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Original Article

Modelling the recruitment of European eel (*Anguilla anguilla*) throughout its European range

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European eel (*Anguilla anguilla*) recruitment has been declining at least since the early 1980s at the scale of its distribution area. Since the population is panmictic, its stock assessment should be carried out on a range-wide basis. However, assessing the overall stock during the continental phase remains difficult given its widespread distribution among heterogeneous and separate river catchments. Hence, it is currently considered by the International Council for the Exploration of the Sea (ICES) more feasible to use glass eel recruitment data to assess the status of the overall population. In this study, we used Glass Eel Recruitment Estimation Model (GEREM) to estimate annual recruitment (i) at the river catchment level, a scale for which data are available, (ii) at an intermediate scale (6 European regions), and (iii) at a larger scale (Europe). This study provides an estimate of the glass eel recruitment trend through a single index, which gathers all recruitment time-series available at the European scale. Results confirmed an overall recruitment decline to dramatically low levels in 2009 (3.5% of the 1960–1979 recruitment average) and highlighted a more pronounced decline in the North Sea area compared to elsewhere in Europe.

Keywords: GEREM, glass eel, panmixia, temperate eel, trend.

Introduction

The European eel (*Anguilla anguilla*) is a facultative catadromous species growing in fresh, brackish, and coastal waters. The continental distribution of the species extends over Europe and northern Africa, from Morocco to Norway and throughout the Mediterranean and the Baltic Sea (Dekker, 2003b; Tesch, 2003). The spawning ground lies far out in the Atlantic Ocean in the south-western Sargasso Sea, around 5000 km from the European and North African coasts (Schmidt, 1923; Righton *et al.*, 2016). After hatching, leptocephali are transported by currents towards the continent. They metamorphose into glass eels when arriving over the continental shelf, and then enter continental waters where they become pigmented yellow eels. This growing stage lasts between 3 years in southern Europe to over 20 in northern Europe (Vollestad, 1992). Then, yellow eels metamorphose into silver eels that migrate back to the oceanic spawning ground.

European eel recruitment has been declining at least since the early 1980s throughout its distribution area (Jacoby and Gollock, 2014; ICES, 2016) and recruitment indices reached their lowest levels in 2009 (<5% of the 1960–1979 average) (ICES, 2015). This decline was preceded by a decline in landings two or more decades earlier, suggesting a decline of the continental stock (Dekker, 2003a). Many reasons have been proposed for this decline: habitat loss, pollution, parasitism, increased migration barriers, changes in oceanographic conditions, reduction of available prey in freshwater habitats, exotic fish invasions, and overexploitation of fisheries (Castonguay *et al.*, 1994; Jacoby *et al.*, 2015; Miller *et al.*, 2016).

In view of this, the IUCN classified the species as critically endangered on its Red List and the species was classified in Appendix 2 of CITES (Jacoby and Gollock, 2014; Nijman, 2015), while the European Union (EU) initiated the European eel regulation (council regulation (EC) no. 1100/2007) for the protection and recovery of the stock. This regulation requires Member States to implement eel management plans setting measures to reduce anthropogenic mortalities in their respective eel management units (EMUs) to achieve a minimum escapement of 40% of the spawner escapement biomass that would have existed in the absence of any anthropogenic impacts. The European eel has been mostly managed at national or regional levels, although the European eel is considered to be panmictic (i.e. recruiting glass eel are considered to originate from one single spawning stock) (Als *et al.*, 2011). Therefore, actions conducted at the local scale should be coordinated throughout the entire distribution area to achieve the objective, namely a substantial increase in spawner escapement. Moreover, assessments carried out at regional substock scales should also be orchestrated over the whole distribution area (Dekker, 2002a, 2016). In this context, developing a stock assessment process across the species' range is one of the priorities set by the European Inland Fisheries and Aquaculture Advisory Commission (EIFAAC)/International Council for the Exploration of the Sea (ICES)/General Fisheries Commission for the Mediterranean (GFCM) Working Group on Eels (WGEEL) (ICES, 2015).

To date, the trend in recruitment for the European eel is one of the indicators used by the WGEEL to assess the stock status and two glass eel recruitment indices called "North Sea" and "Elsewhere Europe" are currently considered (ICES, 2015). It was not possible to merge these indices into a single index since they seem to display different temporal trends (ICES, 2010), and the relative weights of the two zones in the overall population are unknown. As such, an overall recruitment index that gathers all recruitment time-series collected in estuaries distributed over Europe is still lacking. Such a cumulative recruitment index is required since the population is a single panmictic stock and consequently should be assessed as such, especially when attempts in fitting stock–recruitment relationships are undertaken.

Models such as Glass Eel Model to Assess Compliance (GEMAC) (Beaulaton and Briand, 2007), or a model developed by Bru *et al.* (2009), have been used to estimate glass eel exploitation rates and recruitment at the catchment scale but do not provide information at larger scales. At a larger scale, Dekker (2000b) provided a preliminary assessment of the entire European stock through the development of a simple stage-structured model covering the whole life cycle of the species. Among other important indicators, the model provided an estimate of recruitment in two spatial zones (the Bay of Biscay where glass eel is commercially harvested, and elsewhere in Europe). However, given the lack of data, Dekker (2000b) deliberately made a simplistic assumption of stable recruitment and exploitation and it was not possible to estimate recruitment over large geographic scales.

In this context, Drouineau *et al.* (2016) developed a model named glass eel recruitment estimation model (GEREM) to estimate annual absolute glass eel recruitment at different spatial scales, with an initial application to French EMUs and throughout France. This article extends the implementation of GEREM to a large portion of the species distribution area, with the aim of providing a recruitment index for most of the species' range, and a means to robustly compare spatial variation in trends. At present, it was not possible to achieve an estimate at the whole distribution area because of lack of data in specific zones (North Africa, Eastern Mediterranean, and the Baltic Sea).

