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Environmental influences on the recruitment dynamics of juvenile European eels, *Anguilla anguilla*, in a small estuary of the Tyrrhenian Sea, Sardinia, Italy

Cinzia Podda[1] | Francesco Palmas[1] | Giacomo Frau[1] | Giovanna Chessa[2] |
Jacopo Culurgioni[2] | Riccardo Diciotti[2] | Nicola Fois[2] | Andrea Sabatini[1]

[1]Department of Life and Environmental Sciences, University of Cagliari, Cagliari, Italy

[2]Ichthyic Products Research Service, Agris-Agricultural Research Agency of Sardinia, Bonassai, Italy

Correspondence
Francesco Palmas, Department of Life and Environmental Sciences, University of Cagliari, Via Fiorelli 1, 09126 Cagliari, Italy.
Email: fpalmas@unica.it

Abstract

1. The European eel, *Anguilla anguilla*, is a catadromous and migratory species of commercial importance. Its complex life cycle results in its exposure to many risk factors, which have resulted in stock declines across all life stages since the 1970s.

2. The temporal recruitment dynamics of juvenile eels (glass eels and elvers) were investigated in a small Mediterranean estuary (Sardinia, Italy). The composition of the population and the monthly and seasonal variations in the abundances of juvenile eels was assessed over 78 sampling events (from February 2017 to February 2018). Furthermore, the effects of abiotic variables on the abundances of glass eels and elvers were investigated using generalized additive models (GAMs).

3. Glass eels had the greatest abundance during the winter months, whereas elvers had the greatest abundance during spring. Modelling revealed that the abundance of glass eels was mostly explained by the combined effects of water temperature (12.3–14.5 °C), tidal coefficient (40–110 cm), moon phase, season, and river mouth condition, whereas the abundance of elvers was associated with water temperature (14–21 °C), dissolved oxygen content (>7 mg/L), and season. These results suggest that the annual recruitment of juvenile eels occurs throughout the year, with clear seasonal migration dynamics.

4. The use of multiple statistical approaches allowed us to identify the importance of several environmental variables in regulating the recruitment dynamics, providing useful information for conserving eel stocks through the restoration of the natural flow regime and the connectivity between freshwater habitats and the sea.

KEYWORDS
Anguilla anguilla, environmental factors, GAM, juvenile recruitment, Mediterranean Sea, small estuary

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Cinzia Podda and Francesco Palmas contributed equally to this work.

1 | INTRODUCTION

The European eel, *Anguilla anguilla*, is a catadromous, highly migratory, and euryhaline species of commercial importance (Tesch, 2003). The species' continental distribution extends over Europe and northern Africa, from Morocco to Norway, and throughout the Mediterranean and the Baltic Seas (Dekker, 2003; Tesch, 2003). The European eel has a complex life cycle, during which a growth phase occurs in continental waters and panmictic reproduction occurs in the Sargasso Sea (Als et al., 2011; Amilhat et al., 2016; Andrello, Bevacqua, Maes, & De Leo, 2009). After spawning events, leptocephali are transported along the Gulf Stream and North Atlantic Drift on a long journey that lasts 7–12 months (Arai, Otake, & Tsukamoto, 2000; Boëtius & Harding, 1985; Lecomte-Finiger, 1992). On reaching the continental shelf, leptocephalus larvae undergo a first metamorphosis into glass eels and colonize estuarine, coastal, and river habitats (Kleckner & McCleave, 1982; McCleave & Kleckner, 1982). After entering continental waters, eels undergo an acclimation period to adjust to freshwater (Birrel, Cramb, & Hazon, 2000; Ciccotti, Macchi, Rossi, Cataldi, & Cataudella, 1993) before completing their migration into continental feeding habitats as elvers and yellow eels (Van Ginneken & Maes, 2005). After a long feeding and growing period (of more than 20 years) (Naismith & Knights, 1993; Tesch, 2003), eels undergo a second metamorphosis into adult silver eels and finally migrate and spawn in the Sargasso Sea (Amilhat et al., 2016).

This complex life cycle exposes European eels to many risk factors contributing to the decline of the species, although the exact causes have not yet been clearly established because of difficulties in assessing spawning stock abundance (Dekker, 2001; Friedland, Miller, & Knights, 2007; Harrison, Walker, Pinder, Briand, & Aprahamian, 2014; Knights, 2003; Moriarty & Dekker, 1997). Several factors have been proposed as being responsible for this crisis (Dekker, 2003; Miller, Feunteun, & Katsumi, 2016), including potential threats related to the cumulative effects of human impacts, such as overfishing (Dekker, 2004; International Council for the Exploration of the Sea (ICES), 2002), habitat loss (Knights, 2003; McCleave, 2001), the presence of pathogens (Culurgioni et al., 2015; Culurgioni, Sabatini, De Murtas, Mattiucci, & Figus, 2014; Lefebvre, Contournet, & Crivelli, 2007; Palstra, Heppener, van Ginneken, Székely, & van den Thillart, 2007), pollution (Capaldo et al., 2012; Van Ginneken et al., 2009), and ocean climate changes (Castonguay et al., 1994; Jacoby et al., 2015; Miller et al., 2016, 2009). With all life stages of the European eel having been in decline since the early 1970s, the stock reached its lowest level in the last few decades, with variable impacts on fisheries (Aalto et al., 2015; Bornarel et al., 2018; ICES, 2015). In Sardinia, based on commercial fishery data recorded in coastal lagoons, this decline was already evident in the 1950s (Moriarty & Dekker, 1997). As a consequence, in 2007 a European Council Regulation established that all EU members must define and implement protection and conservation measures for the recovery of the European eel stock (European Council, 2007). In Italy, the national plan indicates Sardinia as a single eel management unit (EMU). In Sardinia, the fishing of glass eels is forbidden and it is expected that

any individual with a total length of <28 cm is immediately released (regional decree no. 2617/DECA/53; September 27, 2018). The European eel was also added to CITES Annex II in order to control its international trade, and in 2008 it was listed as Critically Endangered in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2014).

