GEREM (Glass Eel Recruitment Estimation Model): A model to estimate glass eel recruitment at different spatial scales

Hilaire Drouineau, C. Briand, Patrick Lambert, Laurent Beaulaton

GEREM (Glass Eel Recruitment Estimation Model): A model to estimate glass eel recruitment at different spatial scales

Authors: Drouineau, H.[1,*]; Briand, C.[2]; Lambert, P.[1]; Beaulaton, L.[3 4]

1 Irstea UR EABX, 50 avenue de Verdun, centre de Bordeaux, F-33612 Gazinet Cestas, France

2 Institution Aménagement de la Vilaine, 56130 La Roche-Bernard, France

3 Onema, Pôle Gest'Aqua, 65 rue de St Brieuc, 35042 Rennes, France

4 INRA, U3E (1036), Pôle Gest'Aqua, 65 rue de St Brieuc, 35042 Rennes, France

*corresponding author: hilaire.drouineau@irstea.fr, tel: +33 (0)5 57 89 27 09, fax :+33 (0)5 57 89 08 01

1 Abstract

Given the importance of reliable recruitment estimates when assessing temperate eel stocks and enforcing appropriate management measures, surprisingly few analytical tools have been developed to estimate yearly glass eel recruitment. Of the models that do exist, large-scale models generally rely on strong assumptions relating to fishing activity, while other models generally estimate recruitment at the river basin scale. With the aim of filling this gap, we developed the GEREM (Glass Eel Recruitment Estimation Model) to estimate glass eel recruitment at different nested spatial scales. Our model simultaneously estimates annual recruitment at river catchment level, at an intermediate spatial scale such as Eel Management Units (EMUs), and at a larger scale (e.g. a country). Provided enough data become available in the future, the analysis could be extended to the scale of the distribution area, which would be consistent with the population scale. In this study, the model was applied to France, using various recruitment indices obtained from 1960 to 2013. This provided trends and absolute recruitment estimates consistent with current expert knowledge. A sensitivity analysis was carried out to assess the robustness of results to sources of uncertainty. This type of model fills an important gap in the range of quantitative tools presently available to estimate recruitment. It could be used in the future to fix total allowable catches in countries such as France where glass eels are fished commercially.

Keywords: *Anguilla anguilla*, temperate eel, recruitment, stock-assessment model, glass eel

2 Introduction

The European eel (*Anguilla anguilla*) is a catadromous species whose population spans a vast area, stretching from Morocco to Norway (Tesch, 2003). Reproduction takes place in the Sargasso Sea (Schmidt, 1923), after which leptocephalus larvae are passively transported by oceanic currents to the continental shelf, where they metamorphose into glass eels (Tesch, 2003). They then enter continental waters, becoming pigmented glass eels and later yellow eels. Yellow eels grow in freshwater or estuarine habitats, typically for 3 to 15 years (Vollestad, 1992), after which they metamorphose into silver eels and achieve sexual maturity while migrating back to spawning grounds.

The European eel population has been in drastic decline since the late 70s (Castonguay *et al.*, 1994; Dekker, 2003; Dekker *et al.*, 2003; Dekker and Casselman, 2014). The IUCN lists *A. anguilla* as “critically endangered” (Jacoby and Gollock, 2014). Many possible reasons for this population collapse have been suggested, including changes in oceanic conditions (Castonguay *et al.*, 1994), contamination and habitat degradation, parasitoids (Feunteun, 2002), fishing pressure, and massive habitat loss (Kettle *et al.*, 2011).

In the late 2000s, the European Commission introduced Regulation N° 1100/2007, imposing a new set of measures designed to reverse the decline. Because eels spend most of their growth phase in continental waters, implementing these measures was (and remains) the responsibility of EU member states. Under the new rules, member states were required to create Eel Management Units (EMUs). An EMU is a homogeneous group of river basins that are home to eels, and where specific protective measures are applied. These measures are referred to as Eel Management Plans (EMPs). In 2008, each EU Member State submitted its proposed EMUs and EMPs for approval by the EU Commission.

Though management measures are implemented at the national and regional scales, the stock is assessed at the population scale which corresponds to the distribution area since genetic evidence demonstrates that the European eel is totally panmictic (Als *et al.*, 2011). Assessment is carried out yearly by the joint EIFAAC (European Inland Fisheries and Aquaculture Advisory Commission), ICES (International Council for the Exploration of the Sea) and GFCM (General Fisheries Commission for the Mediterranean) working group on eels (WGEEL).

Several abundance indices are collected for stock assessment: recruitment indices, yellow eel abundance indices and silver eel catches. Aside from the questionable quality of some of these data, the fractal dimension of eel stock (Dekker, 2000b) makes it difficult to interpret yellow and silver eel indices. During their growth stage, eels are subject to contrasted environmental conditions (distribution area ranging from Morocco to Norway) and anthropogenic pressures (fishing activity, hydropower mortality, contaminate, etc.) which are difficult to assess at European level (Dekker, 2000). Also, eels display a marked contrast in life-history traits and tactics at the river basin and distribution area scales (Drouineau *et al.*, 2014). This includes sex-ratio (Kettle *et al.*, 2011) and age-at-silvering (Vollestad, 1992), which can vary from 3 years in southern Europe to over 20 in northern Europe. In view of this, it is very difficult to distinguish between local effects and stock status when analysing yellow and silver eel indices. Another issue is that commercial silver eel fishing only takes place in a handful of European regions, and relevant effort data are rarely reported, making silver eel catches difficult to interpret. In view of this, WGEEL considers that while yellow and silver eel indices may be used in the future, they are currently too scarce and uncertain and may be more representative of the local area where they are collected than of overall eel stock (ICES, 2014). On the other hand, glass eels correspond to the first continental stage and are consequently less influenced by local conditions. Several monitoring projects throughout Europe are dedicated to glass-eels. They use sampling methods adapted to this specific eel stage (specific commercial and scientific fishing gear, glass-eel ladder, etc.). In 2002, a European project was set up to list and co-ordinate these monitoring programs (Dekker, 2002).

For the reasons stated above, recruitment indices are of major importance in assessment. They may also be used to assess “non-detriment findings” (CITES) for the issue of export permits, as proposed by ICES (2015). A series of indices is available for sites across Europe. These are analysed by the WGEEL on a yearly basis, and further summarised in three separate indices (ICES, 2013). Two of these indices report glass eel trends, one in the North Sea, and the other for the rest of Europe (referred to as “Elsewhere Europe”). A third index reports trends for young yellow eels, mostly in the Baltic Sea (ICES, 2013).