Material and methods

Available data

Recruitment time-series

Both fishery-based and -independent time-series of recruitment were available in different catchments throughout Europe (ICES, 2016) (Figure 1 and Supplementary Material S1). Most series considered in this article were analysed by Dekker (2002a, b, c) and are currently used by the WGEEL. Throughout this article, we refer to "glass eel recruitment time-series" even if some of these series do include some older age classes in limited proportions. We distinguished four types of time-series: while Type 1 time-series provide information on relative recruitment, Type 4 time-series provide information on absolute recruitment. Types 2 and 3 time-series capture the evolution of recruitment in a relative way but absolute recruitment can be inferred by introducing additional information on the scaling factors (trap efficiency and exploitation rate).

- Type 1: relative time-series with no information on the scaling factor

Regarding commercial data, catch per unit of effort (CPUE) data are generally considered to better estimate changes in fish abundance. However, total catches might better reflect glass eel recruitment when recruitment falls and fishing effort is high (Gascuel *et al.*, 1995; Briand *et al.*, 2003), as is the case in Spain (Dekker, 2002a) or in the Bay of Biscay (Castelnaud, 2001). As a consequence, 11 series correspond to commercial catch time-series and 2 to CPUE time-series (Figure 1 and Supplementary Material S1).

Similarly, scientific surveys have been carried out in various catchments in Europe. In this study, we used scientific surveys from seven sites (Figure 1 and Supplementary Material S1) which provide relative recruitment time-series. These surveys take place in the downstream part of river catchments except the International Young Fish Survey/International Bottom Trawl Survey (IYFS/IBTS) which takes place in marine waters.

- Type 2: relative time-series based on trapping devices with information on trap efficiency

Eleven times-series resulting from the counting of glass eels in standardized gear were available (Figure 1 and Supplementary Material S1). These traps are located at fishways or trapping ladders at migration barriers. All traps are close to the river mouth. They predominantly catch glass eel, and no glass eel fishery takes place downstream of the trap. At such sites, time-series are the product of absolute recruitment and trap efficiency.

- Type 3: relative time-series based on commercial catch with information on exploitation rate

Glass eel catch data were available in the Somme estuary (France) with an estimate of the exploitation rate related to this fishery. The exploitation rate corresponds to the scaling factor between total catches and absolute recruitment.

- Type 4: absolute recruitment

Two models, GEMAC (Beaulaton and Briand, 2007) and a model from Bru *et al.* (2009), provided estimates of absolute recruitment at the catchment scale by using catches per unit of filtered volume multiplied by the total volume of the area. Such estimates were available in six catchments (Supplementary Material S1).

An estimate of absolute recruitment was calculated on the Iberian Coast (Oria River, Spain) (Aranburu *et al.*, 2016). This estimation has been carried out by fitting a generalized additive model based on commercial and experimental glass eel fisheries and environmental covariates, which was used to estimate daily recruitment, then extrapolated to the entire recruitment season.

Finally, estimates of absolute recruitment were available in the Vilaine estuary (France). In this estuary, a 6 year-long mark-recapture experiment estimated an exploitation rate of 95%, and catches were corrected to estimate the absolute recruitment (Briand *et al.*, 2003; Briand, 2009)

Catchment characteristics

The European River and Catchment Database is a Pan-European database of river networks and catchments (Vogt and Foisneau, 2007). It provides comparable characteristics of European catchments, such as their surface areas.

Description of the model

GEREM is a Bayesian model that estimates annual absolute recruitment at three nested spatial scales: at the river catchment level, at an intermediate spatial scale, and at a larger scale over the whole study area (Drouineau *et al.*, 2016). Hence, it allows recruitment at large scales to be inferred from observations carried out at the catchment level. GEREM shares many common features with dynamic factor analysis (DFA—see Discussion), a method that aims at estimating common trends in a set of time-series (Zuur *et al.*, 2003a). As a DFA, GEREM is based on a state-space model framework: the space model describes how the states (here recruitment levels per zone) change over time while the observation model describes how observations (here recruitment time-series) are linked to those states. Here, we apply the model to a large part of the distribution area of the European eel (Figure 1).

State model: temporal evolution of recruitment at different spatial scales

Modelled total annual recruitment at the three different levels is described hereafter:

- River catchment recruitment $R_{c,z}(y)$ corresponds to the absolute glass eel recruitment during year y into a river catchment c, which is located in zone z and is characterized by its catchment surface area $S_{c,z}$.
- Zonal recruitment $R_z(y)$ corresponds to the absolute recruitment of glass eels into a zone z. A zone represents a geographical region of the whole study area (Figure 1) in which n_z catchments are present.
- The recruitment in the whole study area $R(y)$ corresponds to the absolute recruitment of glass eels over the whole study area during year y. The studied area is composed of N_z zones.

We assumed that the overall recruitment is divided into recruitment zones with proportions per zone p_z varying over years:

$$R_z(y) = R(y) \cdot p_z(y). \tag{1}$$

Contrary to the previous implementation of GEREM (Drouineau *et al.*, 2016), we assumed that proportions per zone may change over years because of, for example, changes in oceanographic conditions which would modify larval drift. We assumed that:

$$\{p_z(y)\} \sim \text{Dirichlet}(\lambda \cdot \{p_z(y-1)\}) \tag{2}$$

to mimic a random walk of these proportions per zone. Parameter λ is called the Dirichlet concentration parameter: a strong value of λ implies that proportion is rather stable over time whereas a small value leads to abrupt changes from year to year. We set λ equal to 80 (a rather strong value) to smooth interannual variations at the zone scale. Thus, we focused on the overall trend rather than on short-term oscillations. Those