Juvenile eels (glass eels and elvers) represent the recruitment phase to continental waters (ICES, 2011) and exhibit variable abundances, depending on latitudinal, morphological, climatic, hydrodynamic, and site-specific abiotic factors (Harrison et al., 2014; Trancart, Lambert, Daverat, & Rochard, 2014). The timing of recruitment and the spatial dynamics at a local scale have already been characterized for many estuaries and rivers located on the Atlantic coast of Europe (Arribas, Fernández-Delgado, Oliva-Paterna, & Drake, 2012; Beaulaton & Castelnaud, 2005; Bru, Prouzet, & Lejeune, 2009; Harrison et al., 2014; Walmsley, Bremner, Walker, Barry, & Maxwell, 2018). Only sporadic information is available along the Mediterranean coastline, however, and most of these data are restricted to the northern part of the western basin (Ciccotti, Ricci, Scardi, Fresi, & Cataudella, 1995; Crivelli et al., 2008; Gandolfi, Pesaro, & Tongiorgi, 1984; Leone et al., 2016; Westerberg et al., 2018; Zompola, Katselis, Koutsikopoulos, & Cladas, 2008). Juveniles may settle in coastal waters throughout the year, with recruitment peaks occurring at different times depending on latitudinal gradients (Zompola et al., 2008 and references therein). Along the north-western coast of the Mediterranean Sea the recruitment peaks are usually observed from autumn to spring (Crivelli et al., 1995, 2008;), whereas in the Tyrrhenian Sea the peak also occurs during winter (Ciccotti et al., 1995; Gandolfi et al., 1984).

The recruitment process has been studied along the Mediterranean and Atlantic European coasts and appears to be controlled by an interaction between physiological and abiotic factors (water temperature, river discharge, salinity, lunar phases, tidal cycle, turbidity, rainfall, and water odours) (Edeline, Lambert, Rigaud, & Elie, 2006; Jellyman, Booker, & Watene, 2009; Zompola et al., 2008); however, most of the data currently available almost exclusively concern large estuary systems. The influence of environmental factors on eel recruitment in small-scale systems remains poorly studied. Although the behavioural and environmental processes that modulate recruitment patterns are reasonably well understood, site-specific factors may play a significant role in determining fine-scale distribution patterns at an individual small coastal system level. Therefore, the aims of this study were: (i) to analyse the temporal recruitment pattern of juvenile eels in a small Mediterranean estuary; and (ii) to model the effects of abiotic factors on recruitment dynamics.

2 | METHODS

2.1 | Study area

The study was conducted in the Pramaera River, Sardinia, Italy, a typical Mediterranean small watercourse characterized by a transient

FIGURE 1 Map of the Pramaera River, located on the central–eastern coast of Sardinia
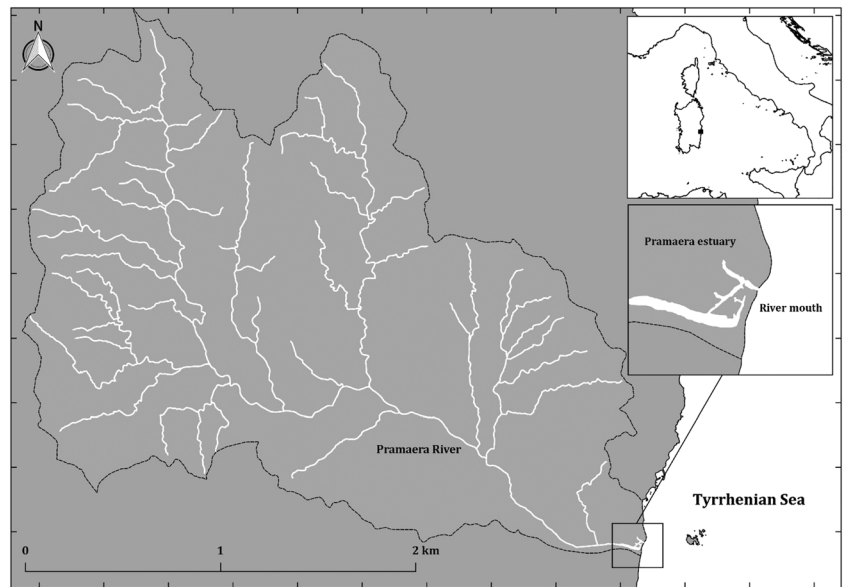
torrential regime and summer dryness. The watercourse is 10 km long, has a catchment basin of 180.7 km^2, and is entirely located in central–eastern Sardinia (Figure 1). The Pramaera River does not currently experience fluvial interruptions of anthropogenic origin (i.e. dams or other artificial barriers). The study focused on the stretch of the river located near the river mouth (39°58.312′N, 9°41.175′E). This area is characterized by brackish water, with a mean river width of 15 m. In the Pramaera estuary, artisanal fishing is carried out in the freshwater habitat and in the river mouth using fyke nets and gillnets to target euryhaline fish species (mullets and seabass), and particularly eels. The Pramaera river mouth has an estuarine typology, assuming a funnel shape when the watercourse flows into the sea, and it is characterized by a substrate that is largely dominated by sand. Such substrate, together with hydrological forces, river flow rate, precipitation, and tidal flow, mainly affects changes in river mouth hydromorphology. Sudden extreme events (such as floods or sea storms) can modify the river mouth morphology very quickly. The shores of the river mouth near to the sea are characterized by a lack of vegetation, whereas the area further back from the sea is characterized by the presence of reeds and rushes, which is typical of the Mediterranean retro-dune environment.