Recruitment estimates are especially important for countries such as France, where glass eels are commercially fished (silver eels can only be fished in the Loire River and in the south of the country, while commercial yellow eel fishing is much less widespread) , meaning that quantitative tools are needed to set permitted glass eel quotas (it should be noted that the equipment used to catch glass eels is completely different from that used to catch silver and yellow eels). In the late 90's, glass eel fishing was important in France (Briand *et al.*, 2008). At that time, eel was the most important species landed in value in the Bay of Biscay (Castelnaud, 2001). In some specific river basins, fishing impact was very high with exploitation rates over 95% (Briand *et al.*, 2003). In view of this, models such as GEMAC (Beaulaton and Briand, 2007), or a model developed by Bru et al. (2006) and Prouzet et al. (2007), have been developed to estimate exploitation rates and recruitment at catchment scale. However, one disadvantage of these models is that they only work at an estuarine scale. From an EU perspective, it would be desirable to have a model capable of estimating recruitment across the entire EMU, or even the whole of Europe. In this paper, we present GEREM (Glass Eel Recruitment Estimation Model): a Bayesian model to estimate recruitment at various nested spatial scales. A hierarchical Bayesian model is one of the most suitable types of model when dealing nested spatial scales. It allows recruitment at large scales to be inferred from observations carried out at smaller scales. The Bayesian approach also makes it possible to incorporate prior information, as well as quantifying uncertainty. To illustrate the model's potential, we provide the results of an initial test on French EMUs. The possibility of using the model at European level is then discussed.

3 Material and methods

3.1 Model description

3.1.1 State models: assumptions relating to recruitment at different spatial scales

The model aims to estimate yearly absolute recruitment of glass eels using recruitment data collected from various river catchments. The model uses three nested spatial scales:

- The overall recruitment: $R(y)$ glass eel within the whole study area year y. The study area is composed of N_z zones.
- Zonal recruitment: $R_z(y)$ glass eel within a zone z. A zone is a homogeneous sub-section of the study area, made up of various river catchments in which glass eel density is assumed to be similar. Each zone is composed of n_z river catchments, each

with its own surface area: $S_{1,z},\dots,S_{n_z,z}$. Catchment surfaces were recorded in the CCM database (Vogt and Foisneau, 2007) (we excluded catchments with a null Strahler rank from the database).

- River catchment recruitment $R_{c,z}(y)$: glass eel over a river catchment c, which is located in zone z and is characterised by its catchment surface $S_{c,z}$.

We assume that the overall recruitment $R(y)$ is divided into different recruitment zones based on a multinomial distribution, with proportions p_z for each zone. This multinomial distribution mimics the random passive distribution of leptocephali generated by oceanic currents. The multinomial distribution is approximated by marginal normal distributions (Johnson *et al.*, 1997):

$$R_z(y) \sim Normal\left(R(y)\cdot p_z, R(y)\cdot p_z\cdot(1-p_z)\right) \qquad (1)$$

Similarly, zonal recruitment is divided into river catchments according to a multinomial distribution with proportions equal to a function of their relative surface area within the zone. As in the previous split level, the multinomial distribution is approximated by marginal normal distributions (Johnson *et al.*, 1997):

$$R_{c,z}(y) \sim Normal\left(R_z(y)\cdot w_{c,z}, R_z(y)\cdot w_{c,z}\cdot(1-w_{c,z})\right) \qquad (2)$$

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

$$w_{c,z} = \frac{S_{c,z}^{\beta}}{\sum_{c_2=1}^{n_z} S_{c_2,z}^{\beta}} \qquad (3)$$

A β value close to 1 would mean that recruitment is proportionate to catchment surface, which can be considered a proxy of available habitat. However, it has previously been observed (at least on small catchments) that river discharge and river plume have an influence on glass eel recruitment (Crivelli *et al.*, 2008; Elie and Rochard, 1994). If river discharge is the main factor influencing the proportions in each catchment, then the power is less than one. This is shown by a meta-analysis carried-out by Burgers et al. (2014), which demonstrates that river discharge is a power function of catchment surface with a power less than 1. A power greater than 1 would imply an over-concentration of glass eels in large catchments. However, this is unlikely, because it would be inconsistent with large commercial catches in small catchments.

The overall recruitment is assumed to follow a random walk:

$$R(y)=R(y-1)\cdot e^{\epsilon(y)} \text{ with } \epsilon(y)\sim Normal\left(0,\sigma_R^2\right) \qquad (4)$$

3.1.2 Observation model

Two types of observed time series are used to fit the model:

$IA_{i,c}(y)$ denotes a relative abundance index i observed in a catchment c, which is assumed to be lognormally distributed:

$$\log\left(IA_{i,c}(y)\right)\sim N\left(\mu_{IA_{i,c}}(y),\sigma_{IA_i}^2\right) \text{with } \mu_{IA_i}(y)=\log\left(q_i\cdot R_{c,z}(y)\right)-\frac{\sigma_{IA_i}^2}{2} \qquad (5)$$

with q_i a scale factor.

$U_{i,c}(y)$ denotes an absolute recruitment estimate series (or a punctual estimation) i observed in a catchment c, which is also assumed to follow a lognormal distribution:

$$\log\left(U_{i,c}(y)\right)\sim N\left(\mu_{U_{i,c}}(y),\sigma_{U_i}^2\right) \text{with } \mu_{IA_i}(y)=\log\left(R_{c,z}(y)\right)-\frac{\sigma_{U_i}^2}{2} \qquad (6)$$

The model requires at least an absolute index (a series or a punctual estimate) per zone to be identifiable: without any absolute index in a zone, the corresponding recruitment zone and consequently the overall recruitment would only be relative estimates.

3.1.3 Bayesian inference

The model is fitted using Stan (Stan Development Team, 2013), a package to obtain Bayesian inference via the No-U-Turn sampler, a variant of the Hamiltonian Monte Carlo, and rstan, an R (R Development Core Team, 2011) interface to Stan. Uninformative or flat priors are used for most parameters (Table 1). For γ, which is often called Dirichlet concentration parameter (a value below 1 leads to sparse distributions while a value above 1 leads to dense distributions), we used an uninformative prior recommended by (Ohlssen *et al.*, 2007). For β, used a uniform prior between 0.01 and 2 because, as previously mentioned, a β above 1 is unlikely.

3.2 Application to French eel substock

3.2.1 EMU description

The model was applied to France. As part of the French eel management plan (Anonymous, 2010) 9 EMUs were defined. In this study, the Rhine-Meuse EMU was discarded, as recruitment does not occur in the French part of this EMU. The Artois-Picardy and Corsica EMUs were merged with the Seine-Normandy and Mediterranean EMUs respectively, as no data were available for the Artois-Picardy and Corsica EMUs. These six (merged) EMUs (Table 2 and Fig. 1) are the six zones from the model ($N_z = 6$).

3.2.2 Recruitment indices

Thirteen series, collected in nine different catchments, were used in this study (Table 3). Of those, eight represent an absolute number of recruits. The characteristics of the nine corresponding catchments are provided in Table 3.

Seven of those data-series (Vil, Loi, SevN, GiS, GiCP, AdCP, Brel) are currently used by the

WGEEL - along with 19 other European series - to derive the Elsewhere-Europe index (ICES, 2014).. Seven data-series covering France are presented by Feunteun et al (2002). Three main types of data were considered as relative indices: (i) commercial catch divided by fishing effort (SevN, GiCP, AdCP) (except for the Loi index for which no effort data were available but catch data were consistent with CPUE from other series), (ii) a scientific index from a standardized monitoring program (GiSc), and (iii) yearly counts in a scientific fish trap (Bres). Fishery-based indices only go as far as 2011. Since 2011, fishing activity in France has been extensively modified due to the introduction of a new quota system. Consequently, fishery-based indices taken before and after these changes cannot be effectively compared.