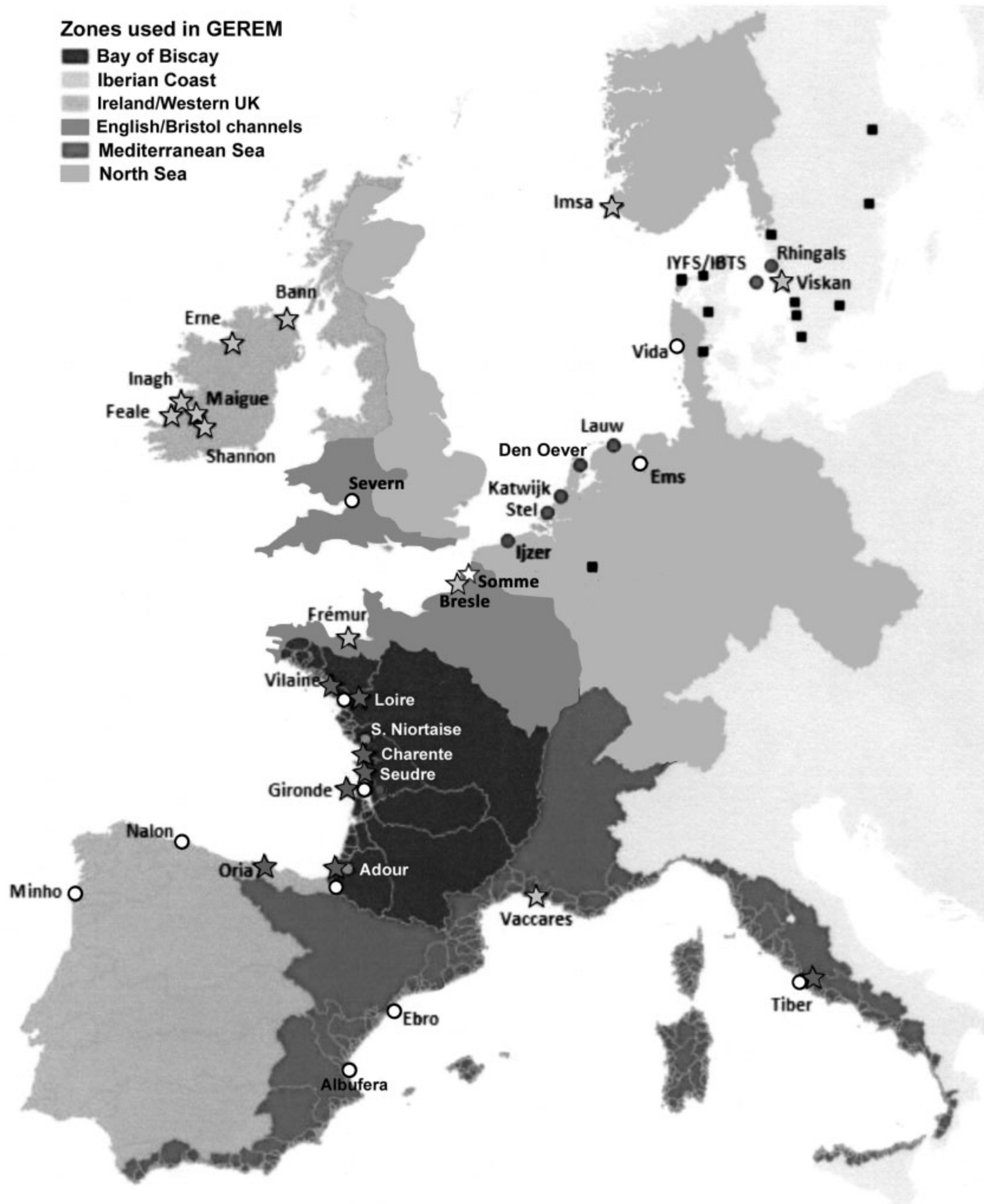

Figure 1. Location of time-series monitoring sites and zones used in GEREM. White circle: glass eel commercial landing time-series (Type 1), light grey circle: glass eel commercial CPUE time-series (Type 1), darker grey circle: glass eel scientific estimate time-series (Type 1), light grey star: recruitment estimate derived from a trapping site (Type 2), white star: the Somme estuary recruitment time-series (Type 3), darker grey star: estimates of absolute recruitment (Type 4), and black square: recruitment time-series not used.

short-term oscillations are considered to be noise at the catchment scale in the observation model (see following section).

Zonal recruitment is then split into river catchments according to a multinomial distribution with proportions as a function of their relative surface areas within the zone. The multinomial distribution is approximated by marginal normal distributions (Johnson *et al.*, 1997):

$$R_{c,z}(y) \sim Normal\ \left(R_z(y) \cdot w_{c,z}, R_z(y) \cdot w_{c,z} \cdot \left(1 - w_{c,z}\right)\right). \quad (3)$$

The weight $w_{c,z}$ of each catchment is calculated as a power function of its surface area:

$$w_{c,z} = \frac{S_{c,z}^{\beta}}{\Sigma_{c_i=1}^{n_z} S_{c_i}^{\beta}}. \quad (4)$$

This means that recruitment into a catchment tends to increase with the catchment weight $w_{c,z}$. We introduced a power function since some catchment attributes, such as river discharge, vary as a power function of catchment surface area (Burgers *et al.*, 2014).

Finally, the overall recruitment is assumed to follow a random walk:

$$R(y) = R(y-1) \cdot e^{\epsilon(y)} \text{ with } \epsilon(y) \sim Normal\left(0, \sigma_R^2\right). \quad (5)$$

Observation model

In the first application of GEREM (Drouineau *et al.*, 2016), only Types 1 and 4 time-series had been considered (no Type 2 time-series was available and Types 3 and 4 were not separated). Consequently, a modification of the observation model was required to account for these new types of series. Following ICES (2015), time-series were assumed to be log normally distributed.

$IA_{f,i,c}(y)$ refers to a Type f recruitment time-series i observed in a catchment c:

$$\log(IA_{f,i,c}(y)) \sim \text{Normal}(\mu_{IA_{f,i,c}}(y), \sigma^2_{IA_{f,i}})$$

$$\text{With } \mu_{IA_{f,i,c}}(y) = \log\left(q_{f,i} \cdot R_{c,z}(y)\right) - \frac{\sigma^2_{IA_{f,i}}}{2} \quad (6)$$

and $q_{f,i,}$ a scaling factor linking Type f recruitment time-series i to absolute recruitment $R_{c,z}$ and $\sigma_{IA_{f,i}}$, the standard deviation of observation regarding Type f recruitment time-series i, which corresponds to the noise within the different time-series.