2.2 | Data collection

Sampling campaigns were carried out monthly from February 2017 to February 2018 during the weeks of the new moon (De Casamajor, Bru, & Prouzet, 1999; Elie & Rochard, 1994), with the goal of catching juvenile eels at different times during their upstream migration and different phases of the settlement process. To evaluate the abundance of juvenile eels entering the watercourse from the sea, three experimental fyke nets (3.2 m long, two chambers, 31 and 28 cm wide, with 2-mm mesh size and two wings of 2.5 m) were installed near the river mouth, approximately 50 m from the sea (with one along each bank

and one in the middle), with their mouths facing to the sea in order to capture individuals arriving from the sea. The sampling started at sunset and ended in the early hours of dawn. The fyke nets were inspected, when possible, every morning over seven consecutive days. Although this sampling allowed all eel stages to be captured, it was designed to be stage selective (with a mesh size of 2 mm). Only glass eels (<7.4 cm, unpigmented eels) and elvers (<15 cm, pigmented eels) were considered separately in the present analysis.

All captured individuals were immediately placed in containers (20 L) filled with river water and anaesthetized by immersion in a bath of clove oil (eugenol dissolved in ethyl alcohol) (Walsh & Pease, 2002). The glass eels and elvers captured on each sampling day were counted and weighed separately. Catch per unit effort (CPUE, hereafter referred to as 'abundance') corresponded to the total number of individuals caught per day divided by the number of fyke nets used on that same day (n individuals/n fyke nets). When total catches were high, a subsample of 50 individuals was randomly selected for further measurements. The total length (TL, to the nearest mm) and total weight (TW, to the nearest 0.01 g) of each individual were measured directly in the field. Once the measurements had been taken, the eels were transferred to another container (20 L) with a continuous supply of river water for recovery and were monitored for 1 hour before their release upstream of the fyke nets.

These biotic data were used to analyse the relationship between TL and TW for both the glass eel and the elver stages using regression analysis (Ricker, 1973, 1975). Monthly and seasonal size differences were compared separately for each stage using the Kruskal–Wallis non-parametric test (K–W, $P < 0.05$). Seasonal variation in abundance was assessed by plotting the mean monthly capture trend (±SE, standard error) for each stage.

Environmental parameters were also measured on each sampling day using a multiparameter probe (smarTROLL Multiparameter Handheld, InSitu Europe, North Moons Moat, Redditch, Worcs. B98 9ND, United Kingdom), including the water and air temperatures (°C),

salinity, pH, dissolved oxygen content (mg/L), and oxygen saturation levels (%). In addition, rainfall (mm), moon phase, tidal coefficient (cm), and river mouth condition were recorded. Rainfall data were provided by the regional meteorological department (Sardinia Environmental Protection Agency, ARPAS) from three meteorological stations situated in the area of the Pramaera River basin and were estimated as the average rainfall recorded during the week before each sampling date. Moon phase data were collected using an online application (https://www.calendario-365.it/luna/calendario-lunare.html). Because sampling was performed during the week of the new moon for each sampling campaign, this covered a period of the waning moon (i.e. the days before the new moon), the new moon, and the waxing moon (i.e. the days after the new moon). The tidal coefficient was also recorded for each day of sampling, which was calculated as the difference in height between consecutive high and low tides. Finally, river mouth condition was considered as a local factor (open or nearly open river mouth). A summary of the environmental features of each season is given in Table S1.

2.3 | Model analysis

Before undertaking the modelling, the abundance data were tested for normality (Shapiro–Wilk test, S–W, $P < 0.01$) and homogeneity of variance (Levene's test, $P < 0.01$), which showed that they had a non-normal distribution. Therefore, to address this and to handle zero inflation, which seriously affects juvenile eel samples, a Tweedie distribution family was fitted to the abundance data (Augustin, Trenkel, Wood, & Lorance, 2013; Shono, 2008).

