



**HAL**  
open science

## **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

► **To cite this version:**

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. *Fisheries Research*, 2016, 174, pp.68-80. 10.1016/j.fishres.2015.09.003 . hal-01706769

**HAL Id: hal-01706769**

**<https://hal.science/hal-01706769v1>**

Submitted on 12 Feb 2018

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

3 Authors: Drouineau, H.<sup>1,\*</sup>; Briand, C.<sup>2</sup>; Lambert, P.<sup>1</sup>; Beaulaton, L.<sup>3,4</sup>

4

5 1 Irstea UR EABX, 50 avenue de Verdun, centre de Bordeaux, F-33612 Gazinet Cestas,

6 France

7 2 Institution Aménagement de la Vilaine, 56130 La Roche-Bernard, France

8 3 Onema, Pôle Gest'Aqua, 65 rue de St Briec, 35042 Rennes, France

9 4 INRA, U3E (1036), Pôle Gest'Aqua, 65 rue de St Briec, 35042 Rennes, France

10

11 \*corresponding author: [hilaire.drouineau@irstea.fr](mailto:hilaire.drouineau@irstea.fr), tel: +33 (0)5 57 89 27 09, fax :+33 (0)5

12 57 89 08 01

13     **1 Abstract**

14 Given the importance of reliable recruitment estimates when assessing temperate eel stocks  
15 and enforcing appropriate management measures, surprisingly few analytical tools have been  
16 developed to estimate yearly glass eel recruitment. Of the models that do exist, large-scale  
17 models generally rely on strong assumptions relating to fishing activity, while other models  
18 generally estimate recruitment at the river basin scale. With the aim of filling this gap, we  
19 developed the GEREM (Glass Eel Recruitment Estimation Model) to estimate glass eel  
20 recruitment at different nested spatial scales. Our model simultaneously estimates annual  
21 recruitment at river catchment level, at an intermediate spatial scale such as Eel Management  
22 Units (EMUs), and at a larger scale (e.g. a country). Provided enough data become available  
23 in the future, the analysis could be extended to the scale of the distribution area, which would  
24 be consistent with the population scale. In this study, the model was applied to France, using

25 various recruitment indices obtained from 1960 to 2013. This provided trends and absolute  
26 recruitment estimates consistent with current expert knowledge. A sensitivity analysis was  
27 carried out to assess the robustness of results to sources of uncertainty. This type of model  
28 fills an important gap in the range of quantitative tools presently available to estimate  
29 recruitment. It could be used in the future to fix total allowable catches in countries such as  
30 France where glass eels are fished commercially.

31

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

33

## 34 **2 Introduction**

35 The European eel (*Anguilla anguilla*) is a catadromous species whose population spans a vast  
36 area, stretching from Morocco to Norway (Tesch, 2003). Reproduction takes place in the  
37 Sargasso Sea (Schmidt, 1923), after which leptocephalus larvae are passively transported by  
38 oceanic currents to the continental shelf, where they metamorphose into glass eels (Tesch,  
39 2003). They then enter continental waters, becoming pigmented glass eels and later yellow  
40 eels. Yellow eels grow in freshwater or estuarine habitats, typically for 3 to 15 years  
41 (Vollestad, 1992), after which they metamorphose into silver eels and achieve sexual maturity  
42 while migrating back to spawning grounds.

43 The European eel population has been in drastic decline since the late 70s (Castonguay *et al.*,  
44 1994; Dekker, 2003; Dekker *et al.*, 2003; Dekker and Casselman, 2014). The IUCN lists *A.*  
45 *anguilla* as “critically endangered” (Jacoby and Gollock, 2014). Many possible reasons for  
46 this population collapse have been suggested, including changes in oceanic conditions  
47 (Castonguay *et al.*, 1994), contamination and habitat degradation, parasitoids (Feunteun,  
48 2002), fishing pressure, and massive habitat loss (Kettle *et al.*, 2011).

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

57 Though management measures are implemented at the national and regional scales, the stock  
58 is assessed at the population scale which corresponds to the distribution area since genetic  
59 evidence demonstrates that the European eel is totally panmictic (Als *et al.*, 2011).

60 Assessment is carried out yearly by the joint EIFAAC (European Inland Fisheries and  
61 Aquaculture Advisory Commission), ICES (International Council for the Exploration of the  
62 Sea) and GFCM (General Fisheries Commission for the Mediterranean) working group on  
63 eels (WGEEL).

