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Original Article

Glass eel recruitment and exploitation in a South European estuary (Oria, Bay of Biscay)

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The size of the European eel population is below safe biological limits. To assess the status of the stock properly, it is necessary to increase the number of recruitment series based on scientific monitoring. In this study, the spatio-temporal variation in glass eel density in a South European Atlantic estuary, the Oria, has been examined using experimental fisheries and fishery data. Glass eel density was predicted using a mixed generalized additive model. Current and depth were selected as covariates and date as a random variable then extrapolated to the whole sampling point volume to obtain the daily recruitment (mean, 12.76 kg; range, 0–72.8 kg). The average seasonal daily recruitment and fishery data were combined to obtain the seasonal recruitment (mean, 1144 kg; range, 682–1593 kg) and exploitation rate (mean, 31.1%; range, 6.2–48.7%). The information of spatio-temporal dynamics in glass eel density gathered in this study will help to improve the design of a recruitment-monitoring scheme at the European level. The integration of glass eel fishery data and scientific estimates is crucial to obtain a recruitment index in the Bay of Biscay, the area with the largest glass eel recruitment in Europe.

Keywords: *Anguilla anguilla*, exploitation rate and Oria estuary, glass eel fishery, recruitment.

Introduction

The European eel (*Anguilla anguilla* L., 1758) has a long and complex life cycle. From the spawning site in the Sargasso Sea, the eel larvae are transported by marine currents towards the continental shelf of the Atlantic coast of Europe and North Africa (Miller *et al.*, 2014). There, they metamorphose into glass eels and colonize coastal, estuarine, and river habitats. Where they will mature into silver eels and migrate back toward the Sargasso Sea.

In the 1980s, a sharp decline in glass eel recruitment began, accompanied by a decrease in the continental stock (Moriarty and Dekker, 1997; Dekker, 2000; Briand *et al.*, 2003; Dekker, 2004, 2008; Iglesias and Lobón-Cerviá, 2012). Nowadays the stock remains outside the safe biological limits (ICES, 2014). This situation drove the European Commission to issue a regulation (Regulation (EC) No 1100/2007) requiring all the member states to produce eel management plans, with the aim to reach 40% pristine escapement to the sea. This regulation added new challenges to eel research, including the task of efficient monitoring of the eel stock at all life stages.

The best available information on the status of the stock is the recruitment trend computed by the ICES-EIFAC Working Group on Eels (WGEEL). Moreover, ICES (2013a) proposed two stock assessment methods for the eel in 2013: "trend-based assessment" and "eel-specific reference points" based on the recruitment indices and stock–recruitment relationships. Quantifying and understanding the recruitment mechanisms is essential in the management of the damaged eel stock. Many assessment methods require an accurate recruitment estimation per estuary to determine escapement (i.e. DECAM, GEM, SMEP; Walker *et al.*, 2011) and compliance with the EC regulations.

Despite the relevance of recruitment, among the 52 European eel recruitment time series used by WGEEL as indices, only ten come from scientific surveys in an estuarine environment. Fishery data may report catches inaccurately and are subject to variable external influences (markets, regulations and technology). In fact, five of the commercial-based series have ended in France between 2008 and 2011 as a consequence of changes in fishing practices brought by the EU regulations (ICES, 2013a). Therefore, WGEEL has repeatedly advised an increase in the number of recruitment series based on scientific monitoring of the stock. This advice is particularly relevant in the southern part of Europe where the recruitment series are mostly based on fishery catches and where the trap-based index used elsewhere in Europe cannot be used since fishery creates a bias in the data. For that reason, it is necessary to find alternative fishery-independent methodologies to determine recruitment.

Other critical factors that have restricted the scope and value of international evaluation of the eel stock are the variability of reporting standards, the level of the detail, and coverage, as has been pointed out by the European eel management plans and post evaluation reports of ICES (2013b). There is an urgent need for coordination and standardization of data collection and assessment methodology, which also applies to the recruitment.

Glass eel migration patterns differ depending on the location, estuary characteristics, and physiological status of the eels. Understanding the recruitment processes in estuaries at different latitudes and ecoregions will help to build a European monitoring programme capable of delivering accurate assessments of the recruitment trend for the whole population. Ideally, each recruitment series should be analysed to disentangle local factors affecting the trend (Dekker, 1986) from the general trend in the number of recruits coming from the sea (ICES, 2010).

In this study, the recruitment volume and dynamics in a South European Atlantic estuary is described using experimental fishing and fishery logbooks from 2003 to 2014. The Oria (Basque Country, Northern Spain) is a medium-size river flowing into the Bay of Biscay. The region has a long glass eel fishing tradition, with current catches being <3% of those in the first part of the 19th century (Gandolfi-Hornyold, 1936).

The specific objectives of the study are to (i) describe the dynamics of the glass eel fishery, (ii) analyse the spatio-temporal variability in recruitment, (iii) analyse the influence of abiotic factors on recruitment dynamics, and (iv) estimate the daily and annual recruitment.

Material and methods

Description of the study area and glass eel fishery

The Oria River (Figure 1) is 77 km long, drains an area of 888 km^2, and flows into the Oria Estuary system with a mean river flow of 25.7 m^3 s^{-1} (Garcia de Bikuna and Docampo, 1990). The estuary is 11.1 km long, the section at the river mouth has an area of 720 m^2, and the flooded area ranges between 0.367 and 2.296 km^2. At mid-tide (tidal height of 2.5 m), the water volume is 3.7×10^6 m^3; it varies between a minimum of 0.8×10^6 m^3 to a maximum of 7.2×10^6 m^3 during the neap and spring tides, respectively.

The estuary has a meander-like profile. The margins of the outer zone of the estuary have been largely modified by the historical settlement of the Oria village and its harbour. In that area, the sediments are mostly sandy and the maximum depth is 10 m. The upper estuary is narrow and has a stony river bed channel, deeper than the middle part of the estuary (Villate *et al.*, 1989). The tide and the river flow are the main factors conditioning the dynamics of the estuary. The mean river flow takes around two tidal cycles to infill the mean volume of the estuary. The average water temperature is 12.4°C.

Surface salinity increases with the tide and decreases with the distance to the sea; it ranges from 20 to 25‰ in the lower estuary and from 4 to 15‰ in the middle area. In the upper estuary, the surface water is always fresh (Villate *et al.*, 1989). The estuary is partly stratified; the stratification reaches its highest level upstream and during low tides, but no stratification is observed under high-flow conditions or during high tides.

The flushing time in the Oria depends on the stratification of the estuary. Under normal (26 m^3 s^{-1}) and high-flow conditions (34 m^3 s^{-1}), it varies from 1 to 5 d (Villate *et al.*, 1989). The tides are semi-diurnal, with a slight asymmetry, and the tidal amplitude varies from ~1 m for neap tides to >4.5 m for spring tides. The tidal waves are of the "standing" type (Ketchum, 1983). The highest tidal current occurs at mid-flood and mid-ebb, and the tide rises and falls simultaneously in the whole estuarine area (Villate *et al.*, 1989).