For the abiotic parameters, the Zuur, Ieno, and Elphick (2010) protocol was followed, whereby collinearity was examined by computing pairwise scatter plots that compared continuous covariates, and those combinations that had relevant Spearman's rho coefficients ($\rho > 0.7$) were discarded prior to modelling. The variance inflation factor (VIF) was also used to check collinearities among the predictive variables, and variables with VIF > 3 were discarded. Data exploration revealed nonlinear patterns among the response variables, so juvenile abundance (dependent variable) and its relationships with environmental, temporal, and site-specific variables were described using generalized additive models (GAMs) by a log link function (Hastie & Tibshirani, 1990; Maunder & Punt, 2004). Seasons and moon phases (waning, new, or waxing moon) were included as temporal factors, whereas river mouth conditions (open or nearly open) were included as a site-specific factor. Only days on which the river mouth was open or nearly open were included in the analysis, because a closed river mouth represents a physical barrier to the ascent of juvenile eels. A GAM can be considered a generalized linear model in which part of the linear predictor is specified as a sum of the smooth functions (smooth function, s) of the predictor variables and where the challenge is to find suitable parametric representations for the smooth functions and to control the degree of smoothness appropriately (Wood & Augustin, 2002). A stepwise backward selection procedure was implemented to identify the best-fitting model, based on the minimization of Akaike's information criterion (AIC) (Akaike, 1973).

At each step in the selection procedure, the variables with the highest P values ($P > 0.05$) were dropped to produce a model with a lower AIC, and backward selection continued until the lowest AIC was reached.

The total explained deviance and the relative contribution of each factor were evaluated for each model, and the performance of the models was evaluated with cross-validation using the Pearson's correlation coefficients between the observed and predicted abundances. All statistical analyses were performed using R 3.3.1, with a significance level of $P < 0.05$ (R Core Team, 2018), and the GAM approach, as proposed by Wood (2006), was performed using the library mgcv 1.8-12.

3 | RESULTS

### 3.1 | Population structure and seasonal migration

Twelve sampling campaigns were carried out from February 2017 to February 2018 during the weeks of the new moon. The river mouth was closed during the campaign of November 2017, so these data were not available for the analysis. The total catches over the entire study period were 28,999 glass eels, weighing 7,212.68 g, and 620 elvers, weighing 640.28 g. A total of 2,064 glass eel and 313 elver specimens were measured during the 78 sampling events. There was a negative allometric relationship between size and weight for the glass eels that favoured body length development ($b = 2.70$, $R^2 = 0.82$, $y = 0.0014x^{2.70}$) (Figure 2a). The mean values for TL and TW (mean ± SD) for glass eels were 6.3 ± 0.33 cm and 0.25 ± 0.04 g, respectively. The largest individual was captured in winter (7.4 cm and 0.33 g), whereas the smallest was captured in spring (5.2 cm and 0.12 g); however, there was no significant difference in the median TL of glass eels among the months and seasons (K–W, $P > 0.05$) (Figure 3a). On average, higher glass eel abundances (mean ± SE) occurred during the winter months (February 2017, 281.8 ± 242.24 individuals per day; January 2018, 371.68 ± 98.63 individuals per day; and February 2018, 555.54 ± 153.66 individuals per day), whereas the lowest recruitment was observed from late spring to early autumn (with a minimum mean value in September of 1.5 ± 0.27 individuals per day) (Figure 3b). Overall, 80.45% of the glass eel catches were recorded in February 2017 and 2018, and in January 2018.

The size–weight relationships for elvers had allometric coefficients of >3 ($b = 3.19$, $R^2 = 0.91$, $y = 0.0008x^{3.19}$, Figure 2b). The mean values for TL and TW (mean ± SD) for elvers were 9.4 ± 2.4 cm and 1.03 ± 7.35 g, respectively, and size differences were detected among months, with the smallest elvers being captured in spring, after which time there was a progressive increase in TL during the summer and autumn months, so that the largest individuals were captured during the winter months (K–W, $P < 0.001$) (Figure 4a). The elver abundance (mean ± SE) was highest during spring, with two peaks in May and June (17.15 ± 4.59 and 12.62 ± 9.54 individuals per day, respectively, Figure 4b), representing 71.60% of the total catches. No elvers were captured in July and December.