64 Several abundance indices are collected for stock assessment: recruitment indices, yellow eel  
65 abundance indices and silver eel catches. Aside from the questionable quality of some of these  
66 data, the fractal dimension of eel stock (Dekker, 2000b) makes it difficult to interpret yellow  
67 and silver eel indices. During their growth stage, eels are subject to contrasted environmental  
68 conditions (distribution area ranging from Morocco to Norway) and anthropogenic pressures  
69 (fishing activity, hydropower mortality, contaminate, etc.) which are difficult to assess at  
70 European level (Dekker, 2000). Also, eels display a marked contrast in life-history traits and  
71 tactics at the river basin and distribution area scales (Drouineau *et al.*, 2014). This includes  
72 sex-ratio (Kettle *et al.*, 2011) and age-at-silvering (Vollestad, 1992), which can vary from 3  
73 years in southern Europe to over 20 in northern Europe. In view of this, it is very difficult to  
74 distinguish between local effects and stock status when analysing yellow and silver eel

75 indices. Another issue is that commercial silver eel fishing only takes place in a handful of  
76 European regions, and relevant effort data are rarely reported, making silver eel catches  
77 difficult to interpret. In view of this, WGEEL considers that while yellow and silver eel  
78 indices may be used in the future, they are currently too scarce and uncertain and may be  
79 more representative of the local area where they are collected than of overall eel stock (ICES,  
80 2014). On the other hand, glass eels correspond to the first continental stage and are  
81 consequently less influenced by local conditions. Several monitoring projects throughout  
82 Europe are dedicated to glass-eels. They use sampling methods adapted to this specific eel  
83 stage (specific commercial and scientific fishing gear, glass-eel ladder, etc.). In 2002, a  
84 European project was set up to list and co-ordinate these monitoring programs (Dekker,  
85 2002).

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

93 Recruitment estimates are especially important for countries such as France, where glass eels  
94 are commercially fished (silver eels can only be fished in the Loire River and in the south of  
95 the country, while commercial yellow eel fishing is much less widespread), meaning that  
96 quantitative tools are needed to set permitted glass eel quotas (it should be noted that the  
97 equipment used to catch glass eels is completely different from that used to catch silver and  
98 yellow eels). In the late 90's, glass eel fishing was important in France (Briand *et al.*, 2008).  
99 At that time, eel was the most important species landed in value in the Bay of Biscay  
100 (Castelnaud, 2001). In some specific river basins, fishing impact was very high with

101 exploitation rates over 95% (Briand *et al.*, 2003). In view of this, models such as GEMAC  
102 (Beaulaton and Briand, 2007), or a model developed by Bru *et al.* (2006) and Prouzet *et al.*  
103 (2007), have been developed to estimate exploitation rates and recruitment at catchment scale.  
104 However, one disadvantage of these models is that they only work at an estuarine scale. From  
105 an EU perspective, it would be desirable to have a model capable of estimating recruitment  
106 across the entire EMU, or even the whole of Europe. In this paper, we present GEREM (Glass  
107 Eel Recruitment Estimation Model): a Bayesian model to estimate recruitment at various  
108 nested spatial scales. A hierarchical Bayesian model is one of the most suitable types of model  
109 when dealing nested spatial scales. It allows recruitment at large scales to be inferred from  
110 observations carried out at smaller scales. The Bayesian approach also makes it possible to  
111 incorporate prior information, as well as quantifying uncertainty. To illustrate the model's  
112 potential, we provide the results of an initial test on French EMUs. The possibility of using  
113 the model at European level is then discussed.

114

### 115 **3 Material and methods**

#### 116 **3.1 Model description**

##### 117 3.1.1 State models: assumptions relating to recruitment at different spatial scales

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

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

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

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

130 We assume that the overall recruitment  $R(y)$  is divided into different recruitment zones based  
 131 on a multinomial distribution, with proportions  $p_z$  for each zone. This multinomial distribution  
 132 mimics the random passive distribution of leptocephali generated by oceanic currents. The  
 133 multinomial distribution is approximated by marginal normal distributions (Johnson *et al.*,  
 134 1997):

$$135 \quad R_z(y) \sim \text{Normal}\left(R(y) \cdot p_z, R(y) \cdot p_z \cdot (1 - p_z)\right) \quad (1)$$