Fishing licenses are issued for two types of fishery: boat and land fishery. Boat fishers fish by trawling two sieves attached to either side of the boat, while land fishers either pull the sieves from the banks of the river or use a dipnet. They also fish from an anchored boat or in the waves at the beach. Fishing is carried out from the river mouth to the tidal limit (10 km upstream). Boat fishing starts ~4–5 h before high tide in the main channel of the river mouth and the fishers move upstream following the glass eel as the tide rises. The boat fishers trawl two circular sieves (1.25–1.80 m in diameter with 2–3 mm mesh size) attached with poles to each side of the boat. The fishing is done against the current for ~10 min at 0.5–2 knots. Most fishing is done with nets placed in the deeper part of the water column. Land fishers start fishing 2.5–3.5 h before high tide all along the estuarine river bank using the stainless or galvanized steel sieves of 0.80–0.90 m in diameter and 2 mm mesh size.

Data collection

Glass eel fishery

Glass eel fishery data in the Oria has been available since 2003, when the fishery was regulated for the first time in the Basque Country by Decree 41/2003 (it obliged fishers to fill log daily catch and effort data). Thus, catch logbooks from 11 seasons (2003–2014) were available for analysis. The fishing period was shortened when the Eel Management Plan for the Basque Country was implemented. In 2003–2008, the season began 1 week before the first new moon in October and ended 1 week after the new moon in March of the following year. From 2009 onwards, it took place from 15 November to 31 January of the following year, and a daily catch quota of 2 kg per fisher was fixed.

Experimental glass eel fishery

Experimental fisheries for glass eel were carried out from 2005 to 2012 during the new and full moon of the fishing season, at four different points of the Oria Estuary (Figure 1). They were established at the river mouth (depth (d) = 6–10.5 m, width (w) = 60 m); under the highway bridge (d = 2.55–7.75 m, w = 130 m); the intermediate point (d = 1.65–7.35 m, w = 20 m), and the upstream point (d = 1.85–2.75 m, w = 13 m).

The timing of the sampling was based on the timing of the Oria boat fishery. The fishing started 4 h before the last high tide at the river mouth (Figure 1) by trawling using the traditional sieves (1.4 m in diameter) attached to either side of the boat. One sieve was fixed near the surface and the other at the maximum depth layer. Trawling was done at a speed of 2–3 knots for 3–8 min.

Each sieve was equipped with a flowmeter (General Oceanics, 2030RC) to determine the volume of filtered water. Every two trawlings, the temperature, salinity, and dissolved oxygen were measured

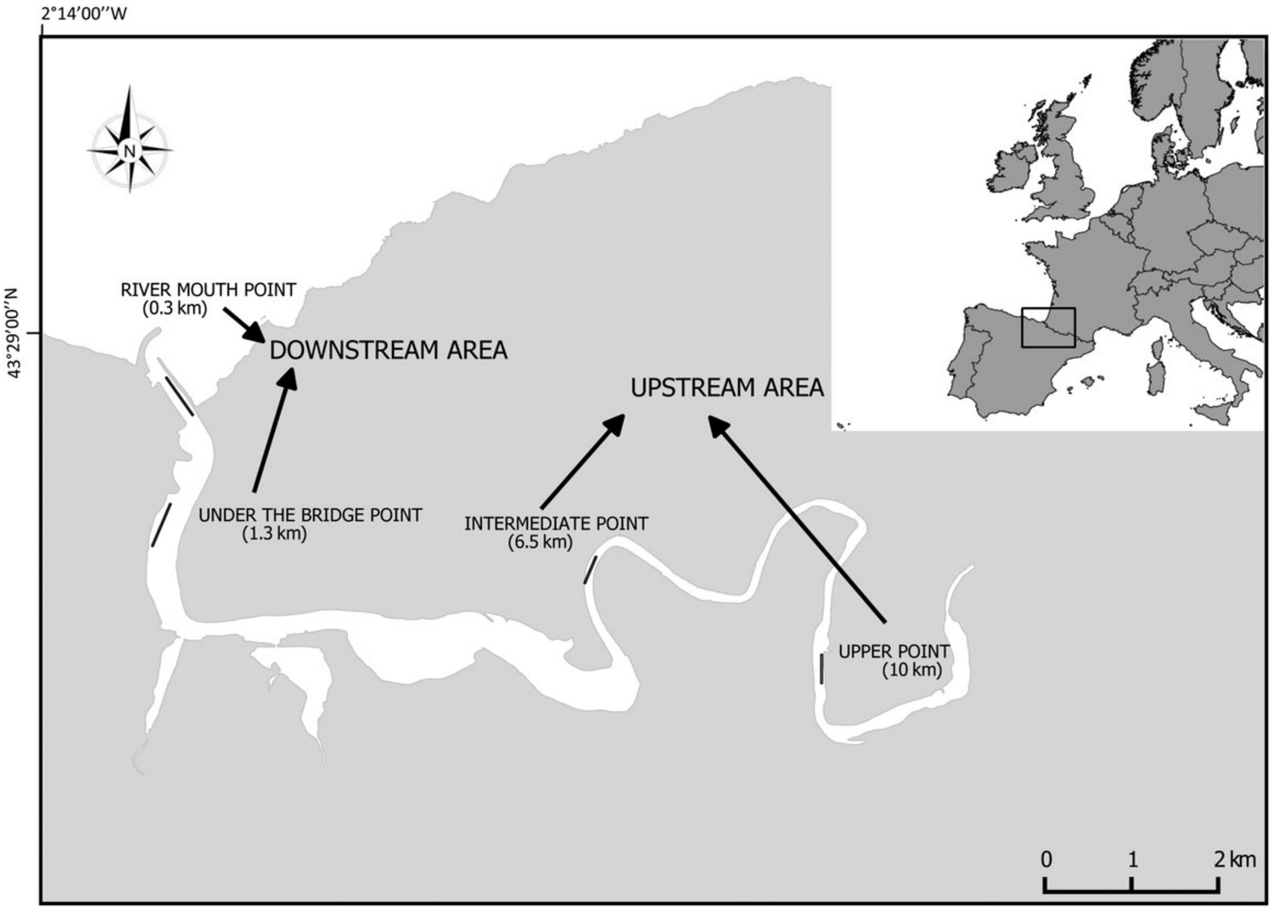

Figure 1. Map of the Oria Estuary showing the location of the *Anguilla anguilla* sampling points grouped in two areas: downstream and upstream. The distances of each sampling point to the river mouth is indicated in brackets.

using a mini CTD (YSI 556 MPS model). Water samples were taken (Niskin Sampling Bottle, Model 1010–1.2 TO30L) at three levels (surface, medium, and deep) to determine turbidity by using an HACH 2100A turbidity meter. Glass eels from each sieve were kept in individual containers and were later examined in the laboratory.