FIGURE 2 Size–weight relationship for (a) glass eels (*n* = 2064) and (b) elvers (*n* = 313) from the Pramaera River
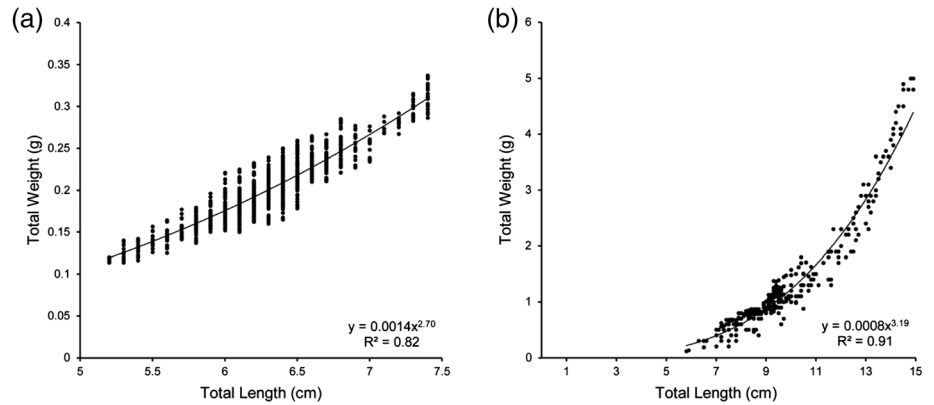
FIGURE 3 (a) Relationship between total length and month of the year for glass eels. (b) Relationship between catch per unit effort (CPUE, i.e. number per trap per day) and month of the year for glass eels. Box lengths represent interquartile ranges, bar lengths represent ranges, horizontal lines represent median values, and black dots represent mean values. Error lines represents the standard errors for each month. The black line denotes the trend of the CPUE data
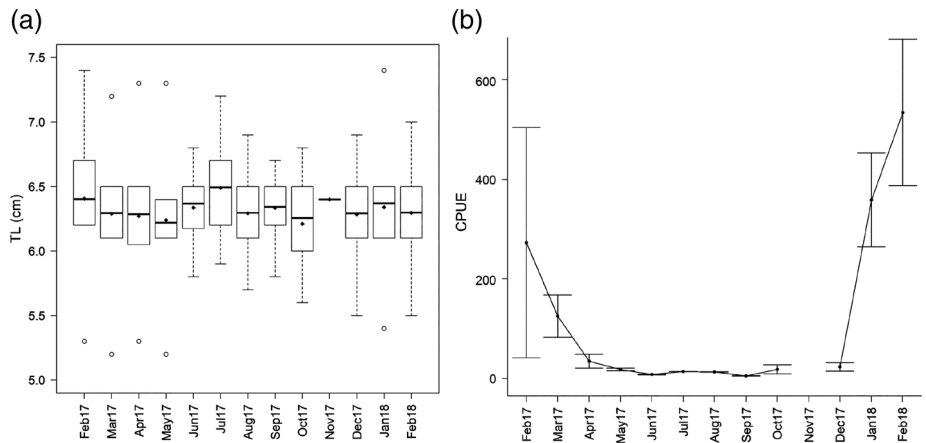
FIGURE 4 (a) Relationship between total length and month of the year for elvers. (b) Relationship between catch per unit effort (CPUE, i.e. number per trap per day) and month of the year for elvers. Box lengths represent interquartile ranges, bar lengths represent ranges, horizontal lines represent median values, and black dots represent mean values. Error lines represents the standard errors for each month. The black line denotes the trend of the CPUE data
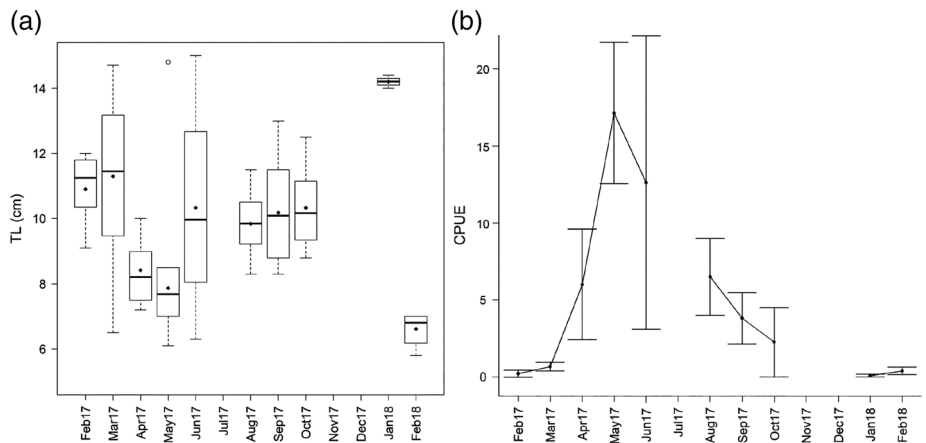

3.2 | Factors affecting juvenile eel abundance

Air temperature (°C), oxygen saturation (%), pH, and salinity were eliminated from the analysis based on the VIF criteria used. Therefore, in the modelling, water temperature (T), dissolved oxygen (DO), rainfall (Rain), and tidal coefficient (Tide) were considered as continuous variables, and season (Season), moon phase (Moon), and river mouth condition (Mouth) were considered as categorical factors.

Three models were tested for glass eels (Table S2). The best model included five exploratory variables (AIC = 842.3): water temperature (T), tidal coefficient (Tide), seasons (Season), moon phase