Prior information and expertise

Regarding Type 1 time-series, no information was available on their scaling factors, so we chose an uninformative large prior for each $q_{1,i}$ which depict in practice catchability of glass eel (Table 1). Type 4 time-series directly provide absolute recruitment estimates, so their scaling factors are $q_{4,i} = 1$.

For Type 2 time-series, scaling factors correspond to trap efficiencies (the result of attraction efficiency and fishway passability) on which we were able to build an informative prior (Table 1). We considered that trap efficiency was equal to fishway passability. Different studies and meta-analysis provided estimates of fishway passability ranging from 0.1 to 0.5 (Jessop, 2000; Briand *et al.*, 2005; Noonan *et al.*, 2012; Drouineau *et al.*, 2015) so we considered that parameters $q_{2,i}$ were all between 0.1 and 0.5.

Regarding Type 3 time-series, the scaling factor corresponds to an exploitation rate. Drouineau *et al.* (2016) assumed an exploitation rate of 75% in the Somme estuary. Rather than considering that this rate is perfectly known, we chose to use a uniform prior around 75% to account for the uncertainty (Table 1).

Modelling assumptions and zone definition

We considered both data availability and ecological information coming from previous studies to define recruitment zones. GEREM uses Types 2–4 time-series along with the "catchment weight vs. catchment surface area" relationship (Equation 4) to estimate absolute recruitment at the catchment and European zone scales, which is similar to a "rule of three" (if a recruitment in a catchment of surface area S_1 is known to be R_1, then the recruitment in a catchment of surface area S_2 in the same zone is $R_1 \cdot S_2^\beta / S_1^\beta$). Those zonal recruitments are then summed up to derive the overall recruitment. In view of this, a first step is to define appropriate zones.

Given the GEREM assumptions, a zone must fulfil three criteria: (i) catchment recruitments within a zone must follow a similar trend (Equation 3), (ii) catchment recruitments within a zone have to follow a similar "catchment weight vs. catchment surface area" rule (Equation 4), and (iii) at least one time-series of Type 2, 3, or 4 is required per zone to be able to apply the "rule of three" and derive zonal recruitment from catchment time-series.

We first divided the study area using the equivalent of ICES ecoregions (Greater North Sea, Celtic Seas, Bay of Biscay and the Iberian Coast, and Western Mediterranean Sea) (ICES, 2004) which correspond to biogeographic and oceanographic zones. We assumed similar currents and environmental conditions would occur within each of these zones, resulting in similar trends in recruitment within each zone. Previous studies demonstrated that there was no clear spatial pattern in recruitment trends, though some time-series from the North Sea might display slightly different trends (Dekker, 2002a; ICES, 2010). In view of this, we built a specific zone for the North Sea and the other zones were based on other criterion. We ended up subdividing the ecoregions into six final zones to meet the two other assumptions since glass eel abundance is maximal along the Bay of Biscay and in the English/Bristol Channels zone (Dekker, 2000b; Bonhommeau *et al.*, 2009). As a consequence, we decided to delimit these two zones from the rest of Europe (Figure 1).

Bayesian inference

The model was fitted using just another Gibbs sampler (JAGS) (Plummer, 2012). The runjags package was used as an interface from R to the JAGS library for Bayesian data analysis (Denwood and Plummer, 2016). The model was fitted to the period 1960–2015 and three chains were run independently in parallel for 80 000 iterations after a burn-in period of 80 000 iterations. Convergence was checked using the Gelman–Rubin diagnostic (Gelman and Rubin, 1992). For each time-series, we computed the root mean square error (RMSE) which measure the average of the squares of the errors, to assess the goodness-of-fit.

Results

Model convergence and quality of fits

The Gelman–Rubin convergence diagnostic has been reported by the potential scale reduction factors (PSRFs) which are all close to 1 (i.e. < 1.1) confirming that the chains converged (Table 1). Posterior distributions of $\tau_{IAf,i}$ ($=1/\sigma^2_{IA_{f,i}}$) were sometimes influenced by their respective prior distributions (Supplementary Material S3). However, since the precision in a lognormal distribution is nearly equal to the inverse of the squared coefficient of variation, we considered that the precision should be >1 (i.e. a coefficient of variation < 1) and we also considered that overfitting was unlikely. Moreover, nine of the 33 scaling factor posteriors were influenced by their priors, mainly for parameters log ($q_{2,i}$) (Supplementary Material S3). Although the quality of fits of the model was variable as illustrated by variable RMSE, the slope was well-fitted in most series. However, the model provided biased estimates or poor slope descriptions for eight abundance indices (SeGEMAC, Tiber, Bresle, Somme, Vaccares, Katwijk, Inagh, and Erne time-series) (Supplementary Material S2).

Recruitment estimates at different spatial scales

According to GEREM, the overall European glass eel recruitment decreased from 1980 onwards to reach a minimum in 2009

Table 1. Parameters used in the model GEREM and their corresponding priors.