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

$$140 \quad R_{c,z}(y) \sim \text{Normal}\left(R_z(y) \cdot w_{c,z}, R_z(y) \cdot w_{c,z} \cdot (1 - w_{c,z})\right) \quad (2)$$

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

$$142 \quad w_{c,z} = \frac{S_{c,z}^\beta}{\sum_{c_2=1}^{n_z} S_{c_2,z}^\beta} \quad (3)$$

143 A  $\beta$  value close to 1 would mean that recruitment is proportionate to catchment surface, which  
 144 can be considered a proxy of available habitat. However, it has previously been observed (at  
 145 least on small catchments) that river discharge and river plume have an influence on glass eel  
 146 recruitment (Crivelli *et al.*, 2008; Elie and Rochard, 1994). If river discharge is the main  
 147 factor influencing the proportions in each catchment, then the power is less than one. This is

148 shown by a meta-analysis carried-out by Burgers et al. (2014), which demonstrates that river  
 149 discharge is a power function of catchment surface with a power less than 1. A power greater  
 150 than 1 would imply an over-concentration of glass eels in large catchments. However, this is  
 151 unlikely, because it would be inconsistent with large commercial catches in small catchments.

152 The overall recruitment is assumed to follow a random walk:

$$153 \quad R(y) = R(y-1) \cdot e^{\epsilon(y)} \text{ with } \epsilon(y) \sim \text{Normal}(0, \sigma_R^2) \quad (4)$$

154

### 155 3.1.2 Observation model

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

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

$$159 \quad \log(IA_{i,c}(y)) \sim N(\mu_{IA_{i,c}}(y), \sigma_{IA_i}^2) \text{ with } \mu_{IA_i}(y) = \log(q_i \cdot R_{c,z}(y)) - \frac{\sigma_{IA_i}^2}{2} \quad (5)$$

160 with  $q_i$  a scale factor.

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

$$163 \quad \log(U_{i,c}(y)) \sim N(\mu_{U_{i,c}}(y), \sigma_{U_i}^2) \text{ with } \mu_{U_i}(y) = \log(R_{c,z}(y)) - \frac{\sigma_{U_i}^2}{2} \quad (6)$$

164

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

168



### 169 3.1.3 Bayesian inference

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

178

## 179 **3.2 Application to French eel substock**

### 180 3.2.1 EMU description

181 The model was applied to France. As part of the French eel management plan (Anonymous,  
182 2010) 9 EMUs were defined. In this study, the Rhine-Meuse EMU was discarded, as  
183 recruitment does not occur in the French part of this EMU. The Artois-Picardy and Corsica  
184 EMUs were merged with the Seine-Normandy and Mediterranean EMUs respectively, as no  
185 data were available for the Artois-Picardy and Corsica EMUs. These six (merged) EMUs  
186 (Table 2 and Fig. 1) are the six zones from the model ( $N_z = 6$ ).

187

### 188 3.2.2 Recruitment indices

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

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

193 WGEEL - along with 19 other European series - to derive the Elsewhere-Europe index (ICES,  
194 2014).. Seven data-series covering France are presented by Feunteun et al (2002). Three main  
195 types of data were considered as relative indices: (i) commercial catch divided by fishing  
196 effort (SevN, GiCP, AdCP) (except for the Loi index for which no effort data were available  
197 but catch data were consistent with CPUE from other series), (ii) a scientific index from a  
198 standardized monitoring program (GiSc), and (iii) yearly counts in a scientific fish trap (Bres).  
199 Fishery-based indices only go as far as 2011. Since 2011, fishing activity in France has been  
200 extensively modified due to the introduction of a new quota system. Consequently, fishery-  
201 based indices taken before and after these changes cannot be effectively compared.

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

- 203 • ChGEMAC, SeGEMAC, GiGEMAC, are recruitments estimates provided by  
204 GEMAC (Beaulaton and Briand, 2007) while AdGERMA and LoGERMA are  
205 recruitment estimates provided developed by Bru et al.'s model (2006, 2009). The two  
206 models were developed to estimate commercial exploitation rates at the river basin  
207 scale. They are essentially based on an estimation of glass-eel density based on catches  
208 divided by sampled volume, which is then multiplied by the total volume of the zone.  
209 The GEMAC model uses either commercial or scientific catches, while the Bru et al.  
210 (2009) model requires the use of scientific catches to estimate glass eel daily  
211 abundance. Since these models work at the river catchment scale, models were fitted  
212 independently to each river basin (using independent data). We assumed that series  
213 were statistically independent, even though they came from similar models.
- 214 • The Vil data-series represents commercial catches. The small additional  
215 number of glass eels arriving after the fishing season was estimated from catches made  
216 at a trapping ladder located at an impassable dam in the Vilaine estuary (Briand,  
217 2008). Commercial fishing takes place just downstream from the dam, where glass  
218 eels aggregate. Statistical analysis shows that commercial fishery is so efficient (over