(Moon), and river mouth condition (Mouth) (Table S3). The final model had a statistically significant goodness of fit and explained 66.1% of the total deviance. Examination of the relative contribution of each variable to the total explained deviance revealed that water temperature was the most important factor (48.7%), followed by tidal coefficient (10.4%). In addition, season, moon phase, and river mouth condition showed some importance, explaining 7% of the total deviance. The response plots for each variable included in the best-fitting GAM are shown in Figure 5. Glass eel abundance decreased at temperatures of 10–12 °C, to reach a local minimum at about 12 °C, and then increased to reach a maximum at approximately 14–15 °C.
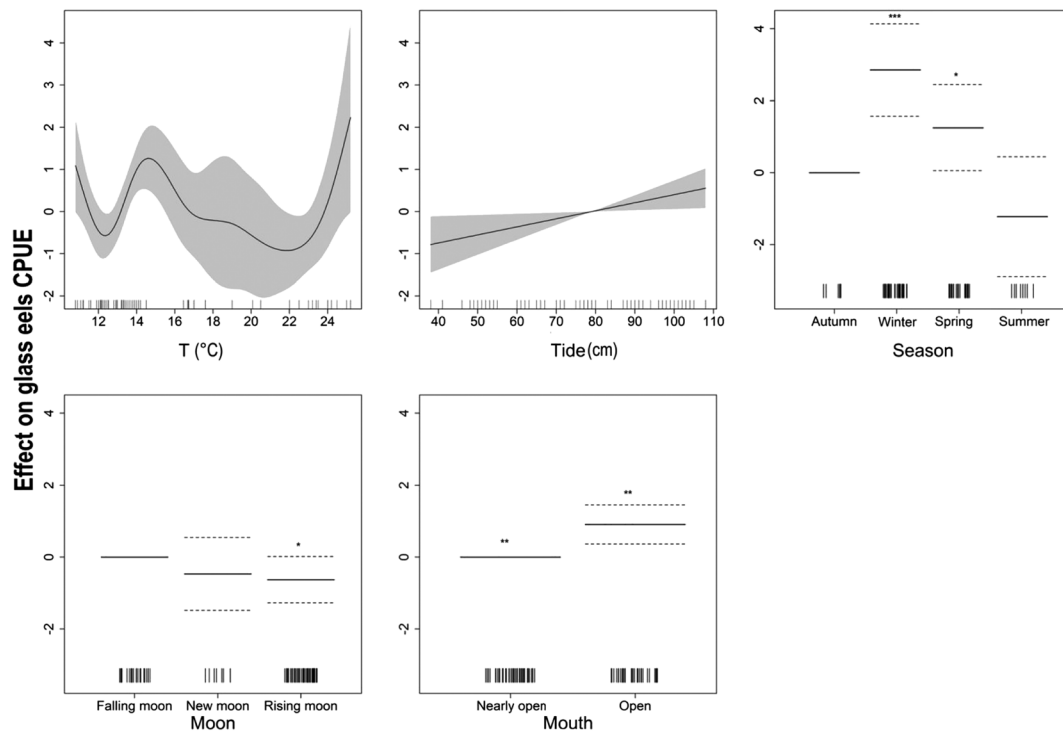
FIGURE 5 Generalized additive model (GAM)-derived effect of covariate modelling for the abundance (catch per unit effort, CPUE) of glass eels. Shaded areas and dashed lines indicate 95% confidence bands; tick marks on the *x*-axes of the depth plots indicate sampling intensity. The *y*-axis represents the partial effect of each variable

Temperatures above this resulted in relatively high variation. The probability of glass eel abundance was also significantly affected by season, reaching a maximum value in winter and a minimum value in summer. The likelihood of a large increase in abundance was clearly associated with an open river mouth condition. The abundance of glass eels increased steadily and positively with tidal coefficient, ranging from 40 to 110 cm. Finally, the model revealed that the waxing moon phase appeared to have a slight, but statically significant, effect on glass eel abundance. Cross-validation indicated a moderate correlation between the observed and fitted abundance values (CPUE, R^2 = 0.52, Figure S1a).

Five GAM models were tested for elvers, the best fitting (AIC = 268.9, Table S4) of which retained three of the nine covariates: water temperature (T), dissolved oxygen (DO), and season (Season) (Table S5). The final model explained 74.1% of the total deviance and all of the terms were significant. Examination of the relative contribution of the individual covariates indicated that water temperature (67.7%) and dissolved oxygen (5.09%) explained the largest level of the observed variation in elver abundance, whereas season had a relatively lower contribution to the model (1.31%). Response plots showed that elver abundance was positively related to water temperature, with the highest abundance occurring at 21 °C (Figure 6). In addition, the abundance of elvers was significantly affected by season, with a greater abundance being observed in spring, and was slightly positively related to the dissolved oxygen content (DO) for values >7 mg/L. The model validation that was developed showed good predictive power (R^2 = 0.68, Figure S1b).

4 | DISCUSSION

The recruitment of juvenile eels in a small estuary on the coast of the Tyrrhenian Sea in Sardinia occurred throughout the year, with evident seasonal migration dynamics. The period of maximum recruitment for glass eels was between winter and early spring, with peaks from January to March, matching the findings of previous studies conducted in estuaries along the Atlantic coast of south-western Europe and in the Mediterranean Sea (Aranburu, Estibaliz, & Briand, 2016; Arribas et al., 2012; Aschonitis et al., 2017; Ciccotti et al., 1995; Gandolfi et al., 1984; Zompola et al., 2008). Our findings also confirmed the results of previous studies conducted in Sardinia, which reported maximum concentrations of glass eels during the first few months of the year (Cau, Cannas, Gandolfi, & Rossi, 1982).

The TL of glass eels recorded in the Pramaera estuary ranged from 5.2 to 7.4 cm, which is lower than previous data reported for the eastern coast of Sardinia (Flumendosa River) (Cau et al., 1982). At a wider geographical scale, data from the Atlantic coast confirmed a decrease in TL in association with a decrease in recruitment (Desaunay & Guerault, 1997). At a seasonal scale, the differences in mean TL were quite moderate, with the lowest values recorded in spring. Similarly, Cau et al. (1982) found that glass eels that were captured in spring were smaller than those caught in the other seasons. Previous studies conducted in the European Atlantic and Mediterranean Tyrrhenian coast reported that glass eels entering the estuary in spring were shorter and lighter than those arriving in autumn and summer (Bardonnet & Riera, 2005; Gandolfi et al., 1984).