When catches were smaller than three glass eels per haul after at least three trawlings, the boat was shifted to the next sampling point where the same procedure was repeated.

Environmental variables

In addition to the parameters measured in the experimental fisheries, the data potentially related to glass eel recruitment were collected. River flow, precipitation, air temperature from the gauging station of Lasarte located 10 km upstream (daily means of 10-min records), daily insolation (sum of insolation time per day), and daily accumulated precipitation registered by Mount Igeldo Meteorological Observatory located 8 km to the east.

An acoustic wave and current profiler (Nortek AWAC 1 MHz) was used to estimate the current speed during the trawlings. It was moored in the main channel of the river mouth during 1 month. The current values were analysed using singular value decomposition (SVD) method (Press *et al.*, 1992) to obtain the harmonic coefficients. The current during each trawling was then estimated using the harmonic signal. The tidal level during each sampling night was also calculated using SVD, from a tide gauge placed at the river mouth for a month.

Data processing

All statistical analyses were performed using R and the significance level was set at $p < 0.05$. An exploratory analysis of all the variables followed the protocol described in Zuur *et al.* (2010). Cleveland dotplots, boxplots, and multipanel scatterplots were used to find the outliers and to investigate relationships between variables. Relationships between covariates were assessed using Pearson correlation coefficients and variance inflation factors (Zuur *et al.*, 2010). The skewness of the distributions required to log turbidity, dissolved oxygen, river flow, precipitation, and daily insolation.

Generalized additive models (GAMs) were applied to both glass eel datasets (fishery and experimental data) to investigate relationships between glass eel abundance and spatio-temporal and environmental variables. Models based on a Gaussian distribution with an identity link function were chosen after preliminary tests on the data distribution. The models were ranked and the best model was selected using Akaike's information criterion (AIC). The total deviance explained and the relative contribution of each factor was evaluated for each model.

For the fishery, the relation between mean daily catch per unit effort (*cpue*) and fishing license type, season, month, number of days from the beginning of the fishing season, and date was assessed. Only the days with the data from more than ten fishers per license were included in the analysis. In 2008–2009, the catches were very low, and the number of fishing operations per day was always <10; this season was excluded from the analysis (Table 1).

Table 1. *Anguilla anguilla*: the number of fishing days per license type and experimental fishing sessions analysed in each fishing season.

	Fishing days		Experimental fishing	
Season	Boat	Land	Downstream	Upstream
2003/2004	24	24		
2004/2005	23	23		
2005/2006	11	11	10 (7)	8
2006/2007	21	21	9 (5)	9
2007/2008	15	14	7 (3)	6
2009/2010	12	12	5 (3)	5
2010/2011	9	9	5 (2)	4
2011/2012	27	27	5 (3)	5
2012/2013	16	16		
2013/2014	29	29		

The number of days used to calculate the glass eel recruitment of the Oria River is indicated in brackets.

For experimental fishery, 42 samplings were performed during the study period (Table 1). To simplify the statistical analysis, the first two sampling points were qualified as the downstream area and the two last points as the upstream area (Figure 1). The glass eel density was calculated by dividing the number of glass eel per haul by the volume of water filtered in each trawling. GAMs were used to analyse the relationship between glass eel density and the depth, sampling area, moon phase, fishing season, month, number of days from the beginning of the fishing season, and date.

Analysis of recruitment

The recruitment trend and its relation to environmental variables were described by a model using glass eel density during each trawling as the dependent variable. The dataset was restricted to samples taken at the "under the bridge" sampling point (Figure 1). This was the area with the highest number of samples, most suited for recruitment estimation, since it was located downstream in a narrow channel with low stratification. Only the data for the sampling nights with glass eel found in more than three trawls per night and with a complete environmental dataset were used. Following these criteria, the data from 19 d were excluded and the working database was reduced to 23 sampling days.

Data exploration revealed non-linear patterns, so generalized additive mixed models (GAMMs; Wood, 2006) were implemented. As the data consisted of densities, a GAMM with a Gaussian distribution and identity link was considered appropriate. In the final model, different variances per sampling nights were used to account for heterogeneity. The best model was selected using AIC. The model validation was based on the independence, homogeneity, normality of the residuals, and the absence of influential observations. Residuals were plotted against fitted values to identify violation of homogeneity and against each explanatory variable within and outside the model. To verify normality, histograms of residuals were made and influential observations were checked by analysing the Cook's distance statistics.

A power transformation was applied to the dependent variable to normalize the residuals. The following explanatory variables were tested in the model: water temperature, salinity, turbidity, dissolved oxygen, current, flow, precipitation, air temperature, tide coefficient, time before the high tide, daily insolation, and seawater temperature as continuous variables and depth, date, month, season, and moon phase as categorical variables.

Estimation of recruitment and rate of exploitation

The following calculation was done every 10 min t for the sampling nights selected in the previous analysis. Glass eel density ($\widehat{\text{dens}_t}$) was predicted by the GAMM model and extrapolated to the volume of water passing at the sampling point. The volume of water (Q_t) corresponds to the section of the sampling area (S_t) multiplied by the current speed (Φ_t) modelled in the estuary. Glass eel density was converted to biomass using the average glass eel weight ($\omega =$ 0.3 g) measured during the scientific surveys. Total daily recruitment ($\widehat{Rd}$) was obtained by summing the biomass as shown below:

$$\widehat{Rd} = \sum_{t=1}^{n} \omega \, \widehat{\text{dens}_t} t \, Q_t \qquad (1)$$
$$Q_t = S_t \times \Phi_t.$$

It was assumed that the recruitment during the day was zero. For those 19 sampling nights when the number of glass eel was too low to use in a model of daily recruitment, a calculation of recruitment was made. Using the same dataset as for recruitment calculation, $\widehat{Rd}$ was related to the average density in the estuary (dens_t) with a simple linear model without intercept. The model was then used to predict those (very low) recruitment values (Rd') (Equation (2)).

$$\widehat{Rd} = \alpha \, \text{dens}_t, \quad Rd = \begin{cases} \widehat{Rd} \; t(\text{dens} > 0) \geq 3 \\ Rd' \; t(\text{dens} > 0) < 3 \end{cases}. \qquad (2)$$

Daily recruitment values were too few and too variable to make a seasonal estimate of recruitment yearly. Thus, all values of $\widehat{Rd}$ and Rd' for all experimental fisheries years were aggregated to obtain an average recruitment. Complementary information from the fishery *cpue* was then used as an indicator of the seasonal strength in recruitment as shown in Equation (3). It was assumed that natural mortality was equal to zero and only the period of maximum recruitment (November, December, and January, $fd =$ 91 d) was taken into account for *cpue* and sampling nights.

$$R_s = d \times Rd_s = fd \times \frac{cpue_s \, (\widehat{Rd})}{(1/s) \sum_{s=1}^{s} cpue_s} \qquad (3)$$
$$ER_s = \frac{100 \times TC_s}{R_s}.$$

where R_s is total recruited biomass for season s; Rd_s, estimated daily recruitment average for season s using experimental surveys and fishery data; fd, number of days in the fishing season, 91 d; $cpue_s$, average *cpue* for season s; ER_s, = exploitation rate for season s; TC_s, = total catch biomass for season s.