The model also requires absolute estimates. These were obtained using three methods:

- ChGEMAC, SeGEMAC, GiGEMAC, are recruitments estimates provided by GEMAC (Beaulaton and Briand, 2007) while AdGERMA and LoGERMA are recruitment estimates provided developed by Bru et al.'s model (2006, 2009). The two models were developed to estimate commercial exploitation rates at the river basin scale. They are essentially based on an estimation of glass-eel density based on catches divided by sampled volume, which is then multiplied by the total volume of the zone. The GEMAC model uses either commercial or scientific catches, while the Bru et al. (2009) model requires the use of scientific catches to estimate glass eel daily abundance. Since these models work at the river catchment scale, models were fitted independently to each river basin (using independent data). We assumed that series were statistically independent, even though they came from similar models.
- The Vil data-series represents commercial catches. The small additional number of glass eels arriving after the fishing season was estimated from catches made at a trapping ladder located at an impassable dam in the Vilaine estuary (Briand, 2008). Commercial fishing takes place just downstream from the dam, where glass eels aggregate. Statistical analysis shows that commercial fishery is so efficient (over

95%) that total catches can be used to estimate total recruitment (Briand *et al.*, 2003). Given this efficiency, local environmental conditions have little impact on the annual catch, and this series is closest to the average of the "Elsewhere Europe" recruitment series (ICES, 2010). Local conditions are fairly similar in the Somme, where commercial fishing also takes place downstream from an estuarine dam. On the basis that glass eels were also blocked by this obstacle, an expert-estimated exploitation rate of 75% was used, although no in-depth analysis was carried out (contrary to the Vilaine estuary). Consequently, we multiplied this data-series by 1.33 and assumed that it provided an absolute estimate of total recruitment.

- The Vaccares series was collected by counting glass eels in a trap upstream from a fish pass. The fish pass is located on a sea wall which blocks the sea channel (Crivelli *et al.*, 2008).

Absolute indices are expressed in tonnes of glass eels, while relative indices are standardised according to their mean values. The model was fitted to the period 1960-2013. Three chains were run independently in parallel for 10,000 iterations after a burn-in period of 10,000 iterations. Convergence was checked using Gelman-Rubin diagnostics (Gelman and Rubin, 1992).

3.3 Sensitivity analysis

The model relies on two main assumptions: (i) absolute recruitment indices are unbiased estimates of real recruitment and (ii) catchment recruitment is derived from zone recruitment with a power function of the catchment surface. Two complementary analyses were carried out to test the influence of those assumptions on the results of the model:

- S1 addresses the consequences of a systematic bias in absolute recruitment indices. The model was fitted successively to 8 altered datasets - one dataset per absolute recruitment index. For each dataset, the absolute recruitment estimate was multiplied by 1.1 to mimic a systematic bias of 10%. Underestimation was considered more likely than overestimation, since our absolute abundance estimates assume that catchability (AdGERMA, SeGEMAC, ChGEMAC, LoGERMA, GiGEMAC) or ladder passability are equal to one (Vaccares). They may also be inferior to 1, in which case, our data underestimate the true value and should be multiplied by a correction factor superior to 1.

- S2 assesses the influence of extrapolation (equation 2). The model was fitted after fixing β at three different values: 0.5, 1 and 1.5.

4 Results

4.1 Recruitment estimates

Gelman and Rubin diagnostics confirmed that the chain converged after 20,000 iterations (10,000 burn-in+10,000 samples for inference). $\bar{R}$ statistics were less than 1.05 for all parameters (Table 1).

A visual inspection of the results confirmed that prior distributions had limited influence on posterior distributions (see supplementary materials). The posterior distribution of γ was limited by the right bound of the prior distribution. However, allowing for a larger Dirichlet concentration parameter would lead to denser Dirichlet distributions, resulting in more informative priors on p_z, which are not suitable.

The model fitted well both relative abundance and absolute abundance indices (Fig. 2 and Fig. 3). Observed data were generally within credibility intervals. As expected, large credibility intervals were occasionally observed for series with missing data. However, since all of the data series were relatively consistent, missing data from a series were made up for by data from other series, resulting in small credibility intervals for most series. Larger credibility intervals were observed for Somme, Vaccares, Bres, and SeGEMAC in certain years. For those catchments, recruitment values were low, either because of a small catchment surface or because the catchment was located in a zone where glass eels were scarce. As a consequence, recruitment $R_{c,z}(y)$ was very low (close to zero) and the normal approximation (equation 2) sometimes led to very small values (even negative), resulting in large credibility intervals in the logarithmic scale (since log(0) tends to negative infinity).

The overall glass eel recruitment estimated by the model was consistent with existing knowledge and strongly correlated to the "Elsewhere Europe" index estimated by the WGEEL (Fig. 4 – Kendall $\tau = 0.87$). The model confirms that recruitment has been on the decline since the late 70s, following a period of stability during the 60s and the 70s. Recruitment was relatively stable at around 4,000 tonnes before 1980 and then dramatically decreased to approximately 140 tonnes in recent years, i.e. less than 5% of the recruitment which was observed before the 80s.

The estimated value of the overall recruitment divided by the surface of the studied area was 0.36 kg/km² (credibility interval: [0.19, 1.26]) in 2010. The ratio was equal to 0.75 kg/km² in 2005 and 0.68 kg/km² in 2006. As a comparison, Cicotti (2006) estimated a ratio of around 0.01 kg/km² in the Tiber River (Italy) in the same period, while Aranburu et al. (in Press) estimated a ratio of 1.68 kg/km² in the Oria River (Spain, Basque Country) in 2013.

The estimated catch rates oscillates between 20% and 30% from 1980 to 2010 with no particular trend (Fig. 4) .

Recruitment is concentrated within three main EMUs: the Loire (median 34.6%), Brittany (median 26.0%) and the Garonne (median 25.0%) (Fig. 5).

The power coefficient β credibility interval is large (median 0.51, credibility interval [0.21,0.75]) but significantly lower than 1.

4.2 Sensitivity analysis

Whatever the scenario (S1 or S2), the estimated trend in the overall recruitment remained similar (Fig. 6). However, the value of β (S2) had a larger influence on results. Recruitment was approximately 25% lower when setting β at 1 than when it was set at 0.5 (close to our estimated value). However, it was approximately 4.57 times higher when β was set at 1.5 (but β greater than 1 are unlikely).

S1 had a limited impact on the distribution of recruitment among the different zones (Fig. 7). The change mostly concerned the zone in which the altered series was collected, but remained small when compared to credibility intervals. Interestingly, changes to one of the three absolute estimates collected in the Garonne zone (GiGEMAC, ChGEMAC, SeGEMAC) did not cause a large variation in β. β was slightly lower when SeGEMAC (smallest catchment) was modified (Fig. 8). As a consequence, the changes in the Garonne zone had limited impact on recruitment in other zones (Fig. 7).