Parameters	Priors	PSRF
β: power parameter of the relation between catchment surface area and catchment weight $w_{c,z}$	$\beta \sim$Unif (0.01,2)	1.04
$p_z(1)$: proportion of recruitment in zone z the first year	$\begin{bmatrix} p_1(1) \\ \vdots \\ p_{N_z}(1) \end{bmatrix} \sim \text{Dirichlet} \begin{bmatrix} \frac{1}{N_z} * \gamma \\ \vdots \\ \frac{1}{N_z} * \gamma \end{bmatrix}$	Min 1.00 Max 1.04
γ: Dirichlet concentration parameter for $p_z(1)$	$1/\gamma \sim$ Gamma (2,1) T (1,2)	1.00
$p_z(y)$: proportion of recruitment in zone z in any given year	$\begin{bmatrix} p_1(y) \\ \vdots \\ p_{N_z}(y) \end{bmatrix} \sim \text{Dirichlet} \begin{bmatrix} p_1(y-1) * \lambda \\ \vdots \\ p_{N_z}(y-1) * \lambda \end{bmatrix}$ With $\lambda = 80$	Min 1.00 Quantile 99%: 1.09 Max 1.43
R (1): recruitment in first year	Log (R (1)) $\sim$ Unif (14,17)	1.04
$q_{1,i}$: uninformative scaling factor depicting catchability of glass eels used for Type 1 time-series i	Log $(q_{1,i}) \sim$ Unif (−13,0)	Min 1.00 Max 1.08
$q_{2,i}$: informative scaling factor representing trap efficiencies used for Type 2 time-series i	Log $(q_{2,i}) \sim$Unif (−2.3,−0.7)	Min 1.00 Max 1.01
$q_{3,i}$: informative scaling factor representing the exploitation rate in the Somme estuary	Log $(q_{3,i}) \sim$ Unif (−0.43,−0.16)	1.00
$q_{4,i}$: scaling factor used for Type 4 time-series i	1	
$\sigma_{IA_{f,i}}$: standard deviation of observation for any recruitment time-series	$\tau_{IA_{f,i}=\frac{1}{\sigma^2_{IA_{f,i}}}} \sim$ Gamma (2,1) T (1,15)	Min 1.00 Max 1.06
σ_R: recruitment random walk standard deviation	$\tau_{R=\frac{1}{\sigma^2_R}} \sim$ Gamma (2,1) T (1,15)	1.03

The Gelman–Rubin diagnostic is reported for each parameter by PSRF. A PSRF value lower than 1.1 generally indicates that the chains have converged. The notation "log" refers to the natural logarithm.

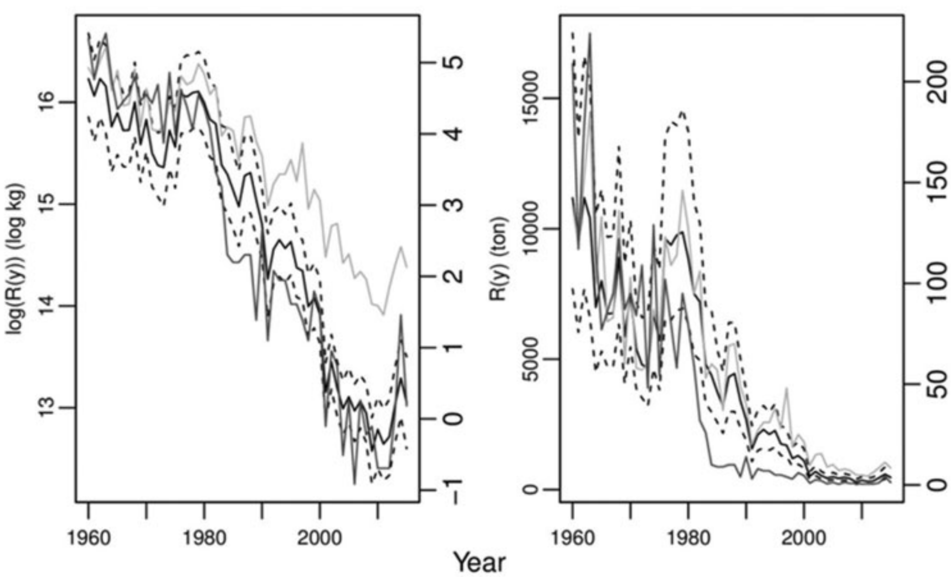

Figure 2. European glass eel recruitment estimated by GEREM in log-scale (left panel) and in tons (right panel) over time. Black solid lines: median and dashed lines: credibility intervals (95%). Light grey line: "Elsewhere" WGEEL recruitment index. Darker grey line: "North Sea" WGEEL recruitment index.