The effect of environmental variables on $\widehat{Rd}$ was tested by linear regression analysis after normalizing $\widehat{Rd}$ with log transformation.

Results

In the Oria, no licensing system (which would register the number of fishers) had existed until 2003 when the fisheries became regulated and 44 boat and 183 land licenses were issued. Subsequently, the number of licenses increased to a maximum of 50 boats in 2004/2005 and 262 land licenses in 2005/2006. Later, this number gradually decreased and stabilized at 30 boat and 80 land licenses in the season of 2013/2014.

The model that explained the fishery *cpue* best was the GAM_f model (Equation (4), adjusted $R^2 = 0.60$) and is expressed as follows:

$$\sqrt{cpue} \sim \alpha + \beta \text{ License}_i + \gamma \text{ Season}_i + f(\text{Doy})_i + \epsilon_i \qquad (4)$$
$$\epsilon_i \sim N(0, \sigma_i^2)$$

where $\sqrt{cpue}$ is the square root of the mean daily glass eel fishery *cpue*; License is the fishing mode (boat or land); Season corresponds to the fishing seasons from 2003 to 2014; and f(Doy) denotes a spline smoother function of the covariate Doy (number of days from the beginning of the fishing season).

Daily *cpue* was higher in the boat fisheries than in the land fisheries ($p < 0.001$) and, for both fishery types, *cpue* varied significantly between the seasons ($p < 0.001$). From 2011 to 2014, both the catches and *cpue* increased, and *cpue* was significantly higher than in the preceding seasons (Figure 2; Supplementary Tables SA-2 and SA-3).

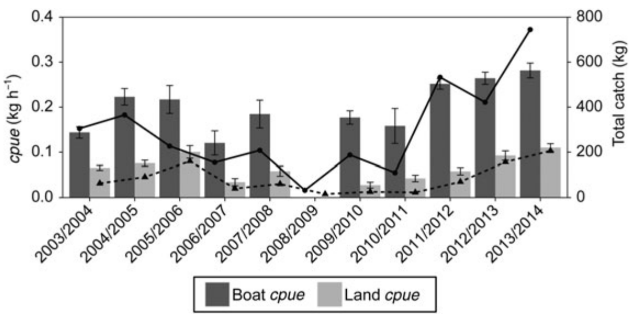

Figure 2. Seasonal evolution of total glass eel (*Anguilla anguilla*) catch and mean *cpue* ($\pm$ SE) in the Oria Estuary glass eel fishery for the two license types (*Note*: only November, December, and January are included).

The intraseasonal variability was also high and showed different trends depending on the season the highest *cpue* reached in changing months (Figure 3). However, on average, the highest boat-fishing *cpue* was obtained in December and January. There was a positive correlation between the *cpue* of the two license modalities (Pearson's coefficient, $R^2 = 0.43$, $p < 0.001$).

Spatio-temporal variation in recruitment

The model that best explained the experimental fishery densities was the GAM_{ef} model (Equation (5), adjusted $R^2 = 0.25$):

$$\text{dens}^{0.02} \sim \alpha + \beta \text{ Depth}_i + \gamma\, SP_i + \delta \text{ Season}_i + \lambda \text{ Moon}_i + f(\text{Doy, by} = SP)_i + \epsilon_i \qquad (5)$$
$$\epsilon_i \sim N(0, \sigma_i^2)$$

where dens is the mean glass eel density, *SP* is the sampling area (downstream or upstream), Depth is the trawling depth (surface or deep), Season corresponds to the fishing seasons from 2005 to 2012, Moon is the moon phase (full or new), and f(Doy) denotes a spline smoother function of the covariate Doy (number of days from the beginning of the fishing season).

Glass eel densities were significantly greater in the deeper layer ($p < 0.001$) and during the new moon ($p < 0.001$). There was a highly significant seasonal variability in glass eel density at both sampling points ($p < 0.001$, Figure 4). The temporal density trend differed significantly between the sampling areas ($p < 0.05$); it decreased downstream and increased upstream (Figure 5; Supplementary Tables SA-2 and SA-3).

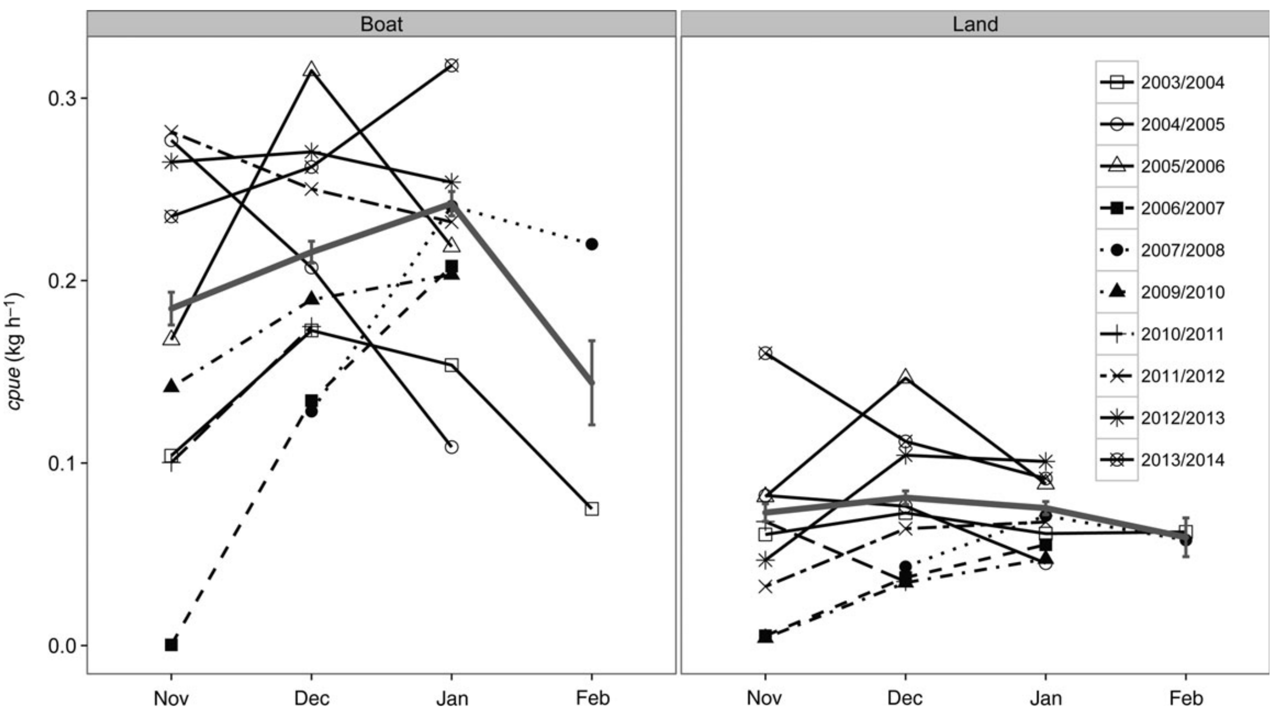

Figure 3. Monthly trends of mean glass eel (*Anguilla anguilla*) *cpue* for the two license types in the Oria Estuary (2003–2014). The overall mean *cpue* ($\pm$ SE) for each month is shown in grey.