β was the parameter with the largest influence. Changes mostly affected three zones: Brittany, Garonne and Rhone-Mediterranea-Corsica. Estimated recruitment for Brittany decreased as β increased, while, conversely, it increased for the Rhone-Mediterranea-Corsica zones. Unsurprisingly, sensitivity to β tended to decrease for zones where absolute estimates were collected from the largest catchments in each zone (Table 3). It explains the difference in variation of β between Brittany and Rhone-Mediterranea-Corsica and Seine-Artois: for the Brittany zone, the absolute estimate was collected in the largest catchment of the zone (the Vilaine) whereas it was collected in relatively small catchments for the two other zones (Vaccarès is a 6.5km² catchment in a 129,586 km² zone, and the Somme is a 6,550 km² catchment in a 114,293 km² zone). For the Garonne zone, absolute indices were collected in both large and small catchments resulting in a less straightforward response.

5 Discussion

5.1 GEREM – a model to fill a gap in the range of existing quantitative assessment tools

The GEREM model addresses the estimation of absolute glass eel recruitment at various nested spatial scales. As such, it provides new insights into eel recruitment dynamics, the fractal nature of which is highlighted by Dekker (2000b). Glass eel recruitment is equally fractal. Because it covers the entire eel population, the distribution area is the most appropriate spatial scale when for stock assessment. Analysing recruitment at EMU scale is consistent with the spatial management scale, while the river basin scale is consistent with anthropogenic pressures (fishing activity, hydropower production, level of contamination, habitat degradation) and the scale of data collection.

Assessing glass eel recruitment is essential for stock management (Moriarty and Dekker, 1997). Many traditional reference points used in fisheries management are based on stock-recruitment relationships, and therefore require a recruitment time-series. Current limitations stemming from the interpretation of yellow and silver eel indicators make recruitment indices even more crucial when assessing the status of eel stocks (ICES, 2013). The procrustean model proposed by Dekker (Dekker, 2000a) estimates recruitment at stock level, requiring strong assumptions about the stability of recruitment and fishing activity (Dekker notably assumed that silver eel catch rates and life cycle duration were similar in the whole distribution area and that catches were known without errors). On the other hand, GEMAC (Beaulaton and Briand, 2007) provides recruitment estimates at the catchment scale, but cannot be applied at a larger spatial scale. GEREM fills a gap within the existing range of tools by providing estimates at spatial scales consistent with biological and management scales. In Europe, these scales may be used in the future to fix total allowable catches in countries like France, where glass eels are fished commercially.

The modelling approach used in GEREM could form the basis for a patch-based population dynamics model (Wu and Levin, 1997) for the whole eel continental phase, similar to the model currently being developed by Koops et al. (2014). In such a patch-based model, the recruitment zones we have proposed may be subdivided into smaller patches that would be homogeneous in terms of eel sub-population characteristics and anthropogenic pressure. In those sub-patches, a simple stage-based model similar to the model proposed by Dekker (2000a) could be applied using GEREM recruitment estimates for each patch and incorporating new fishing effort data that were recently reconstructed by the WGEEL (ICES, 2013). The nested spatial scales, ranging from distribution area to recruitment zones, subpatches, and river catchments would appear to be especially relevant in addressing the fractal geometry of the eel population (Dekker, 2000b).

5.2 Rationales of underlying assumptions and robustness of results

To estimate absolute recruitment, the model is based on an assumption of two nested multinomial distributions of the overall recruitment. At the finest spatial scale, the proportion of recruitment in each river catchment is assumed to be a function of its surface area raised to a power β. Currently, the model estimates for the β parameter encompasses the power coefficient of the relationship between maximum discharge and catchment area estimated by Burgers et al. (2014), i.e. [0.57–0.69]. However, the estimation is only based on three series (SeGEMAC, GiGEMAC and ChGEMAC) from the Garonne zone, which was the only zone where more than one river basin absolute abundance estimate was provided.

The estimation of β raises the question of how glass eels heading for coastal environments navigate at sea, and whether they distribute themselves according to river flows or simply at random in the area of their arrival. European leptocephalus larvae generally metamorphose into glass eels when they cross the continental slope (Tesch, 2003). They use tidal (Tesch,

2003) and wind driven currents (Westerberg, 1998) to progress towards the coast. Experiments have shown that energy reserves and highly efficient swimming of American glass eels allow them to sustain active swimming over long distances (Wuenschel and Able, 2008). Glass eels possess an acute sense of smell (Sorensen, 1986; Tesch, 2003) which is thought to allow them to identify freshwater plumes and navigate as they approach the coast. The final distribution of glass eels is the result of two mechanisms. The first is passive transport by currents, which is described in the model by the first multinomial distribution between different zones. The second is active navigation within a zone, which is probably achieved by active migration but also the use of the tidal currents, which is described by the second multinomial distribution.

The model is very sensitive to the value of β. Therefore, including more series with absolute recruitment, or at least indices with standardised protocols and similar catchability values, could significantly improve the model's estimates, as well as helping to work out the relationship between catchment recruitment and catchment surface area. In the French Management Plan, 10 “index rivers” have been identified (Anonymous, 2010) Within these areas, specific efforts are made to quantify yearly eel recruitment and escapement. This ought to provide valuable data in the near future. In the absence of any further data, comparing model estimates with different values of β could suffice. In our case study, the trend remained similar, irrespective of β values. However, overall recruitment was sensitive to β (25% lower when setting β at 1) especially in zones where absolute estimates made up an insufficient proportion of the surface area of the zone.

As mentioned earlier, recruitment indices are of major importance for eel stock assessment. As is the case with many stock assessment models, GEREM assumes that glass eel indices, including commercial CPUE, are proportional to true abundance. However, Harley et al. (2001) pointed out for many stocks that CPUE are not strictly proportionate to true abundance but rather display a power relationship. The most common situation, called hyperstability, occurs when CPUE remains stable while abundance decreases (Hilborn and Walters, 1992). Hyperstability can arise when fishermen modify their behaviour as a function of abundance (Hilborn and Walters, 1992). However, the commercial CPUE used in this article, display similar trends to other types of data (including scientific trap) which should not display hyperstability. It has been observed at European level that most commercial CPUE collected across Europe display a similar trend, despite very distinct fishery types between river catchments. This trend is also similar to non fishery-based indices (ICES, 2010, p 201). In view of this, we considered that hyperstability or hyperdepletion could be ignored in the model.

Additionally, we carried out a simulation exercise where we fit the model to simulated datasets to check that model performs adequately when assumptions are correct. Results are presented in supplementary material

5.3 Application to French eel sub-population

The application of the model to France as a case study would appear especially relevant, given that France is assumed to receive a significant proportion of population recruitment (Lambert, 2008; Moriarty and Dekker, 1997). Estimating recruitment is of particular importance in France, where glass eels are commercially fished - an industry which flourished up until the early 2000s (Castelnaud, 2001). Data were available for 9 different river catchments covering 47% of mainland France, and accounting for (according to the model) about 35% of overall recruitment. The model estimates fit well with the different series, and the trend is not sensitive to data uncertainty. Consequently, the estimated trend can be considered reliable. The overall recruitment is not particularly sensitive to bias or uncertainty in the data, even for the Somme catchment, where absolute estimates are based on an expert assessment of exploitation rate.