219 95%) that total catches can be used to estimate total recruitment (Briand *et al.*, 2003).  
220 Given this efficiency, local environmental conditions have little impact on the annual  
221 catch, and this series is closest to the average of the “Elsewhere Europe” recruitment  
222 series (ICES, 2010). Local conditions are fairly similar in the Somme, where  
223 commercial fishing also takes place downstream from an estuarine dam. On the basis  
224 that glass eels were also blocked by this obstacle, an expert-estimated exploitation rate  
225 of 75% was used, although no in-depth analysis was carried out (contrary to the  
226 Vilaine estuary). Consequently, we multiplied this data-series by 1.33 and assumed  
227 that it provided an absolute estimate of total recruitment.

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

231 Absolute indices are expressed in tonnes of glass eels, while relative indices are standardised  
232 according to their mean values. The model was fitted to the period 1960-2013. Three chains  
233 were run independently in parallel for 10,000 iterations after a burn-in period of 10,000  
234 iterations. Convergence was checked using Gelman-Rubin diagnostics (Gelman and Rubin,  
235 1992).

236

### 237 **3.3 Sensitivity analysis**

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

242 • S1 addresses the consequences of a systematic bias in absolute recruitment indices.  
243 The model was fitted successively to 8 altered datasets - one dataset per absolute

244 recruitment index. For each dataset, the absolute recruitment estimate was multiplied  
245 by 1.1 to mimic a systematic bias of 10%. Underestimation was considered more  
246 likely than overestimation, since our absolute abundance estimates assume that  
247 catchability (AdGERMA, SeGEMAC, ChGEMAC, LoGERMA, GiGEMAC) or  
248 ladder passability are equal to one (Vaccares). They may also be inferior to 1, in which  
249 case, our data underestimate the true value and should be multiplied by a correction  
250 factor superior to 1.

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

253

## 254 **4 Results**

### 255 **4.1 Recruitment estimates**

256 Gelman and Rubin diagnostics confirmed that the chain converged after 20,000 iterations  
257 (10,000 burn-in+10,000 samples for inference).  $\bar{R}$  statistics were less than 1.05 for all  
258 parameters (Table 1).

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

264 The model fitted well both relative abundance and absolute abundance indices (Fig. 2 and Fig.  
265 3). Observed data were generally within credibility intervals. As expected, large credibility  
266 intervals were occasionally observed for series with missing data. However, since all of the  
267 data series were relatively consistent, missing data from a series were made up for by data

268 from other series, resulting in small credibility intervals for most series. Larger credibility  
269 intervals were observed for Somme, Vaccares, Bres, and SeGEMAC in certain years. For  
270 those catchments, recruitment values were low, either because of a small catchment surface or  
271 because the catchment was located in a zone where glass eels were scarce. As a consequence,  
272 recruitment  $R_{c,z}(y)$  was very low (close to zero) and the normal approximation (equation 2)  
273 sometimes led to very small values (even negative), resulting in large credibility intervals in  
274 the logarithmic scale (since  $\log(0)$  tends to negative infinity).

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

282 The estimated value of the overall recruitment divided by the surface of the studied area was  
283  $0.36 \text{ kg/km}^2$  (credibility interval: [0.19, 1.26]) in 2010. The ratio was equal to  $0.75 \text{ kg/km}^2$  in  
284 2005 and  $0.68 \text{ kg/km}^2$  in 2006. As a comparison, Cicotti (2006) estimated a ratio of around  
285  $0.01 \text{ kg/km}^2$  in the Tiber River (Italy) in the same period, while Aranburu et al. (in Press)  
286 estimated a ratio of  $1.68 \text{ kg/km}^2$  in the Oria River (Spain, Basque Country) in 2013.

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

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

291 The power coefficient  $\beta$  credibility interval is large (median 0.51, credibility interval  
292 [0.21,0.75]) but significantly lower than 1.