FIGURE 6 Generalized additive model (GAM)-derived effect of covariate modelling for the abundance (catch per unit effort, CPUE) of elvers. Shaded areas and dashed lines indicate 95% confidence bands; tick marks on the *x*-axes of the depth plots indicate sampling intensity. The *y*-axis represents the partial effect of each variable
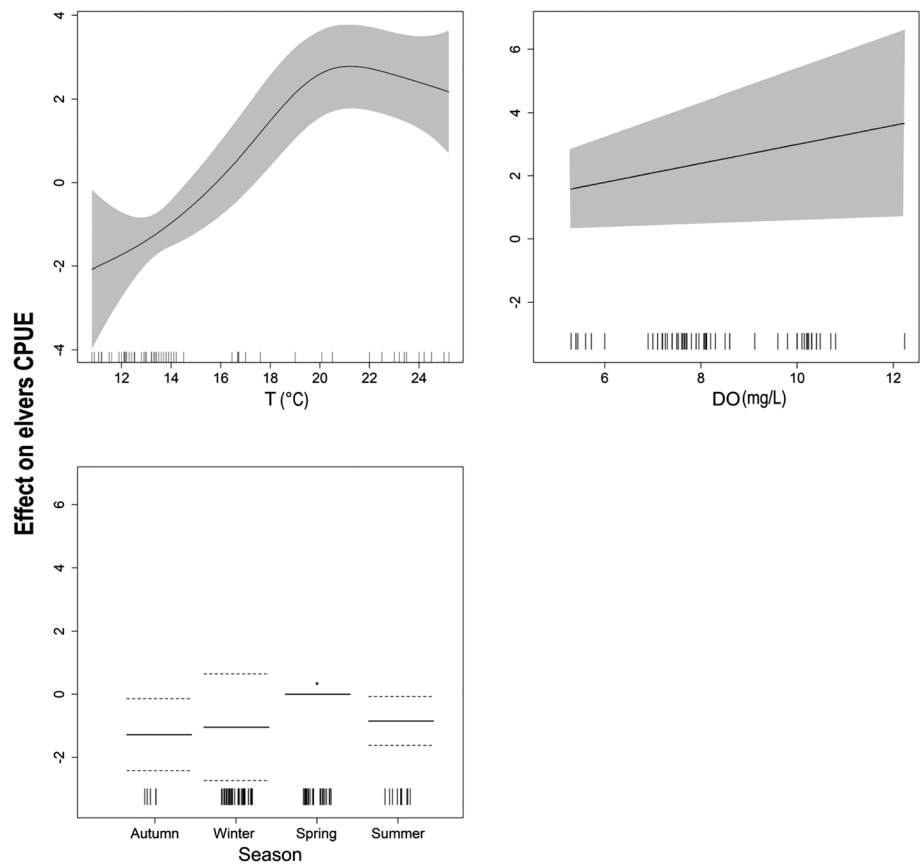
Recruitment of the elver stage in the Pramaera estuary began in late winter, peaked sharply in May, and persisted through October, supporting the findings of other studies conducted in both Mediterranean (Boëtius & Boëtius, 1989; Ezzat & El-Serafy, 1977; Gandolfi et al., 1984; Leone et al., 2016) and Atlantic estuaries (Naismith & Knights, 1988). The seasonal occurrence of elvers near the river mouth suggests a temporary period of residency during their upstream migration, and results in an increase in abundance and therefore an increase in their catchability. This pattern, which has also been observed in many previous studies (Bardonnet & Riera, 2005; Gascuel, Feunteun, & Fontenelle, 1995; Laffaille, Caraguel, & Legault, 2007; Naismith & Knights, 1988), was confirmed by the fact that the mean size of elvers in the Pramaera estuary increased from May to October. We hypothesize a horizontal active movement of the elvers from the river to the estuary, because they are prone to use the sandy area near the river mouth as a foraging ground.

The use of multiple statistical approaches allowed us to identify the importance of some environmental variables in the recruitment of juvenile eels. Our models, which were based on correlational observations in the field, revealed that water temperature is the most important factor controlling the abundance of glass eels. Similarly, water temperature has previously been reported as being one of the most significant predictors of the periodicity and magnitude of upstream eel migration among the numerous potential environmental factors (Arribas et al., 2012; Crivelli et al., 2008). Our results support the

findings of previous studies that glass eels become inactive and less susceptible to capture when the water temperature drops below a threshold of 10–12 °C (Edeline et al., 2006; Gascuel, 1986); however, the active migration of glass eels was associated with temperatures of 12.3–14.5 °C, which were often recorded during the winter season (12 ± 0.15 °C), and this was statistically confirmed by the model.