Using glass eel fishery data from 1993 and 1994, Moriarty and Dekker (1997) estimated that recruitment in France, Spain, Portugal, and the Bristol Channel area in the United Kingdom was around 538 tonnes, approximately 76% of total European recruitment, resulting in a glass eel exploitation rate of 95% in this area. A similar approach to the same data, carried out by Lambert (2008), led to a recruitment of approximately 1,500 tonnes in the same area, 74% of total European recruitment, and an exploitation rate of 26%. GEREM estimates for the same period were similar, with a median of 1,490 tonnes in 1993 (credibility interval 784 to 5,020 tonnes), although this only applies to France.

The resulting exploitation rates were slightly lower, and recruitment estimates slightly higher than estimates provided by a group of experts preparing French Management Plans in 2007 (unpublished data). There are two possible explanations for these differences. The first is that the experts based their estimates on commercial catch data in commercially fished catchments, and then had to extrapolate an overall exploitation rate for both fished and unfished basins, possibly resulting in a small underestimation of abundance. The second is that GEREM recruitment estimates were possibly slightly exaggerated for the Brittany EMU. Catchments located on the west and north coasts of Brittany probably have smaller recruitment levels (closer to those in the Seine-Artois zone) than catchments located on the south coast (closer to Loire catchments). Since the Vilaine estuary, which is the only absolute estimate series for this EMU, is located on the south coast, recruitment estimates in this zone are probably over-optimistic.

On the contrary, the EDA model estimated that there were 6 times more silver eels in the Seine Normandy EMU than in the Picardie EMU (Briand *et al.*, 2015). The recruitment estimated by GEREM for both of these EMUs combined is based on the data of the Somme, which are probably lower than the potential number of recruits further west. In view of this, recruitment in the Seine-Artois zone may have been underestimated.

For the Rhone-Mediterranea-Corsica estimates, it is important to take into account that

Vaccares is a lagoon, and as such, the assumption we made relating to catchment surface area and discharge relationship may not have been appropriate. New series and absolute recruitment estimates could prove valuable in improving estimates made by the model.

The estimated overall recruitment displayed very large credibility intervals (Fig. 4). This can be explained by several factors. Firstly, the uncertainty attached to β due to the limited levels of absolute recruitment series in a single zone is especially problematic, because the model is highly sensitive to this parameter. Secondly, quantifications of uncertainty surrounding available recruitment data series were not available. In view of this, we assumed that standard deviations for each data series were independent (equations 5 and 6) and used uninformative priors. However, it would be possible to use similar standard deviations for similar types of data series (for example for data series provided by the same model). Model selection criterion may be used to select the appropriate numbers of independent standard deviations. In the future, if estimates of uncertainty on those data-series were provided, they could be used to build more informative prior that would probably lead to smaller credibility intervals.

5.4 Possible application to the whole stock

The trend estimated by the model is very similar to the trend in the “Elsewhere-Europe” index provided by the WGEEL (ICES, 2012a). With some minor modifications, GEREM could be useful in taking into account differences in trends between the “Elsewhere-Europe” and North Sea indices.

Instead of assuming constant proportions per zone through time (13), we can assume that those proportions are time-dependent:

$[p_1(y),\ldots,p_n(y)] \sim Dirichlet(\lambda \cdot [p_1(y-1),\ldots,p_n(y-1)])$. Assigning a high value to λ (approximately 100) would be a suitable way to smooth inter-annual time-variations and avoid erratic variations. The model would provide a single absolute recruitment estimate.

Should this model be applied to the whole of Europe, the main limitation would once again be the limited amount of absolute number estimates. Such an application would require aggregation of EMUs into larger zones. ICES eco-regions (Celtic Sea, Atlantic coast, Mediterranean area, North and Baltic Seas) would therefore appear a suitable spatial scale in the future. Extension of the "index rivers" plan of action at European scale could be a valuable source of information, as proposed by Dekker (2002, 2005) and ICES (2012b, 2014). Standardisation of some monitoring programs throughout Europe could provide similar catchabilities between recruitment indices so that they can be directly compared.

5.5 Glass eel recruitment indices

In the current version of the model, only recruitment indices collected in river catchments (i.e. continental waters) are used. However, it would be possible to use recruitment series collected at the zone level (i.e. marine waters). For example, when working at the European scale, the recruitment indices provided by the ICES-International Young Fish Survey (Hagstrom and Wickström, 1990) (part of the International Bottom Trawl since 1993) used by the WGEEL (ICES, 2013), or the new Baltic eel recruitment estimates proposed by Westerberg and Wickström (2014), may be used as zone abundance indices in the model. Tesch (1980) proposed an index based on catches of leptocephali on the west of the European continental shelf. Similarly, an index based on a survey in the Sargasso Sea may be used in the future as an indicator of the population recruitment (Hanel *et al.*, 2014; Hanel and Miller, 2014).

Regarding glass eel abundance estimates in rivers, Harrison et al. (2014) have recently proposed an interesting review of the various methods that can be implemented to estimate recruitment in estuaries. They underline the importance of an appropriate sampling design and propose three main kinds of methods: combining trap and commercial catch data (Jessop, 2000), depletion methods (Tzeng, 1984) or models similar to those used in this study

(Beaulaton and Briand, 2007; Bru *et al.*, 2009). In some situations, when fishery exploitation rates are close to 1, commercial landings can be good estimators of recruitment, such as in the Vilaine estuary (Briand *et al.*, 2003). Tag and recapture experiments may also be a relevant method when recapture rate is significant (Briand *et al.*, 2005; Dekker and van Willigen, 1997). In the future, the development of new video tracking methods (Delcourt *et al.*, 2013) may also provide relevant abundance estimates (Doehring *et al.*, 2011; Grote *et al.*, 2014), although glass eels remain too small for those techniques.

In this paper, the model was applied to European eel, however the model is generic enough to be applied to the two other temperate eels (*Anguilla rostrata* and *Anguilla japonica*) provided enough data are available.

6 Acknowledgments

Authors would like to thank two anonymous referees for their suggestions and comments. Data series used in this study were collected by Irstea, Institution Aménagement de la Vilaine, Onema, Station Biologique de la Tour du Valat, Association Migrateurs Rhône Méditerranée, Ifremer, tableau de bord Loire, Cellule Migrateurs Charente and Département halieutique -Ecole Nationale Supérieure Agronomique de Rennes.

7 References

Als, T. D., Hansen, M. M., Maes, G. E., Castonguay, M., Riemann, L., Aarestrup, K., Munk, P., *et al.* 2011. All roads lead to home: panmixia of European eel in the Sargasso Sea. Mol Ecol, 20: 1333–1346.

Anonymous. 2010. Plan de gestion Anguille de la France - Application du règlement (CE) n°1100/2007 du 18 septembre 2007 - Volet national. Ministère de l'Ecologie, de l'Energie, du Développement durable et de la Mer, en charge des Technologies vertes et des Négociations sur le climat, Onema, Ministère de l'Alimentation, de l'Agriculture et de la Pêche.