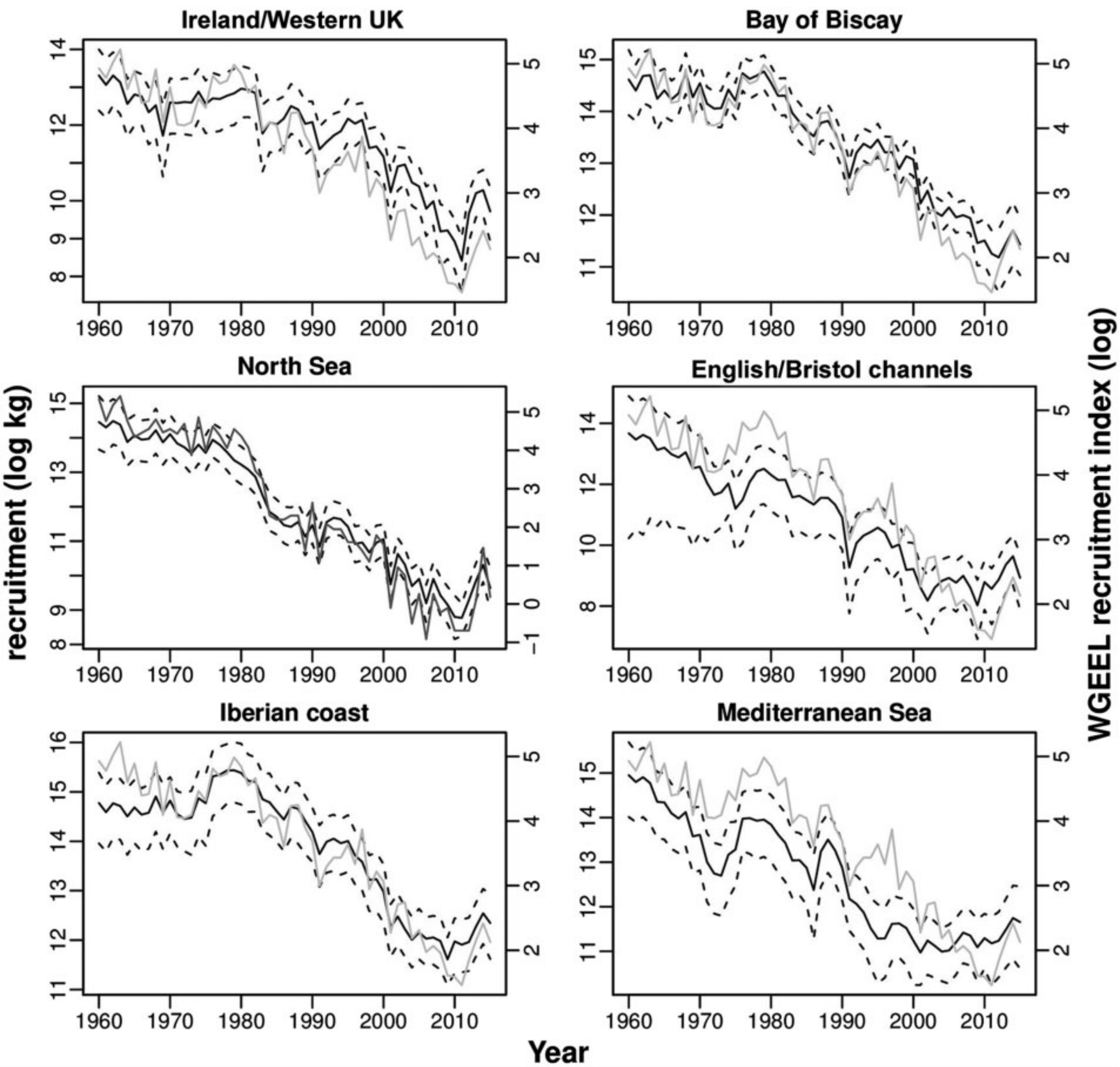

Figure 3. Estimated glass eel recruitment within each zone of the model GEREM in log-scale. Black solid lines: median and dashed lines: confidence intervals (95%). Light grey line: "Elsewhere" WGEEL recruitment index and darker grey line: "North Sea" WGEEL recruitment index.

(Figure 2). GEREM estimated an overall recruitment of 10 825 t in 1960 compared with 440 t in 2015, the latter corresponding to only 6% of the 1960–1979 average. Estimates were consistent with WGEEL estimates (R^2 between the European glass eel recruitment and the WGEEL "Elsewhere" and "North Sea" indices were 0.98 and 0.89, respectively) (Figure 2 right panel).

Zonal recruitments started to decline from 1980 in the Bay of Biscay, Iberian Coast, and Ireland/Western UK after a stable period from 1960 to 1980, while recruitments may have decreased from the beginning of the study period in the Mediterranean Sea and English/Bristol channels zones (Figure 3). However, in these two zones, few data series were available before the 1980s so that estimates were partly extrapolated from data in other zones (North Sea and Bay of Biscay) and from the two random walks (Equations 2 and 5), leading to very large credibility intervals especially in the English/Bristol Channel zone (Figure 3). In the North Sea, recruitment also decreased from the beginning of the study period and the decrease accelerated from the late 1970s. This fast decrease in the North Sea led to a drop in the proportion of total estimated recruitment $p_z(y)$ occurring in this zone from ~20% at the beginning of the study period to ~5% from the 1990s (Figure 4). Conversely, proportions to total recruitment tended to increase in the Iberian Coast and Bay of Biscay zones. The North Sea estimated recruitment in 2015 was 0.88% of the North Sea recruitment level occurring in 1960. For other zones, this ratio varied between 2.77% (Ireland/Western UK) and 8.58% (Iberian Coast).

The North Sea recruitment estimate correlated well with the "North Sea index" estimated by WGEEL (correlation coefficient $r = 0.86$) and the other zones were consistent with the WGEEL "Elsewhere Europe" index (Ireland/Western UK $r = 0.90$, Bay of Biscay $r = 0.91$, English/Bristol Channels $r = 0.65$, Iberian Coast $r = 0.82$, and Mediterranean Sea $r = 0.72$).

Estimated recruitment was concentrated within two main zones: the Bay of Biscay accounted for between 20 and 45% of

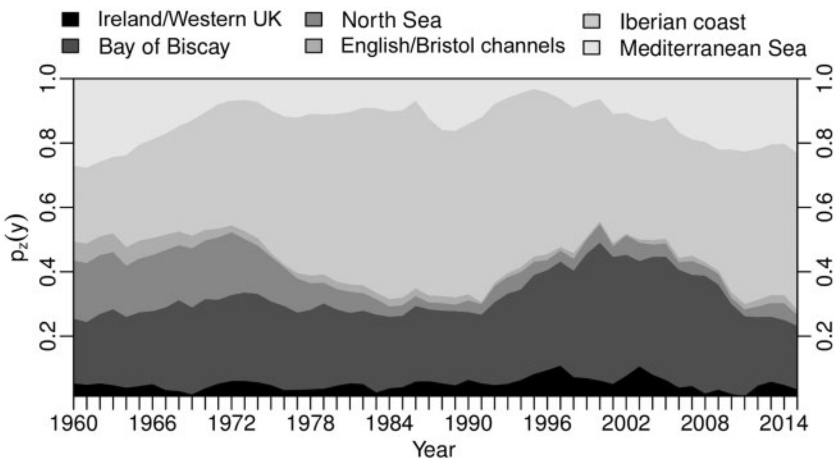

Figure 4. Proportion of total recruitment attributed to each zone in the model simulation with no measurement unit.

Table 2. Minimum and maximum absolute recruitment (in kg) estimated by the model GEREM for each zone.

	Min	Max
Ireland/Western UK	4 214 (2011)	571 496 (1962)
Bay of Biscay	68 873 (2012)	2 566 766 (1979)
North Sea	6 439 (2011)	1 959 079 (1962)
English/Bristol Channels	2 726 (2009)	627 539 (1960)
Iberian coast	107 035 (2009)	4 829 283 (1979)
Mediterranean Sea	55 887 (2001)	2 854 552 (1960)

Years of minimum and maximum recruitment are presented in brackets.

total recruitment while the Iberian Coast accounted for between 20 and 50% of total recruitment (Figure 4). In most zones, recruitment peaked in the early 1960s but peaked in the late 1970s for the Bay of Biscay and Iberian Coast. On the other hand, recruitment minima occurred between 2009 and 2012 in most zones, except for the Mediterranean region where it occurred in 2001 (Table 2), suggesting that the decrease may have slowed or even stopped in recent years.