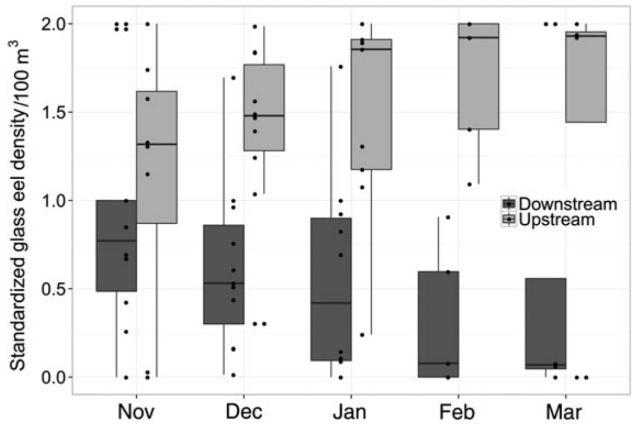

Figure 4. Spatio-temporal trends of standardized *Anguilla anguilla* glass eel density (the density at each sampling point divided by the average daily densities of each sampling area) in the Oria estuary obtained in the experimental fisheries (2005–2012).

Analysis of recruitment

The daily recruitment at the bridge sampling point (Figure 1) was best described by a GAMM selecting the current and depth as covariates and the date as a random variable (Equation (6), adjusted $R^2 = 0.59$). All three covariates were significant (current $p < 0.05$, date $p < 0.001$, depth $p < 0.001$; Table 2 and Supplementary Table SA-1).

$$\begin{aligned} \text{dens}_{dt}^{0.2} &\sim f\,(\text{current})_{dt} + \text{date}_d + \text{depth}_{dt} + \epsilon_{dt} \\ \epsilon_{dt} &\sim N(0, \sigma_d^2), \quad d = 1, \ldots, 2, 3, \end{aligned} \tag{6}$$

where d denotes date, t denotes trawl, and f is a cubic regression spline with 5 degrees of freedom. Glass eel densities were higher near the bottom but followed the same trend in both layers as there was no significant crossed effect between the current and depth. Densities increased with the current and reached the maximum values when the currents were ~0.4 m s^{-1}, 3–5 h before high tide (depending on the tidal height). Then they decreased for the currents above that value (Figure 6). The GAM model gave a better fit using the current than using the timing of the tide as a covariate (Supplementary Model (2) in Table SA-4).

Estimation of recruitment and overall rate of exploitation

The estimated daily recruitment (*Rd*) showed a high daily and seasonal variability (Figure 7; Supplementary Table SA-5). The correlation with the daily value of *cpue* was low (Pearson's coefficient, $R^2 = 0.225$, d.f. = 10, $p = 0.48$). The average daily recruitment was 12.76 kg. The highest daily recruitment was observed in December 2011 (72 kg, range 31–149 kg). Null recruitment was extrapolated from zero catches in the downstream area in 2 d in both 2006/2007 and 2007/2008, 1 d in 2009/2010, and 2 d in 2011/2012. Among the analysed parameters, only turbidity was related to log-transformed *Rd* ($R^2 = 0.52$, d.f. = 14, $p < 0.01$). River flow and precipitation were not significant in the regression even when lagged.

The average seasonal daily recruitment (R_s) varied among seasons and did not show any clear trend during the 2003–2011 period (mean: 1144 kg, range: 682–1593 kg), though the highest three values were obtained in the 2012–2014 period (Table 3). The minimum value was observed during the 2006–2007 season, coinciding with low *cpue* and catch values. However, the daily recruitment calculated from the experimental fishery in that season ($\overline{Rd, Rd'}_s$) was among the highest. For the remaining seasons, the daily recruitment (*Rd* and *Rd'*), the estimated daily recruitment (Rd_s), *cpue* ($cpue_s$), and catches (TC_s) followed the same trends.

The exploitation rate (ER_s) of the Oria River during the study period was estimated as 31.1% (range 6.2–48.7%). In general, the exploitation rate increased together with *cpue*, catches, and recruitment. However, in 2003/2004, the exploitation rate was high, although the *cpue*, catches, and recruitment values were low (Table 3).

Discussion

Estimating recruitment during a flood tide event in an estuary requires good understanding of the changes in glass eel density and its relation to the timing of tides and environmental factors (Harrison *et al.*, 2014). This study provides a description of the glass eel abundance dynamics during the flood current in the Oria Estuary. It also examines the spatial and seasonal variation in the abundance of these fish.

Density trend during the tide

Within a day, the flow and depth were the only significant descriptors of density. Glass eel in the Oria used a selective tidal stream transport to progress into the estuary (Creutzberg, 1958). The current was a better predictor than timing before the high tide, so the local cues based on the current were better descriptors of glass eel activity than a simple timing of the ascent in the water column based on the theoretical tide. This indicates that the current is the main synchronizer of the rhythmic swimming activity as has been shown in other studies (Wippelhauser and McCleave, 1988; Bolliet *et al.*, 2007; Trancart *et al.*, 2012). In the Adour, Bru *et al.* (2006) have found a linear relationship between the glass eel density and flood tide currents. However, in the Oria Estuary this relationship was clearly not linear: glass eel density increased with the flow, reaching a maximum at ~0.3 to 0.4 m/s then decreased for higher current values.

A linear relation between the density and current could be obtained if there were a large source of glass eel scattered in the downstream area of the estuary. Such a large source of the glass eel does not exist in the Oria. During each experimental sampling, the glass eel density decreased after a while. This indicated that after some time, most of the fish moved upstream, pursued by the fishery activities. As the Adour Estuary is much wider than the Oria, it is likely that more glass eel were available in the bay to participate in the migration during the tide. In cases where the upstream migration of the glass eel is blocked, a density peak is also found at the mid-flood tide; however, large densities of glass eel remain below the dam till the end of ebb tide (Laffaille *et al.*, 2007).