Aranburu, A., Diaz, E., and Briand, C. in Press. Glass eel recruitment and exploitation in a South European estuary (Oria Bay of Biscay). ICES Journal of Marine Science.

Beaulaton, L., and Briand, C. 2007. Effect of management measures on glass eel escapement. ICES Journal of Marine Science: Journal du Conseil, 64: 1402–1413.

Beaulaton, L., Briand, C., Lambert, P., Castelnaud, G., Drouineau, H., Chapon, P. M., Pénil, C., *et al.* 2014. Report on the eel stock and fishery in France 2013/2014. In Report of the Joint EIFAC/ICES Working Group on Eels (WGEEL), pp. 274–346.

Bertand, L. 2009. Etude de l'impact de la pêche à la civelle sur les estuaires de la Seudre et de la Charente dans le cadre du règlement européen R(CE) 1100/2007 sur l'anguille. UFR Sciences & Techniques Côte Basque. 69 pp.

Briand, C. 2008. Dynamique de population et de migration des civelles en estuaire de vilaine. Rennes, ENSA. http://www.theses.fr/2009NSARH076 (Accessed 26 May 2015).

Briand, C., Beaulaton, L., Chapon, P. M., Drouineau, H., and Lambert, P. 2015. Estimation de l'échappemement en anguilles argentées (*Anguilla anguilla*) en France. rapport Onema.

Briand, C., Bonhommeau, S., Castelnaud, G., and Beaulaton, L. 2008. An appraisal of historical glass eel fisheries and markets: landings,trade route and future prospect for management. *In* IFM 38th Annual Conference , 15/10/2007 - 18/10/2007, p. 21. Ed. by C. Moriarty. Wesport, IRL. http://cemadoc.irstea.fr/cemoa/PUB00030466.

Briand, C., Buard, E., and Postic-Puivif, A. 2012. Modélisation de la capture de civelles dans l'estuaire de la Seudre par l'utilisation du modèle GEMAC. Modélisation de la capture de civelles dans l'estuaire de la Seudre par l'utilisation du modèle GEMAC. Traitement des données des saisons 2008-2009 et 2009-2010. http://www.fleuvecharente.net/bibliotheque/poissons-migrateurs/documents/files/rapport-sur-limpact-de-la-peche-a-la-civelle-en-charente-et-en-seudre-via-limplementation-du-modele-gemac-bertrand-loic.pdf/attachment_download/attachedFile.

Briand, C., Fatin, D., Feunteun, E., and Fontenelle, G. 2005. Estimating the stock of glass eels in an estuary by mark-recapture experiments using vital dyes. Bulletin Français de la Pèche et de la Protection des Milieux Aquatiques, 378-379: 23–46.

Briand, C., Fatin, D., Fontenelle, G., and Feunteun, E. 2003. Estuarine and fluvial recruitment of the European glass eel, *Anguilla anguilla*, in an exploited Atlantic estuary. Fish Manag Ecol, 10: 377–384.

Bru, N., Bouvet, J.-C., and Prouzet, P. 2006. Quantification par une méthode analytique de la biomasse saisonnière de civelles (*Anguilla anguilla*) dans l'estuaire de l'Adour et estimation du taux d'exploitation saisonnier de la pêche professionnelle de 1998 à 2005. Rapport Ifremer – projet Indicang http://www.ifremer.fr/ indicang/sites-thematiques/pdf/estim-civelle-1998-2005.pdf, 2006, Rapport Ifremer – projet Indicang http://www.ifremer.fr/ indicang/sites-thematiques/pdf/estim-civelle-1998-2005.pdf.

Bru, N., Prouzet, P., and Lejeune, M. 2009. Daily and seasonal estimates of the recruitment and biomass of glass eels runs (*Anguilla anguilla*) and exploitation rates in the Adour open estuary (Southwestern France). Aquatic Living Resources, 22: 509–523.

Burgers, H. E., Schipper, A. M., and Jan Hendriks, A. 2014. Size relationships of water discharge in rivers: scaling of discharge with catchment area, main-stem length and precipitation. Hydrological Processes, 28: 5769–5775.

Castelnaud, G. 2001. Localisation de la pêche, effectifs de pêcheurs et production des espèces amphihalines dans les fleuves français. Bulletin Français de la Pêche et de la Pisciculture: 439–460.

Castonguay, M., Hodson, P. V., Moriarty, C., Drinkwater, K. F., and Jessop, B. M. 1994. Is there a role of ocean environment in American and European eel decline? Fisheries

Oceanography, 3: 197–203.

Cicotti, E. 2006. Nuovi metodi ecologici per la valutazione del reclutamento di ceche di anguilla europea (*Anguilla anguilla* L.) per la gestione sostenibile di questa risorsa. Relazione finale MiPAF, VI Piano Triennale n. 6°21.

Crivelli, A. J., Auphan, N., Chauvelon, P., Sandoz, A., Menella, J.-Y., and Poizat, G. 2008. Glass eel recruitment, *Anguilla anguilla (L.)*, in a Mediterranean lagoon assessed by a glass eel trap: factors explaining the catches. *In* Fish and Diadromy in Europe (ecology, management, conservation), pp. 79–86. Ed. by S. Dufour, E. Prévost, E. Rochard, and P. Williot. Springer Netherlands. http://link.springer.com/chapter/10.1007/978-1-4020-8548-2_6 (Accessed 20 December 2013).

Dekker, W. 2000a. A Procrustean assessment of the European eel stock, 57: 938–947.

Dekker, W. 2000b. The fractal geometry of the European eel stock. ICES Journal of Marine Science: Journal du Conseil, 57: 109–121.

Dekker, W. 2002. Monitoring of glass eel recruitment. Netherlands Institute of Fisheries Research. report C007/02-WD.

Dekker, W. 2003. Did lack of spawners cause the collapse of the European eel, *Anguilla anguilla*? Fish Manage Ecol, 10: 365–376.

Dekker, W. 2005. Report of the Workshop on National Data Collection for the European Eel, S\a anga Säby (Stockholm, Sweden), 6–8 September 2005. Fiskeriverket Swedish Board of Fisheries, 282.

Dekker, W., Casselman, J., Cairns, D. K., Tsukamoto, K., Jellyman, D., and Lickers, H. 2003. Worldwide decline of eel resources necessitates immediate action: Québec Declaration of Concern. Fisheries, 28: 28.

Dekker, W., and Casselman, J. M. 2014. The 2003 Québec Declaration of Concern About Eel Declines—11 Years Later: Are Eels Climbing Back up the Slippery Slope? Fisheries, 39: 613–614.

Dekker, W., and van Willigen, J. 1997. Hoeveel glasaal trekt het IJsselmeer in? Verslag van een merkproef met glasaal te Den Oever in 1997. DIVO-DLO Rapport, C062/97. DLO-Rijksinstituut voor Visserijonderzoek.

Delcourt, J., Denoël, M., Ylieff, M., and Poncin, P. 2013. Video multitracking of fish behaviour: a synthesis and future perspectives. Fish and Fisheries, 14: 186–204.