293

294 **4.2 Sensitivity analysis**

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

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

307  $\beta$  was the parameter with the largest influence. Changes mostly affected three zones: Brittany,  
308 Garonne and Rhone-Mediterranea-Corsica. Estimated recruitment for Brittany decreased as  $\beta$   
309 increased, while, conversely, it increased for the Rhone-Mediterranea-Corsica zones.

310 Unsurprisingly, sensitivity to  $\beta$  tended to decrease for zones where absolute estimates were  
311 collected from the largest catchments in each zone (Table 3). It explains the difference in  
312 variation of  $\beta$  between Brittany and Rhone-Mediterranea-Corsica and Seine-Artois: for the  
313 Brittany zone, the absolute estimate was collected in the largest catchment of the zone (the  
314 Vilaine) whereas it was collected in relatively small catchments for the two other zones  
315 (Vaccarès is a 6.5km<sup>2</sup> catchment in a 129,586 km<sup>2</sup> zone, and the Somme is a 6,550 km<sup>2</sup>  
316 catchment in a 114,293 km<sup>2</sup> zone). For the Garonne zone, absolute indices were collected in  
317 both large and small catchments resulting in a less straightforward response.

318

## 319 **5 Discussion**

### 320 **5.1 GEREM – a model to fill a gap in the range of existing quantitative assessment tools**

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

329 Assessing glass eel recruitment is essential for stock management (Moriarty and Dekker,  
330 1997). Many traditional reference points used in fisheries management are based on stock-  
331 recruitment relationships, and therefore require a recruitment time-series. Current limitations  
332 stemming from the interpretation of yellow and silver eel indicators make recruitment indices  
333 even more crucial when assessing the status of eel stocks (ICES, 2013). The procrustean  
334 model proposed by Dekker (Dekker, 2000a) estimates recruitment at stock level, requiring  
335 strong assumptions about the stability of recruitment and fishing activity (Dekker notably  
336 assumed that silver eel catch rates and life cycle duration were similar in the whole  
337 distribution area and that catches were known without errors). On the other hand, GEMAC  
338 (Beaulaton and Briand, 2007) provides recruitment estimates at the catchment scale, but  
339 cannot be applied at a larger spatial scale. GEREM fills a gap within the existing range of  
340 tools by providing estimates at spatial scales consistent with biological and management  
341 scales. In Europe, these scales may be used in the future to fix total allowable catches in  
342 countries like France, where glass eels are fished commercially.

343 The modelling approach used in GEREM could form the basis for a patch-based population  
344 dynamics model (Wu and Levin, 1997) for the whole eel continental phase, similar to the  
345 model currently being developed by Koops et al. (2014). In such a patch-based model, the  
346 recruitment zones we have proposed may be subdivided into smaller patches that would be  
347 homogeneous in terms of eel sub-population characteristics and anthropogenic pressure. In  
348 those sub-patches, a simple stage-based model similar to the model proposed by Dekker  
349 (2000a) could be applied using GEREM recruitment estimates for each patch and  
350 incorporating new fishing effort data that were recently reconstructed by the WGEEL (ICES,  
351 2013). The nested spatial scales, ranging from distribution area to recruitment zones,  
352 subpatches, and river catchments would appear to be especially relevant in addressing the  
353 fractal geometry of the eel population (Dekker, 2000b).

354

## 355 **5.2 Rationales of underlying assumptions and robustness of results**

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

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



368 2003) and wind driven currents (Westerberg, 1998) to progress towards the coast.

369 Experiments have shown that energy reserves and highly efficient swimming of American  
370 glass eels allow them to sustain active swimming over long distances (Wuenschel and Able,  
371 2008). Glass eels possess an acute sense of smell (Sorensen, 1986; Tesch, 2003) which is  
372 thought to allow them to identify freshwater plumes and navigate as they approach the coast.

373 The final distribution of glass eels is the result of two mechanisms. The first is passive  
374 transport by currents, which is described in the model by the first multinomial distribution  
375 between different zones. The second is active navigation within a zone, which is probably  
376 achieved by active migration but also the use of the tidal currents, which is described by the  
377 second multinomial distribution.