The influence of environmental factors

Many factors, individual or combined, have been identified as recruitment short- or medium-term drivers for the glass eel in estuaries. Some of these factors are the wind (Prouzet, 2002; Arribas *et al.*, 2012), river flow (Gandolfi *et al.*, 1984; Domingos, 1992), turbidity (de Casamajor *et al.*, 1999; Prouzet, 2002; Bouvet *et al.*, 2006; Arribas *et al.*, 2012), temperature (Gandolfi *et al.*, 1984; Gascuel, 1986; Elie and Rochard, 1994), and local rainfall (Arribas *et al.*, 2012). However, the above studies differ in ranking the importance of these factors, probably because of their interactions and because their effect might depend on the location, estuary characteristics, and physiological status of the glass eel (Elie and Rochard, 1994;

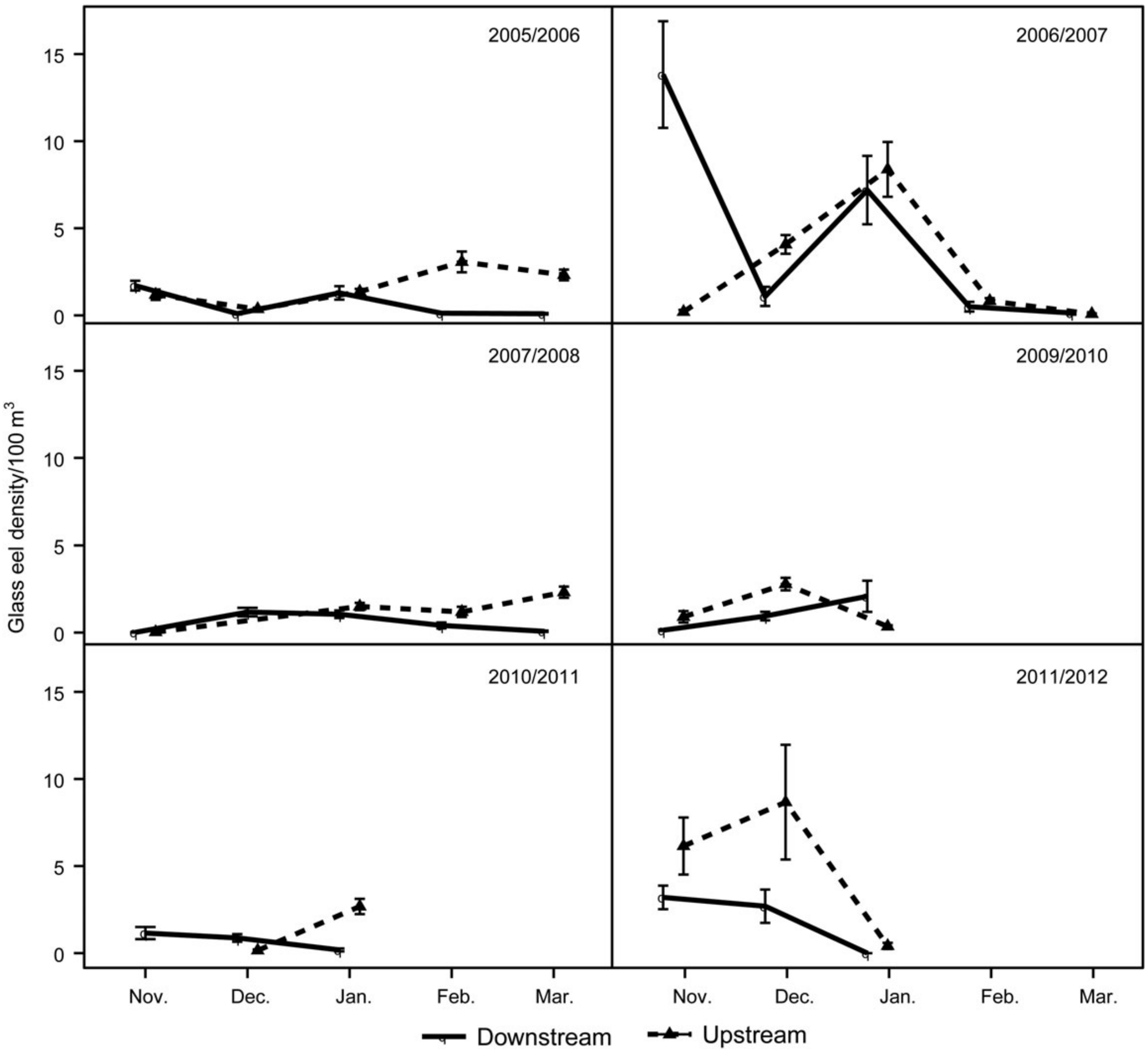

Figure 5. Glass eel (*Anguilla anguilla*) mean monthly density evolution (± SE) during the experimental fishery seasons from 2005 to 2012 in two sampling areas of the Oria Estuary.

Table 2. Deviance table of the mixed model (GAMM) defined by Equation (6) analysing the relationships between daily *A. anguilla* glass eel recruitment and environmental variables in the Oria estuary.

Covariate		d.f.	*F*-value	*p*-value
Parametric terms				
Date		22	19	0.001
Depth		1	26.9	0.001
Approximate significance of smooth terms				
Covariate	EDF	Ref.df	*F*-value	*p*-value
Current	1.57	3	2.39	0.018

d.f., degree of freedom; EDF, effective degrees of freedom for the regression spline; Ref.df, reference degrees of freedom used to compute the *p*-value.

Zompola *et al.*, 2008). In the Oria, the high daily recruitment values were significantly related to turbidity. However, the temperature was not a conditioning factor, probably because it remained above the migration-blocking threshold of 4–6°C (Deelder, 1952, 1958; Elie, 1979; Cantrelle, 1981) (November: 12–16°C, December: 11–15°C, and in January 10–12°C). Temperatures >12°C have been linked to a decrease in *cpue* and an increased rate of settlement (Désaunay *et al.*, 1987; Briand, 2009). However, these temperatures probably would not affect the glass eel in the early phases of estuarine migration. Similarly, neither flow nor precipitation, even when lagged, was a significant predictor of daily recruitment.

Seasonal trend

At the seasonal level, the period of maximum recruitment in the Oria Estuary fits into the latitude gradient, which has been extensively studied (Tesch, 2003; Zompola *et al.*, 2008; Arribas *et al.*, 2012). There is a clear south–north trend along the coast of Biscay and further north to Ireland and the English Channel, with the earliest recruitment occurring in the south, and the latest found in Ireland. The recruitment in the Oria, as reflected by the glass eel *cpue*, varies during the year. It follows a symmetrical curve with a peak in December–January, 1 month later than in the Guadalquivir (November, Arribas *et al.*, 2012) and 1 and 2 months earlier than in the French Atlantic coast (January–February, Gascuel *et al.*, 1995), and Ireland, respectively (Moriarty, 1999). This delay could be explained by the differences in the seasonal dynamics of water temperature (Tesch, 2003). It might be also associated with different routes followed by glass eel, using either a southern migration pathway (through the Canary Islands and Madeira then to the Mediterranean) or moving further north in the main North Atlantic current, and possibly departing from this current using an active tidal-assisted migration (Creutzberg, 1958).