Doehring, K., Young, R. G., Hay, J., and Quarterman, A. J. 2011. Suitability of Dual-frequency Identification Sonar (DIDSON) to monitor juvenile fish movement at floodgates. N Z J Mar Freshwater Res, 45: 413–422.

Drouineau, H., Rigaud, C., Daverat, F., and Lambert, P. 2014. EvEel (evolutionary ecology-based model for eel): a model to explore the role of phenotypic plasticity as an adaptive response of three temperate eels to spatially structured environments. Canadian Journal of Fisheries and Aquatic Sciences, 71: 1561–1571.

Elie, P., and Rochard, E. 1994. Migration des civelles d'anguilles (*Anguilla anguilla* L.) dans les estuaires, modalités du phénomène et caractéristiques des individus. Bulletin Français de la Pêche et de la Pisciculture: 81–98.

Feunteun, E. 2002. Management and restoration of European eel population (*Anguilla anguilla*): An impossible bargain. Ecol Eng, 18: 575–591.

Feunteun, E., Castelnaud, G., Briand, C., Prouzet, P., Menella, J. Y., and De Roton, G. 2002. Monitoring of glass eel recruitment in France. *In* Monitoring of glass eel recruitment vol. 2B: Country Reports; Southern part, DEKKER W., pp. 179–217. Netherlands Institute of Fisheries Research, Ijmuiden, NLD. http://cemadoc.irstea.fr/cemoa/PUB00013143.

Gelman, A., and Rubin, D. B. 1992. Inference from iterative simulation using multiple sequences. Statistical Science, 7: 457–511.

Grote, A. B., Bailey, M. M., Zydlewski, J. D., and Hightower, J. E. 2014. Multibeam sonar

(DIDSON) assessment of American shad (Alosa sapidissima) approaching a hydroelectric dam. Canadian Journal of Fisheries and Aquatic Sciences, 71: 545–558.

Hagstrom, O., and Wickström, H. 1990. Immigration of Young Eels to the Skagerrak-Kattegat Area 1900 to 1989. Internationale Revue der gesamten Hydrobiologie und Hydrographie, 75: 707–716.

Hanel, R., and Miller, M. J. 2014. Changes in Abundance of Anguillid Leptocephali in the Sargasso Sea. Afs. https://afs.confex.com/afs/2014/webprogram/Paper16276.html (Accessed 2 October 2014).

Hanel, R., Stepputtis, D., Bonhommeau, S., Castonguay, M., Schaber, M., Wysujack, K., Vobach, M., *et al.* 2014. Low larval abundance in the Sargasso Sea: new evidence about reduced recruitment of the Atlantic eels. Naturwissenschaften, 101: 1041–1054.

Harrison, A. J., Walker, A. M., Pinder, A. C., Briand, C., and Aprahamian, M. W. 2014. A review of glass eel migratory behaviour, sampling techniques and abundance estimates in estuaries: implications for assessing recruitment, local production and exploitation. Reviews in Fish Biology and Fisheries: 1–17.

Hilborn, R., and Walters, C. J. 1992. Quantitative Fisheries Stock Assessment. Chapman and Hall, New York. 570 pp.

ICES. 2010. Report of the 2010 session of the Joint EIFAC/ICES Working Group on Eels. ICES CM 2010/ACOM:18. Hamburg.

ICES. 2012a. Report of the Joint EIFAAC/ICES Working Group on Eels (WGEEL). ICES CM 2012/ACOM:18. Copenhagen.

ICES. 2012b. Report of the Workshop on Eel and Salmon DCF Data (WKESDCF). ICES CM / ACOM:62. Copenhagen.

ICES. 2013. Report of the Joint EIFAAC/ICES Working Group on Eels (WGEEL). ICES CM 2013/ACOM:18. Copenhagen.

ICES. 2014. Report of the Joint EIFAAC/ICES Working Group on Eels (WGEEL). ICES CM

2014/ACOM:18. Rome.

ICES. 2015. EU request on criteria for CITES non-detriment finding for European eel (Anguilla anguilla). *In* ICES Advice 2015, book 9. ICES. ICES.

Jacoby, D., and Gollock, M. 2014. *Anguilla anguilla*. *In* The IUCN Red List of Threatened Species. Version 2014.2. http://www.iucnredlist.org.

Jessop, B. M. 2000. Size, and exploitation rate by dip net fishery, of the run of American eel, *Anguilla rostrata* (LeSueur), elvers in the East River, Nova Scotia. Dana, 12: 43–57.

Johnson, N. L., Kotz, S., and Balakrishnan, N. 1997. Discrete Multivariate Distributions. Wiley-Interscience. 328 pp.

Kettle, A. J., Asbjørn Vøllestad, L., and Wibig, J. 2011. Where once the eel and the elephant were together: decline of the European eel because of changing hydrology in southwest Europe and northwest Africa? Fish and Fisheries, 12: 380–411.

Koops, M. A., Young, A., and Cairns, D. K. 2014. Meta-Population Dynamics in the American Eel and the Importance of Larval Distribution. Afs. https://afs.confex.com/afs/2014/webprogram/Paper16645.html (Accessed 9 October 2014).

Lambert, P. 2008. Évaluation des effets possibles de différents niveaux de réduction des impacts sur le temps de restauration du stock d'anguille européenne. Convention de partenariat Onema-Cemagref. http://cemadoc.irstea.fr/cemoa/PUB00028119.

Moriarty, C., and Dekker, W. 1997. Management of the European Eel. Irish Fisheries Bulletin, 15: 1–125.

Ohlssen, D. I., Sharples, L. D., and Spiegelhalter, D. J. 2007. Flexible random-effects models using Bayesian semi-parametric models: applications to institutional comparisons. Stat Med, 26: 2088–2112.

Prouzet, P., Bouvet, J.-C., Bru, N., and Boussouar, A. 2007. Quantification de la biomasse saison-nière de civelles (*Anguilla anguilla*) dans l'estuaire de la Loire et estimation du taux d'exploitation saisonnier de la pêche professionnelle pour les saisons de pêche 2003 à 2005. Rapport Ifremer – projet Indicang http://www.ifremer.fr/indicang/boite-bassins-versants/pdf/rapport-saison-bv-loire.pdf, Rapport Ifremer – projet Indicang http://www.ifremer.fr/indicang/boite-bassins-versants/pdf/rapport-saison-bv-loire.pdf.

R Development Core Team. 2011. R: A Language and Environment for Statistical Computing. http://www.R-project.org/.

Schmidt, J. 1923. Breeding places and migrations of the eel. Nature, 111: 51–54.

Sorensen, P. W. 1986. Origins of the freshwater attractant(s) of migrating elvers of the American eel, *Anguilla rostrata*. Environmental Biology of Fishes, 17: 185–200.

Stan Development Team. 2013. Stan: A C++ Library for Probability and Sampling, Version 1.3. URL http://mc-stan.org/.

Tesch, F.-W. 1980. Occurrence of eel *Anguilla anguilla* larvae west of the European continental shelf, 1971–1977. Environmental Biology of Fishes, 5: 185–190.

Tesch, F. W. 2003. The Eel. Blackwell Publishing.