At a finer scale (i.e. river basin), recruitment estimates were not supported by the modelling approach. The power coefficient β had a median value of 0.76 (credibility interval 0.69–0.79). This parameter is thus significantly lower than 1.

Discussion

Model structure: mixing a DFA and a "rule of three"

Relation with a DFA

GEREM aims to derive an overall recruitment index through an analysis of trends in available recruitment time-series. GEREM shares many common features with a DFA (Zuur *et al.*, 2003a), a method used to detect common trends in a set of time-series. Similar to a DFA, GEREM is based on a state-space modelling structure, with a state-model describing the common trends and an observation model which links observed time-series to those trends. Following the DFA method, GEREM assumes that trends follow random walks. Those random walks ensure that the model focuses on long-term trends while short-term variations are assumed to be noise in the observation model. Random walk is the simplest form of time-series smoother but have proved to be efficient in many situations (Chatfield, 1989; Harvey, 1989; Zuur *et al.*, 2003a, b; Zuur and Pierce, 2004). More complex structures would perhaps improve our estimates since many time-series display rather constant slope over long periods. For example, it would be possible to add a stochastic slope by imposing the existence of a slope between two successive yearly recruitment, with the slope following a random walk. This solution has proved to be robust to different kind of misspecifications such as slope breaks or heteroscedasticity (Delle Monache and Harvey, 2011). Although random walks are generally assumed to be independent from one to another in a DFA, GEREM assumes there is an overall common trend at a larger spatial scale which follows a random walk, and that the different trends among zones are the result of a second random walk of a vector of proportions at the intermediate spatial scale. We considered that this structure was well-suited because of population panmixia which leads to an overall trend, and then possible long-term changes in oceanographic conditions that may have modified larval drift and the distribution of larvae among zones.

A second difference is that in GEREM, each time-series follows the corresponding zonal trend while in a DFA, a time-series is assumed to be a mixture of different trends with mixed weights estimated in the analysis. This modification was necessary to apply the "rule of three" aiming at deriving zonal recruitment from time-series of absolute recruitment. Finally, while DFA are generally fitted using a maximum likelihood approach, GEREM is based on a Bayesian approach that facilitates the propagation of uncertainties at different spatial scales.

The "rule of three"

At the smaller scale, we assumed that glass eels are distributed among catchments proportionally to an unknown power function of their surface area. The model estimated a power parameter β of 0.78 (credibility interval [0.72,0.85]). This value falls within the [0.71,0.85] confidence interval of a power function linking catchment surface area and average discharge estimated by Burgers *et al.* (2014) through a meta-analysis. This would be consistent with river discharge and estuarine plume playing a role in glass eel attraction (Tosi *et al.*, 1990; Aida *et al.*, 2003).

However, river discharge is not the only parameter that might influence glass eel distribution, a process influenced by a number of interacting factors over temporal and spatial scales (Harrison *et al.*, 2014). It has been suggested for instance, in reference to coastal lagoons and brackish water habitats in the Mediterranean area, that a sparse glass eel recruitment sustains local stocks

(Aalto *et al.*, 2016). Indeed, the quantity of available habitats and their typology might play a role, since density-dependence is known to be an important trigger of eel behaviour (Geffroy and Bardonnet, 2012; Podgorniak *et al.*, 2016) and conspecific odour concentration attracts glass eel (Schmucker *et al.*, 2016).

GEREM quality of fits

GEREM relies on latent smoothing functions over time which makes it possible to reproduce the trend of most time-series. However, eight time-series were poorly fitted by the model. These poor fits might be explained by several causes. First, it might reveal local conditions not described in the model which could influence glass eel recruitment at the catchment scale in terms of density and/or temporal trends. Such phenomena, occurring at local scales, have been shown to contribute to between-year variability in glass eel recruitment to estuaries (Arribas *et al.*, 2012; Aranburu *et al.*, 2016) and a quantitative difference in recruitment strength might also occur within a zone. For example, Arribas *et al.* (2012) showed that rainfall and westerly winds may generate more productive environmental conditions in local shelf waters off the Guadalquivir estuary, benefiting growth, survival, and retention of leptocephali during the final stage of their oceanic migration. Ideally, local effects should be taken into consideration in the modelling procedure. Residuals per time-series may also be analysed in the future to depict site-specific deviations from the common trend. Yellow eel abundance in the lower reaches of rivers, as modelled by Eel Density Analysis (De Eyto *et al.*, 2016), could be used in future applications of GEREM to set more realistic abundance priors at the finest spatial scale. Second, most of these time-series correspond to Type 2 (Bresle, Vaccares, Inagh, and Erne) or Type 3 (Somme) time-series. A poor fit may indicate priors that are too restrictive on their respective scaling factors. Indeed, we observed that corresponding posterior distributions were influenced by priors (Supplementary Material S3), confirming this assumption. Although the prior on trap efficiency was based on values from the literature (Jessop, 2000; Briand *et al.*, 2005; Noonan *et al.*, 2012; Drouineau *et al.*, 2015), fishway passability and consequently trap efficiency greatly depends on the geographical location, the distance of the trap from the sea, the trap design, and the type of river system as well as environmental conditions such as river flow and water temperature (Edeline *et al.*, 2006; Crivelli *et al.*, 2008; Acou *et al.*, 2009; Piper *et al.*, 2012). We assumed that trap efficiencies were constant through time. However, trap efficiency depends on local conditions and these interannual variations may be considered as observational noise. More importantly, some traps were occasionally modified to improve their efficiency. In such a situation, it would have been necessary to estimate efficiency before and after the modification to avoid a systematic bias. Such information is probably beyond our reach for most series. In view of this, further discussion is needed with local experts to validate priors on those scaling factors. Third, some series are shown to deviate from the common trend. The reason for that deviation might be a lowering effort after fishery collapse (Tiber), under or overestimation of recruitment for Type 4 series (Oria, Tiber) (Supplementary Material S5).