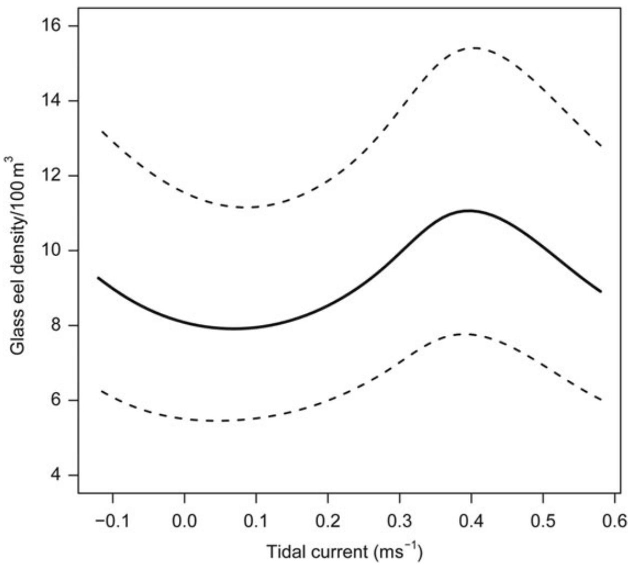

Figure 6. *Anguilla anguilla* glass eel density prediction ($\pm$95% confidence limits) from fitted GAMM model (Equation 6) depending on the current in the deep layer, obtained on 13-12-2011 (sampling point: under the bridge).

At the annual level, there is a relation between the indices of eel abundance and the ocean-atmosphere conditions. Many authors have speculated about a possible relationship between oceanic factors and the long-term changes in recruitment (Bonhommeau *et al.*, 2008; Kettle *et al.*, 2008; Baltazar-Soares *et al.*, 2014). Some authors have pointed out that variation in the ocean currents, especially in the subtropical gyre region, might trigger the onset of recruitment decline (Pacariz *et al.*, 2014), but it cannot explain the continuous decline since the 1980s. The recent upwards trend might be the result of an increasing number of spawners available due to management measures (Baltazar-Soares *et al.*, 2014).

Vertical position

In both the downstream and upstream areas, the densities of glass eel were higher near the bottom than at the surface. Higher densities in the deep layer might be caused by the penetration of the tidal front along the Oria Estuary bed. However, the estuary was not stratified in the upper section and the crossed effect between the tide and current was not significant. Thus, the densities at the deep layer

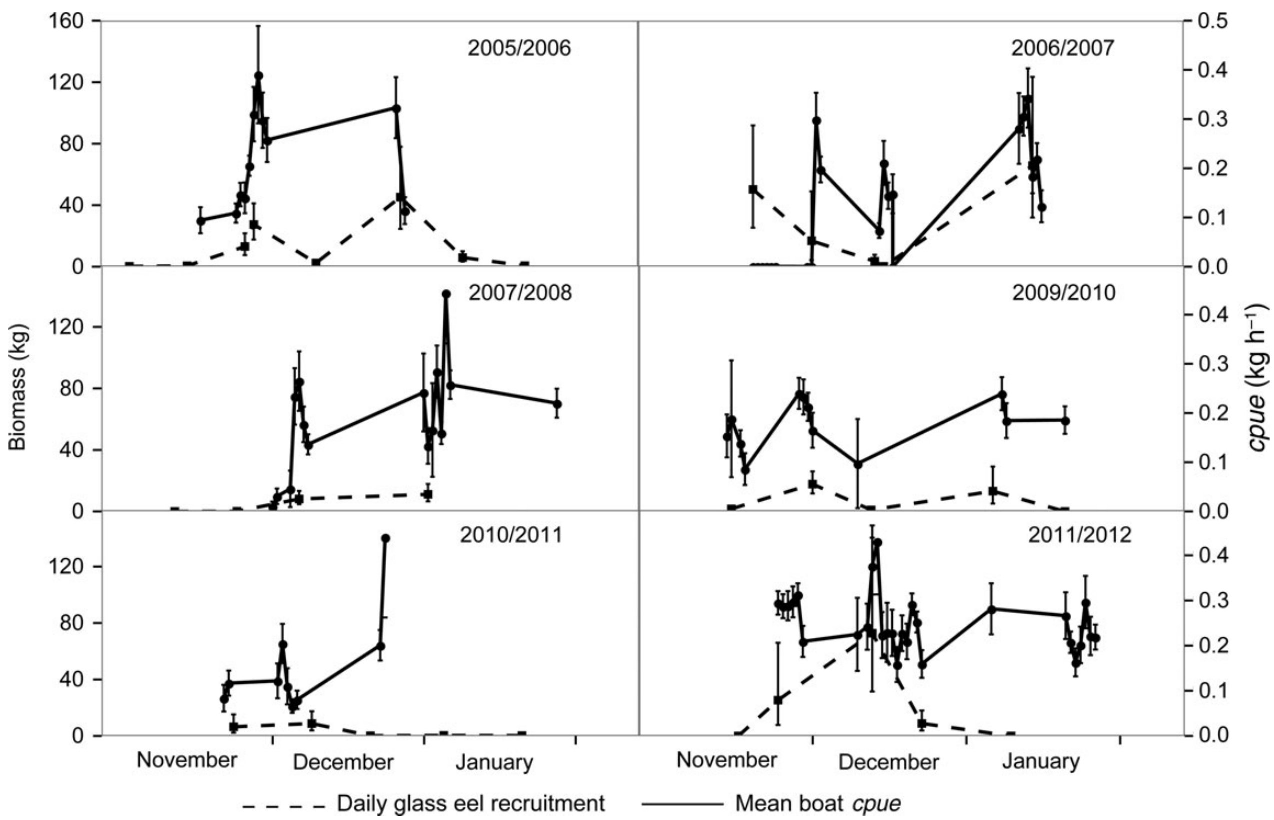

Figure 7. *Anguilla anguilla* glass eel daily recruitment (*Rd′*, kg) prediction from fitted GAMM and mean *cpue* ($\pm$SE) for the boat fishery (only the days with data from >10 fishers have been included) for each season.

Table 3. Summary of glass eel (*A. anguilla*) recruitment in the Oria.