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

389 As mentioned earlier, recruitment indices are of major importance for eel stock assessment.

390 As is the case with many stock assessment models, GEREM assumes that glass eel indices,  
391 including commercial CPUE, are proportional to true abundance. However, Harley et al.  
392 (2001) pointed out for many stocks that CPUE are not strictly proportionate to true abundance  
393 but rather display a power relationship. The most common situation, called hyperstability,

394 occurs when CPUE remains stable while abundance decreases (Hilborn and Walters, 1992).  
395 Hyperstability can arise when fishermen modify their behaviour as a function of abundance  
396 (Hilborn and Walters, 1992). However, the commercial CPUE used in this article, display  
397 similar trends to other types of data (including scientific trap) which should not display  
398 hyperstability. It has been observed at European level that most commercial CPUE collected  
399 across Europe display a similar trend, despite very distinct fishery types between river  
400 catchments. This trend is also similar to non fishery-based indices (ICES, 2010, p 201). In  
401 view of this, we considered that hyperstability or hyperdepletion could be ignored in the  
402 model.

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

406

### 407 **5.3 Application to French eel sub-population**

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

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

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

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

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

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

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

459

#### 460 **5.4 Possible application to the whole stock**

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

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

467  $[p_1(y), \dots, p_n(y)] \sim \text{Dirichlet}(\lambda \cdot [p_1(y-1), \dots, p_n(y-1)])$  . Assigning a high value to  $\lambda$

468 (approximately 100) would be a suitable way to smooth inter-annual time-variations and  
 469 avoid erratic variations. The model would provide a single absolute recruitment estimate.

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

478

#### 479 **5.5 Glass eel recruitment indices**

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

490 Regarding glass eel abundance estimates in rivers, Harrison *et al.* (2014) have recently  
491 proposed an interesting review of the various methods that can be implemented to estimate  
492 recruitment in estuaries. They underline the importance of an appropriate sampling design and  
493 propose three main kinds of methods: combining trap and commercial catch data (Jessop,  
494 2000), depletion methods (Tzeng, 1984) or models similar to those used in this study

495 (Beaulaton and Briand, 2007; Bru *et al.*, 2009). In some situations, when fishery exploitation  
496 rates are close to 1, commercial landings can be good estimators of recruitment, such as in the  
497 Vilaine estuary (Briand *et al.*, 2003). Tag and recapture experiments may also be a relevant  
498 method when recapture rate is significant (Briand *et al.*, 2005; Dekker and van Willigen,  
499 1997). In the future, the development of new video tracking methods (Delcourt *et al.*, 2013)  
500 may also provide relevant abundance estimates (Doehring *et al.*, 2011; Grote *et al.*, 2014),  
501 although glass eels remain too small for those techniques.

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

505

## 506 **6 Acknowledgments**

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

512

## 513 **7 References**

514 Als, T. D., Hansen, M. M., Maes, G. E., Castonguay, M., Riemann, L., Aarestrup, K., Munk,  
515 P., *et al.* 2011. All roads lead to home: panmixia of European eel in the Sargasso Sea.  
516 Mol Ecol, 20: 1333–1346.  
517 Anonymous. 2010. Plan de gestion Anguille de la France - Application du règlement (CE)  
518 n°1100/2007 du 18 septembre 2007 - Volet national. Ministère de l'Ecologie, de

- 519 l'Energie, du Développement durable et de la Mer, en charge des Technologies vertes  
520 et des Négociations sur le climat, Onema, Ministère de l'Alimentation, de  
521 l'Agriculture et de la Pêche.
- 522 Aranburu, A., Diaz, E., and Briand, C. in Press. Glass eel recruitment and exploitation in a  
523 South European estuary (Oria Bay of Biscay). ICES Journal of Marine Science.
- 524 Beaulaton, L., and Briand, C. 2007. Effect of management measures on glass eel escapement.  
525 ICES Journal of Marine Science: Journal du Conseil, 64: 1402–1413.
- 526 Beaulaton, L., Briand, C., Lambert, P., Castelnaud, G., Drouineau, H., Chapon, P. M., Pénil,  
527 C., *et al.* 2014. Report on the eel stock and fishery in France 2013/2014. In Report of  
528 the Joint EIFAC/ICES Working Group on Eels (WGEEL), pp. 274–346.
- 529 Bertand, L. 2009. Etude de l'impact de la pêche à la civelle sur les estuaires de la Seudre et de  
530 la Charente dans le cadre du règlement européen R(CE) 1100/2007 sur l'anguille.  
531 UFR Sciences & Techniques Côte Basque. 69 pp.
- 532 Briand, C. 2008. Dynamique de population et de migration des civelles en estuaire de vilaine.  
533 Rennes, ENSA. <http://www.theses.fr/2009NSARH076> (Accessed 26 May 2015).
- 534 Briand, C., Beaulaton, L., Chapon, P. M., Drouineau, H., and Lambert, P. 2015. Estimation de  
535 l'échappement en anguilles argentées (*Anguilla anguilla*) en France. rapport  
536 Onema.
- 537 Briand, C., Bonhommeau, S., Castelnaud, G., and Beaulaton, L. 2008. An appraisal of  
538 historical glass eel fisheries and markets: landings, trade route and future prospect for  
539 management. In IFM 38th Annual Conference , 15/10/2007 - 18/10/2007, p. 21. Ed.  
540 by C. Moriarty. Wespport, IRL. <http://cemadoc.irstea.fr/cemoa/PUB00030466>.
- 541 Briand, C., Buard, E., and Postic-Puivif, A. 2012. Modélisation de la capture de civelles dans  
542 l'estuaire de la Seudre par l'utilisation du modèle GEMAC. Modélisation de la capture  
543 de civelles dans l'estuaire de la Seudre par l'utilisation du modèle GEMAC.  
544 Traitement des données des saisons 2008-2009 et 2009-2010.