The conspicuous abundance of glass eels was predicted to be associated with the open river mouth condition. Sardinian rivers tend to represent intermittently estuarine systems as a result of the large water-level fluctuations that are caused by summer drought conditions (Sabatini et al., 2011; Sabatini et al., 2018). Such estuaries are closed off from the sea for varying periods by a sandbar that develops at the mouth when there is little to no water discharge (Suari et al., 2019). These systems are also subject to rapid changes over short periods of time during mouth opening and river flooding events, however, which are generally associated with heavy rainfall. In these types of estuaries, prolonged mouth closure leads to a cumulative discharge of fresh water, which acts as a lure that guides glass eel migration (Crivelli et al., 2008). Supporting this, laboratory experiments have shown that chemical stimuli, such as geosmine, play an important role as inland water markers that are involved in the orientation of glass eels towards fresh water (Tosi & Sola, 1993; Tosi, Spampanato, Sola, & Tongiorgi, 1989). The recruitment of glass eels was also associated with an increase in the tidal coefficient. Even if the tidal range is extremely reduced in the Mediterranean Sea in comparison with the Atlantic Ocean, the tides would continue to move water in and out of

the estuary, potentially exerting a strong influence on glass eels, which might be carried by the tidal currents. This result confirms previous experimental evidence, indicating that the tidal cycle plays a pivotal role as a migration vector to fresh water for glass eels (Aranburu et al., 2016; Ciccotti et al., 1995; Gandolfi et al., 1984). The moon phase also influenced the upstream migration of glass eels in the estuary, with higher catches being obtained around the time of the waxing moon. An association between glass eel migration and lunar phases has been widely reported in the literature (Leone et al., 2016; Milardi, Lanzoni, Gavioli, Fano, & Castaldelli, 2018; Sorensen & Bianchini, 1986), but this link has been mainly attributed to the coupled relationship between the moon and the tide (Tesch, 2003). Finally, the results revealed that oxygen concentration, salinity, and rainfall were not significantly correlated with glass eel abundance in the study area. Other environmental factors, not investigated in this study, could explain the observed patterns in glass eel abundance. In this regard, coastal storms from the sea, and wind speed and direction have been suggested to affect glass eel migration towards the river mouth (Arribas et al., 2012; Lecomte-Finiger & Razouls, 1981; Leone et al., 2016).

Temperature was also found to be the most important predictor of the abundance of elvers in the Pramaera estuary, with higher abundances being observed at temperatures of 14–21 °C, which occur during spring. Seasonal water temperatures are often considered to influence the movements of elvers in lagoons (Leone et al., 2016), with most studies arguing that seasonal increases in water temperature are positively correlated with active swimming, upstream migration, growth, metabolism, and pigmentation along both the Atlantic and Mediterranean coasts (Boëtius & Boëtius, 1989; Edeline et al., 2006; Ezzat & El-Serafy, 1977). Dissolved oxygen showed remarkable temporal variability as a result of the combined effects of climatic factors, anthropogenic activities, and the specific features of the system. Seasonally, the maximum of dissolved oxygen recorded in spring could be related to the autotrophic production of oxygen by phytoplankton. Therefore, we hypothesize that the association with dissolved oxygen for values above 7 mg/L could be interpreted as an indirect effect related to the greater abundance of elvers during spring rather than an active preference. On the other hand, the European eel is able to tolerate relatively high levels of hypoxia (Trischitta, Takei, & Sébert, 2014), thanks to its ability to use both branchial and cutaneous modes of respiratory gas exchange (Tesch, 2003).

The present study has provided, for the first time, information on the behavioural and environmental factors that control juvenile eel recruitment in a small Mediterranean estuary. In this context, site-specific data represent valuable and robust tools to assess stock status, especially in data-poor situations, as asserted by ICES (2016). Our analysis suggests that the seasonal recruitment of European eels at the study site is similar to the patterns seen along the Atlantic coast of south-western Europe and the Mediterranean coast. Furthermore, the model demonstrated that the migration dynamics of juvenile eels is related to environmental, temporal, and site-specific factors, such as the water temperature, tidal coefficient, oxygen concentration, moon phase, and river

mouth condition. One key management measure to preserve juvenile eel recruitment in small Mediterranean watersheds could be to restore the thermal regime through river flow control. In particular, many of the small estuaries in Sardinia are intermittently and partly closed as a result of the reduction of natural freshwater flow as a consequence of the presence of dams and weirs. In this context, many authors have stressed the critical importance of maintaining natural flow conditions and connectivity between freshwater habitats and the sea (Besson et al., 2016; Ciccotti et al., 2014; ICES, 2011; Lafaille et al., 2005; Moriarty & Dekker, 1997). Therefore, further studies should be carried out to investigate the role of marine currents on the differences in the fluctuation dynamics of juvenile eels that are observed between the western and eastern sides of Sardinia (Cau et al., 1982). The use of Lagrangian models, which are already used to assess other species with pelagic larval forms in the Sea of Sardinia (Palmas, Olita, Addis, Sorgente, & Sabatini, 2017), could represent an important tool for investigating the dispersion and recruitment of larvae in the Mediterranean Sea. Such studies will be important not only to understand the recruitment dynamics of European eels in the Mediterranean Sea but also to predict the time of arrival of glass eels in proximity of the estuaries and the development of local management strategies.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

Conceptualization: AS, CP, FP, GC, JC, NF, and RD. Software: CP and FP. Formal analysis: AS, CP, FP, and RD. Investigation: AS, CP, FP, GF, JC, and RD. Writing – original draft preparation: AS, CP, and FP. Writing – review and editing: AS, CP, FP, GC, GF, JC, NF, RD. Funding acquisition: NF, GC, and AS.

ORCID

Francesco Palmas https://orcid.org/0000-0001-7171-6987

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.