Tzeng, W.-N. 1984. An estimate of the exploitation rate of Anguilla-japonica elvers immigrating into the coastal waters off Shuang-Chi River, Taiwan. Bulletin of the Institute of Zoology, Academia Sinica, 23: 173–180.

Vogt, J., and Foisneau, S. 2007. European river and catchment database, version 2.0 (CCM2) analysis tools. Report. Luxembourg : Publications Office of the European Union. http://www.envia.bl.uk//handle/123456789/4533 (Accessed 2 October 2014).

Vollestad, L. A. 1992. Geographic variation in age and length at metamorphosis of maturing European eel - Environmental effects and phenotypic plasticity, 61: 41–48.

Westerberg, H. 1998. Oceanographic aspects of the recruitment of eels to the Baltic Sea. Bulletin Français de la Pêche et de la Pisciculture: 177–185.

Westerberg, H., and Wickström, H. 2014. Baltic Eel Recruitment and Escapement; Quantitative Estimates from Survey Data. Afs.

https://afs.confex.com/afs/2014/webprogram/Paper15498.html (Accessed 2 October 2014).

Wuenschel, M. J., and Able, K. W. 2008. Swimming ability of eels (*Anguilla rostrata*, *Conger oceanicus*) at estuarine ingress: contrasting patterns of cross-shelf transport? Marine Biology, 154: 775–786.

Wu, J., and Levin, S. A. 1997. A patch-based spatial modeling approach: conceptual framework and simulation scheme. Ecological Modelling, 101: 325–346.

8 Tables

Table 1. Estimated parameters and corresponding prior and Rhat (Vogt and Foisneau, 2007)

Parameters	priors	Rhat
σ_R : recruitment random-walk standard-deviation	$\sigma_R^2 \sim InverseGamma(0.01, 0.01)$	1.001
σ_{U_i} : standard-deviation of observation for absolute index i	$\sigma_U^2 \sim InverseGamma(0.01, 0.01)$	min 1.000 max 1.001
σ_{AI_i} : standard-deviation of observation for relative index i	$\sigma_{IA}^2 \sim InverseGamma(0.01, 0.01)$	min 1.000 max 1.011
q_i ; catchability of relative index i	$\log(q_i) \sim Unif(-10, 10)$	min 1.000 max 1.002
$R(1)$: recruitment in first year	$\log(R(1)) \sim Unif(5, 10)$	1.000
β : power parameter of the relation between catchment surface and proportion of the recruitment	$\beta \sim Unif(0.01, 2)$	1.000
p_z Proportion of recruitment in zone z	$\begin{bmatrix} p_1 \\ \vdots \\ p_{nb_z} \end{bmatrix} \sim Dirichlet \begin{bmatrix} \alpha_1 \\ \vdots \\ \alpha_{nb_z} \end{bmatrix}$ with $\alpha_1 = \ldots = \alpha_{nb_z} = \frac{1}{nb_z} \cdot \gamma$ and nb_z the number of zones.	min 1.001 max 1.002
γ Dirichlet concentration parameter (a value below 1 leads to sparse distributions while a value above 1 leads to dense distributions)	$\gamma \sim Unif(0.3, 10)$	1.001

Table 2. Zone characteristics (Vogt and Foisneau, 2007)

EMU	Catchment area (km²)
Seine – Artois	114,293
Bretagne	30,561
Loire	127,813
Garonne	97,340
Rhone – Mediterranea – Corsica	129,586
Adour	20,228

Table 3. Recruitment data series (type I = index, A = absolute). Absolute abundance indices are either provided in catchments where exploitation rates are closed to 1 (Briand *et al.*, 2003) or by model estimations (Beaulaton and Briand, 2007; Prouzet *et al.*, 2007). In the Bresle River, the index is based on a trap device that collects recruits composed of a few glass eels and mostly pigmented elvers.

Catchment characteristics				Recruitment indices			
Zone	Catchment	Area (km²) (%zone)	River length (km)	Index short name	Type	Extent (missing data)	Ref
Seine – Artois	Bresle	748 (0.6%)	72	Bres	I	1994 – 2010	(Beaulaton *et al.*, 2014)
Seine – Artois	Somme	6,550 (5.7%)	245	Somme	A	1992-2012 (1)	
Bretagne	Vilaine	10,500 (34%)	218	Vil	A	1971 – 2011	(Beaulaton et al., 2014)
Loire	Loire	117,000 (92%)	1013	LoGERMA	A	2004 – 2006	(Prouzet *et al.*, 2007)
Loire	Loire			Loi	I	1950 – 2008	(Beaulaton et al., 2014)
Loire	Sèvre Niortaise	3,650 (2.9%)	159	SevN	I	1962 – 2008 (25)	(Beaulaton et al., 2014)
Garonne	Charente	9,855 (10%)	381	ChGEMAC	A	2007 – 2008	(Bertand, 2009)
Garonne	Seudre	855 (0.9%)	68	SeGEMAC	A	2007 – 2008	(Bertand, 2009; Briand *et al.*, 2012)
Garonne	Garonne	78,870 (81%)	647	GiGEMAC	A	1999	(Beaulaton and Briand, 2007)
Garonne	Garonne			GiCP	I	1961 – 2008 (1)	(Beaulaton et al., 2014)
Garonne	Garonne			GiSc	I	1992 – 2013	(Beaulaton et al., 2014)
Adour	Adour	16,880 (83%)	309	AdGERMA	A	1999 – 2005	(Bru *et al.*, 2006)
Adour	Adour			AdCP	I	1966 – 2008 (6)	(Beaulaton et al., 2014)
Rhone – Mediterranea – Corsica	Vaccarès	6.5 (<0.1%)	245	Vaccares	A	2004 – 2011	(Crivelli *et al.*, 2008)

9 Figures

Fig. 1. Maps of considered zones (solid lines indicates EMUs border)

Fig. 2. Estimated (black solid lines) and observed (grey line and points) absolute estimates. Dashed lines represent 95 % credibility intervals for $\mu_{U_{i,c}}$ while solid lines represent the median.

Fig. 3. Estimated (black solid lines) and observed (grey line and points) relative indices. Dashed lines represent 95 % credibility intervals for $\mu_{IA_{i,c}}$ and solid lines represent the median

Fig. 4. Estimated French glass eel recruitment in tonnes (bottom panel) and in log-scale (top panel). Solid line indicates the median while dashed lines represent the corresponding credibility interval (95%). Darker grey line represents Elsewhere-Europe WGEEL index (ICES, 2013) while light grey line represents the catches estimated by Briand et al. (2008).

Fig. 5. Estimated proportions of the recruitments in the different EMUs.

Fig. 6. Recruitment (median) estimated by the model when fitting the model on altered datasets according to S1 (left panel) and S2 (right panel).

Fig. 7. Zone recruitments estimated by the model for the last year when the model is fitted on altered datasets according to S1 (top panel) and S2 (bottom panel). Bars represent the median while vertical segments represent the 97.5 % quantile of the a posteriori distributions

Fig. 8. Medians (circles) and 2.5 and 97.5 % quantiles (segments) of β estimated by the model when the model is fitted on altered datasets according to S1.