Season	$cpue_s$ (kg h^{-1})	TC_s (kg)	Rd (kg)	Rd' (kg)	Rd_s (kg)	R_s (kg)	ER_s (%)
2003/04	0.14	304.9			8.9	814 (601–2461)	37.4 (12.3–50.7)
2004/05	0.22	365.1			13.8	1261 (931–3814)	28.9 (9.5–39.2)
2005/06	0.21	227.0	14.9	11.9	13.50	1228 (907–3714)	20.8 (8.0–22.9)
2006/07	0.12	154.9	30.3	27.3	7.50	682 (503–2063)	6.2 (2.5–10.8)
2007/08	0.18	208.1	11.5	4.8	11.48	1044 (771–3159)	47.2 (14.6–40.6)
2008/09							
2009/10	0.17	187.7	10.8	6.7	11.00	1001 (739–3028)	30.6 (10.6–34.6)
2010/11	0.15	110.1	7.6	3.2	9.84	895 (661–2708)	37.5 (7.3–38.7)
2011/12	0.25	533.0	35.6	21.3	15.66	1425 (1052–4309)	27.3(7.5–40.7)
2012/13	0.26	421.9			16.4	1495 (1104–4523)	28.2 (9.3–38.2)
2013/14	0.28	745.2			17.51	1593 (1176–4818)	46.7 (15.4–63.3)

$cpue_s$, average *cpue* for season; TC_s, total catch biomass for season; Rd, total daily recruitment estimated using experimental fishing; Rd_s, estimated daily recruitment average for the season using experimental surveys and fishery data; R_s, total recruited biomass during a season; ER_s, exploitation rate for the season.

were higher at all times, even when no stratification occurred. The more plausible explanation is the strong negative phototaxis of glass eels (Tesch, 2003). Under low turbidity conditions found in the Oria (*NTU* ranges 0–100), the moonlight penetrating the water can affect the vertical distribution of glass eel in the water column (de Casamajor *et al.*, 1999; Bardonnet *et al.*, 2005). This hypothesis of photophobic behaviour is corroborated by the significantly higher glass eel densities during the new moon phase than during the full moon. In addition, the noise or disturbance generated by the fishery operating around the sampling point might drive the glass eel to the deeper part of the estuary.

Accumulation at the tidal limit

The symmetrical downstream decrease and asymmetrical upstream increase in the glass eel density (Figure 5) suggest that, as the season progresses, the glass eels tend to migrate and accumulate upstream close to the tidal limit. There they switch from selective use of tidal currents (Creutzberg, 1958; McCleave and Kleckner, 1982; Trancart *et al.*, 2012) to a countercurrent migration behaviour (Briand, 2009). This results in the natural accumulation of glass eels at the limit of the flood tide (Deelder, 1958; Gascuel, 1986). In the Oria, the river recruitment period starts in May (data from the eel pass at the tidal limit). It is likely that glass eel arriving from the open sea gradually accumulate at the upper tidal limit during the season and continue their migration upstream into the riverine system from May onwards.

Recruitment estimates

The estimated seasonal recruitment ranged from 700 kg (500–2000 kg) in 2006/2007 to 1600 kg (1000–4600 kg) in 2013–2014. However, these values may be overestimated and should only be considered as an order of magnitude since experimental fisheries were concentrated during the new and full moon phases when the highest tidal levels occur. In general, the daily recruitment (Rd), the estimated daily recruitment (Rd_s), *cpue* ($cpue_s$), and catches (TC_s) followed the same trends. However, during 2006/2007, low *cpue* and catch corresponded to high Rd values (Table 3). There is a positive correlation between the Oria seasonal *cpue* ($cpue_s$) and the recruitment index used by the ICES WGEEL for locations outside the North Sea (series elsewhere Europe). Nevertheless, this correlation is not significant ($R^2 = 0.53$, $p = 0.11$; ICES, 2014) due to the presence of two outliers: low $cpue_s$ in 2003/2004 and 2006/2007. In 2006/2007, the experimental surveys pointed to high recruitment. Therefore, perhaps the underreporting of catches caused the difference between average $cpue_s$ and daily recruitment. The lack of correlation might be also related to the behaviour of the fishers, they actively pursue the glass eel along the estuary, while only downstream samplings have been used to estimate the recruitment. Implementation of a more integrative model of population dynamics would improve daily recruitment estimation and allow the natural and fishing mortality and settlement to be determined (GEMAC model; Beaulaton and Briand, 2007).

Exploitation rate

The estimated mean exploitation rates for the Oria during the study period (31.1%; range 6.2–48.7%) are similar to the rates for some other glass eel fisheries, e.g. East River in Canada 30.8–51.8% (Jessop, 2000) and the Adour 13–30% (Prouzet, 2002). However, they are lower than the rates for Shang-Chi (Taïwan), 44.1–75.4% (Tzeng, 1984), and the Vilaine (France), 78.1–99.7% (Briand, 2009). Probably reflect the non-commercial nature of the Oria fishery. Although the Oria has the highest total catch within the Basque Country (391–1023 kg during the 2003–2014 period), it is a low quantity compared with the surrounding estuaries with commercial fisheries. There are several such estuaries: Vilaine (3000–7000 kg, 400 km North, 71 $m^3 s^{-1}$ flow), Minho (300–2000 kg, 575 km Southwest, 340 $m^3 s^{-1}$), Nalon (400–2900 kg, 320 km West, 56.40 $m^3 s^{-1}$), and even the smaller Seudre (1000–3000 kg, 300 km North, 5 $m^3 s^{-1}$).

In general, exploitation rate increased together with *cpue*, catches, and recruitment. However, in 2003/2004, the exploitation rate was high, although the *cpue*, catches, and recruitment values were low, possibly because of an increase in price that year (ICES, 2013a). As mentioned above, there was also a mismatch between the average $cpue_s$ and daily recruitment in that season; underreporting of catches might have caused this disparity.

Implications for management and future work

Glass eel recruitment series are a valuable and robust tool to assess stock status, especially in data-poor situations (ICES, 2014). The biomass of eel population depends largely on recruitment; thus, its quantification and understanding of its mechanisms are essential in the management of the damaged eel stock.

The spatio-temporal variation in glass eel density in the Oria Estuary is now well understood and the local factors affecting the recruitment are identified. Our results will contribute to the overall knowledge of recruitment dynamics at different latitudes in various ecoregions and should aid the design of monitoring programmes in other estuaries. Furthermore, we demonstrated the suitability of estuarine recruitment monitoring as an alternative to trap-based monitoring in locations affected by downstream glass eel fisheries.

However, our monitoring programme estimating seasonal recruitment could be further improved. First, the sampling should be performed on days with different tidal levels to avoid overestimation by sampling only on the days with potentially high recruitment (new moon and full moon phases). Second, the percentage of daytime migration should be examined. In a tributary of Gironde, 30% of glass eel migrants have been observed during the daytime, although this has been compensated by the fish moving back during the ebb tide (Lambert, unpublished data). Finally, the sampling should cover the whole tide at the downstream sampling point to ensure that all the glass eel entering during the tide are recorded.

Supplementary data

Supplementary Material is available at *ICESJMS* online.

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