between April and September, i.e. during spring and summer.

Fig. 3 Boxplot for total length (mm) of juvenile eels moving upstream in the Mondego River, by Season, and grouped by Years 2017 (white rectangle) and 2018 (grey rectangle). The slash (–) and the dot (●) across the box marks represent the median and mean, respectively. Extreme values are indicated by stars above and beneath the boxplots (*). N represents the number of individuals used in the analysis



Discussion

In the Mondego River, located in the southern part of *A. anguilla* distribution area, a strong peak of upstream movements of juvenile yellow eels

consistently occurs in spring, with a start in April and a peak in May–June (74% of the annual upstream movements). This study complements the latitudinal gradient reported (ICES 2020), showing that there is a difference of almost 2 months in the peak

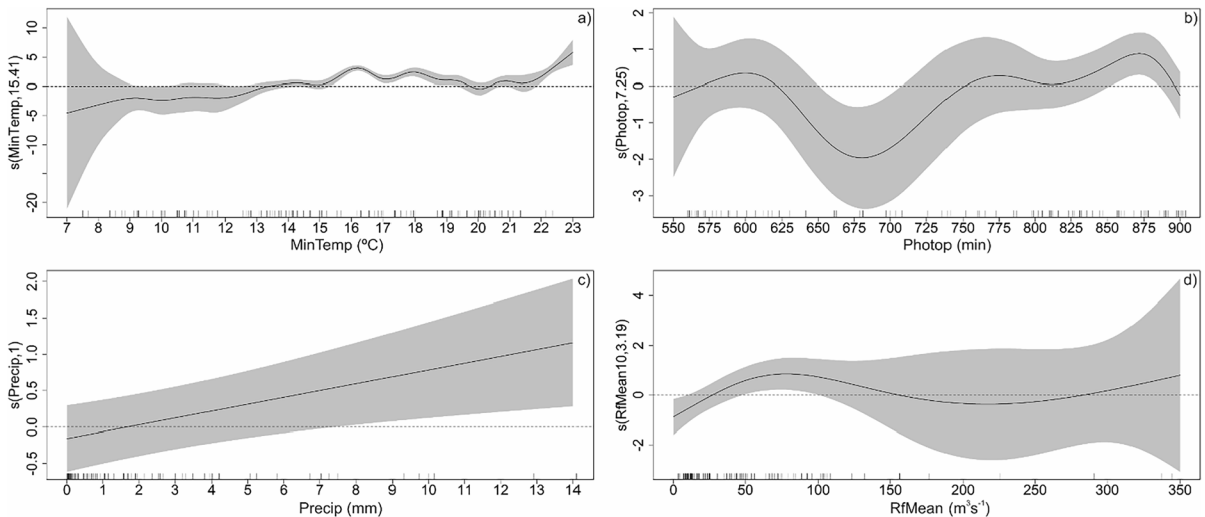


Fig. 4 Response curves of the upstream movement of juvenile eels ($Mean_{ind}$) to environmental predictors selected by the GAM model (centre lines): **a** minimum water temperature; **b** photoperiod; **c** precipitation; **d** mean 10-day river flow. The y-axes are based on partial residuals and show the relative influence of each explanatory variable on the prediction.

The values in brackets in the y-axes are the smooth criterion applied automatically. The shades that accompany the centre line are the 95% confidence band. Thick marks in the x-axes represent the observations. Horizontal dashed line represents the zero y-axes

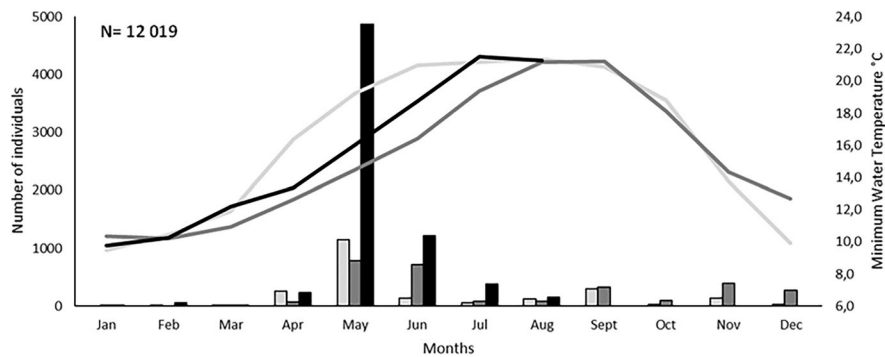


Fig. 5 Monthly variation in the total number of individuals trapped in the eel ladder over the study period (bars: 2017 (white bar); 2018 (grey bar); 2019 (black bar)) and in the mean

daily minimum water temperature, one of the most relevant environmental predictor selected in the GAM model (lines: 2017 (white line); 2018 (grey line); 2019 (black line))