Comparisons of results with existing knowledge on trends

This study developed a single recruitment index across much of the species' range. Unsurprisingly, the overall trend in recruitment produced by GEREM lies between the two WGEEL indices (i.e. "North Sea" and "Elsewhere" indices). However, GEREM shows a stronger correlation (0.98) with the "Elsewhere" index (Figure 2), where most recruitment time-series included in this study was located, and where glass eel is most abundant (Dekker, 2000b). Indeed, according to GEREM estimates, the "Elsewhere" areas accounted for 80% of the overall recruitment in 1960, while the percentage increased to 95% in 2015, suggesting that the trends in the North Sea time-series have a minor weight in the overall trend, particularly in recent years.

Previous studies did not highlight any clear spatial patterns in recruitment trends (Dekker, 2000a), except possibly for some series in the North Sea area (ICES, 2010). The analysis of estimated zonal recruitments (Figure 3) and proportions (Figure 4) showed a sharper decline in North Sea than in the rest of Europe, consistent with the sharper decline of the "North Sea" index compared with the "Elsewhere Europe" index provided by the WGEEL. GEREM also estimated that the declines in the Mediterranean and English/Bristol channels zones started earlier than in the Bay of Biscay, Iberian Coast, and Ireland/Western UK zones. However, the limited number of time-series at the beginning of the study period led to large credibility intervals and consequently those differences should be viewed with caution.

An index of recruitment at the population scale?

Is the index representative of the overall population recruitment?

Our study area does not cover the entire population distribution area. Data were available for 30 river catchments across Europe and the Kattegat-Skagerrak area was covered by the IYFS scientific survey. Even though Westerberg and Wickström (2016) have recently proposed an assessment method for the Baltic Sea, this region could not be included in the present analysis given that recruitment time-series are composed of young yellow eels with unknown age distributions so that an additional assumption would be required to convert yellow eel abundance into glass eel recruitment. The situation is even more difficult in the eastern and southern Mediterranean zone as well as in northwest Africa where no series are currently available. The participation of GFCM in the WGEEL since 2014 can sustain the involvement of more Mediterranean countries and hence stimulate the implementation of new monitoring programmes in this zone and/or contribute to the availability of new recruitment time-series.

Moreover, most data relate to recruitment to continental areas, and do not include the proportion of glass eel recruiting to coastal waters in which some individuals settle (ICES, 2009). However, there are almost no indices of glass eel recruitment to these marine habitats. The IYFS/IBTS survey provides a glass eel time-series in marine habitats before settlement, but likely, a large part of them may recruit into rivers afterwards. The trend in abundance found in this time-series corresponds well to the trend of the North Sea index generated in this article (Supplementary Material S2). Other surveys targeting eels have occurred in coastal areas of the southern North Sea (ICES, 2009), but several age classes are usually caught, making the use of these data difficult to analyse the recruitment of a given year. Moreover, these surveys target eels in open waters of the North Sea whereas eels settling in marine habitats commonly occupy sheltered waters in bays, lagoons, and estuaries which were not covered. Overall, ICES (2009) indicated that fresh and saline waters probably contribute roughly equally to total French eel landings, suggesting that a substantial fraction of the European eel population may use saline waters as growth habitat.

Although the study area does not cover the entire distribution area of the species, GEREM estimated an overall index using most available time-series. Many time-series originated from zones which are thought to receive the greatest proportion of the recruitment (Dekker, 2000b) and where glass eels are commercially harvested. Few opportunities are available to validate the estimation of absolute recruitment. Dekker (2000b) estimated a recruitment of 582 t in 1993 through a procrustean assessment of catch data. Lambert (2008) carried out a similar analysis with the same data (but making assumption on the glass eel fishery in the Bay of Biscay zone rather than an assumption on the silver eel fishery as in Dekker (2000b) and estimated a recruitment of 1780 t for the same year. In 1993, GEREM estimated a recruitment of ∼2000 t but the comparison is difficult since it was based on only 1 year and the study areas do not completely match. More importantly, a sensitivity analysis of the model demonstrated that, while absolute zonal recruitments were quite sensitive to model misspecification or data corruptions, the overall trend was quite robust (Supplementary Material S4).

A need for additional data

Though there is no option for a standardized monitoring protocol at the European scale (Dekker, 2000a, 2002a), a better spatial coverage through the implementation of new monitoring programmes has already been proposed (Dekker, 2002a), and the latest EU multiannual programme management and use of data in the fisheries sector (EC 2016/1251) requires Member States to collect information on eel recruitment in at least one river per EMU, so such data should become available, although it will take many years before these time-series will be suitable for long-term trend analysis.

There is also a need to further estimate absolute recruitment in certain parts of Europe and increase the number of Types 2, 3, or 4 recruitment time-series. This would improve the estimation of the parameter β and the quality of the "rule of three" used to estimate absolute recruitments. For example, the high recruitment estimated over the Iberian Coast might be surprising but the only absolute recruitment time-series available in this zone comes from the Oria River which is a small catchment close to the Bay of Biscay zone, for which the authors also indicate that recruitment might have been overestimated (Aranburu *et al.*, 2016). Consequently, the level of recruitment in this river is probably more similar to that of the French Atlantic coast than to that of Portugal, probably making the recruitment estimate for the Iberian Coast overly optimistic. The same arguments apply to the Mediterranean region where series are few and Type 4 time-series relatively uncertain (Supplementary Material S5). Currently, our zone definition was strongly constrained by data availability and so largely based on operational considerations.

Conclusion

GEREM provides a methodological framework to estimate the recruitment of temperate eels at various spatial scales, from the catchment level (which is consistent with the scale of anthropogenic pressures and data collection) to the extrapolation across the species' range—the scale at which the stock assessments should be conducted—provided sufficient data are available. In this study, the model has been applied to the European eel to derive a single recruitment index gathering all recruitment time-series available across Europe. This application has made it possible to obtain an overview on the distribution of recruitment across different regions as well as an insight into the different regional recruitment trends. The main result of this study points out a more severe recruitment decline in the North Sea compared with elsewhere in Europe supporting the suggestion of the WGEEL.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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