of upstream movements between the southern (this study) and northern areas of the species distribution (Vøllestad and Jonsson 1988). In Norway, located at higher latitudes in the Northeast Atlantic, juvenile yellow eels colonise the watersheds in summer, between June and September, peaking in July (Vøllestad and Jonsson 1988). In the UK rivers, movements start with small quantities of eels in late April, peaking in June–July with a consistent decrease to zero (Naismith and knights 1988; White and Knights 1997a). In Ireland, at a similar latitude to the UK, upstream movements begin in May, also peaking in June–July, and decreasing again to almost zero values from September onward (Moriarty 1986). In France, upstream movements peak in May–July with a progressive decline starting in the autumn (e.g. Acou et al. 2009). This evident latitudinal gradient has already been described in the literature (ICES 2020), but a striking difference in the present study is that, after the peak of ascending individuals in May–June, a sharp decline was consistently observed in the following months (July–August), followed by a modest increase of movements until December (13.2% of all movements). There was almost no movement between January and March. What can cause the reduction in upstream movements?

Water temperature, a well-known predictor ruling the upstream movements of both tropical (e.g. Sloane 1984) and temperate eels (Moriarty 1986; Vøllestad and Jonsson 1988; White and Knights 1997a; Acou et al. 2009; Welsh and Liller 2013; Kume et al 2022), was also identified in the present study as an important factor in regulating A.

anguilla movements. Temperatures above 13.0 °C, which in the Mondego River usually start to occur in April, seem to favour the beginning of movements, with 51% of movements occurring between 15.0 and 19.0 °C. These values are within the range of previous findings at distinct latitudes (Moriarty 1986; White and Knights 1997a; Feunteun et al. 2003; Acou et al. 2009). However, contrary to these (i.e. Moriarty 1986; Vøllestad and Jonsson 1988; White and Knights 1997a), the continued increase in water temperature during the summer months was not associated with a consistent increase in upstream movements. On the contrary, during the period with higher minimum water temperatures (> 20.0 °C), a decrease of movements is observed. The continuous recruitment in Mondego along the year (Domingos 1992), and the fact that the smallest individuals were caught in summer, suggests that minimum water temperature constantly above 20.0 °C may suspend the upstream movement of juvenile eels. Nevertheless, given the positive rheotactic behaviour exhibited by yellow eels (Tesch 2003) and the fact that the reduction in river flow is abrupt in the summer, comparatively to more northerly river basins, one cannot exclude the possibility that reduced river flow values may also restrict the upstream movement intensity, as supported by the model for average river flows below 30 m³s⁻¹. Juvenile eels preferred to move upstream during late Spring (May–June), a period associated with a longer duration of the light hours per day. Although there is a perception that eels move during night, this increase of movements during shorter nights

might be related with the impact of sun exposition in river water warming that allows them to progress upstream at night benefiting from warmer water.

Although water temperature is usually favourable until December (average water temperature = 14.3 °C, ranging between 8.4 °C and 21.3 °C), the increase of movements from September onwards can also be explained by the positive relationship found with precipitation, as already shown by Feunteun et al. (2003) and Santos et al. (2016). As the first rains start to occur, with the subsequent increase in river flow (Supplemental Fig. 2), movements resumed, which does not occur in the northern regions where the movements cease in the autumn. Thus, it is likely that the prolonged favourable water temperature, the increase in river flow and continuous recruitment throughout the year, is the reason for this increase in movements in autumn. The period with lower movements, January to March, corresponds precisely to the period where water temperature is lower (constantly below 13.0 °C) and river flow values higher, both promoting less favourable conditions for upstream movement (Supplemental Fig. 2).

This study points out the importance of temperature and river flow in ruling the upstream movement of juvenile eels. Considering these findings in a global warming scenario, a shift in the peak of movements may occur, or the sharp decline of movements observed in the warmer summer months may extend over longer periods in the southern distribution area of *A. anguilla*. Thus, a reduction in the time window used by juvenile eels to colonise upstream habitats, associated with increased temperature and reduced river flow, may promote increased densities downstream, especially below obstacles when they are present. These changes can extend to the species northern distribution range, promoting an extension of the colonisation period. From a management perspective, the results herein presented can be used to establish the appropriate time window to monitor eel ladders and ensure all the conditions necessary to promote efficient passage. This is particularly relevant for obstacles where manual upstream transposition actions are conducted, or in situations where the period of functioning (and monitoring) of eel ladder devices needs to be maximise on a cost–benefit principle.

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Data availability Data will be available upon reasonable request.

Declarations

Ethical approval This study was carried out in strict accordance with the recommendations present in the Guide for the Care and Use of Laboratory Animals of the European Union 62/2010—in Portugal under DL no. 129/92, Portaria no. 1005/92 and DL 113/2013. Individual permissions to collect specimens were provided by the Institute for Nature Conservation and Forestry, I.P. (ICNF, IP).

Conflict of interest The authors declare no competing interests.

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