- 545 [charente.net/bibliotheque/poissons-migrateurs/documents/files/rapport-sur-limpact-de-](http://charente.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)  
546 [la-peche-a-la-civelle-en-charente-et-en-seudre-via-limplementation-du-modele-](http://charente.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)  
547 [gemac-bertrand-loic.pdf/attachment\\_download/attachedFile](http://charente.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).
- 548 Briand, C., Fatin, D., Feunteun, E., and Fontenelle, G. 2005. Estimating the stock of glass eels  
549 in an estuary by mark-recapture experiments using vital dyes. *Bulletin Français de la*  
550 *Pêche et de la Protection des Milieux Aquatiques*, 378-379: 23–46.
- 551 Briand, C., Fatin, D., Fontenelle, G., and Feunteun, E. 2003. Estuarine and fluvial recruitment  
552 of the European glass eel, *Anguilla anguilla*, in an exploited Atlantic estuary. *Fish*  
553 *Manag Ecol*, 10: 377–384.
- 554 Bru, N., Bouvet, J.-C., and Prouzet, P. 2006. Quantification par une méthode analytique de la  
555 biomasse saisonnière de civelles (*Anguilla anguilla*) dans l'estuaire de l'Adour et  
556 estimation du taux d'exploitation saisonnier de la pêche professionnelle de 1998 à  
557 2005. Rapport Ifremer – projet Indicang [http://www.ifremer.fr/indicang/sites-](http://www.ifremer.fr/indicang/sites-thematiques/pdf/estim-civelle-1998-2005.pdf)  
558 [thematiques/pdf/estim-civelle-1998-2005.pdf](http://www.ifremer.fr/indicang/sites-thematiques/pdf/estim-civelle-1998-2005.pdf), 2006, Rapport Ifremer – projet Indicang  
559 <http://www.ifremer.fr/indicang/sites-thematiques/pdf/estim-civelle-1998-2005.pdf>.
- 560 Bru, N., Prouzet, P., and Lejeune, M. 2009. Daily and seasonal estimates of the recruitment  
561 and biomass of glass eels runs (*Anguilla anguilla*) and exploitation rates in the Adour  
562 open estuary (Southwestern France). *Aquatic Living Resources*, 22: 509–523.
- 563 Burgers, H. E., Schipper, A. M., and Jan Hendriks, A. 2014. Size relationships of water  
564 discharge in rivers: scaling of discharge with catchment area, main-stem length and  
565 precipitation. *Hydrological Processes*, 28: 5769–5775.
- 566 Castelnaud, G. 2001. Localisation de la pêche, effectifs de pêcheurs et production des espèces  
567 amphihalines dans les fleuves français. *Bulletin Français de la Pêche et de la*  
568 *Pisciculture*: 439–460.
- 569 Castonguay, M., Hodson, P. V., Moriarty, C., Drinkwater, K. F., and Jessop, B. M. 1994. Is  
570 there a role of ocean environment in American and European eel decline? *Fisheries*



- 571 Oceanography, 3: 197–203.
- 572 Cicotti, E. 2006. Nuovi metodi ecologici per la valutazione del reclutamento di ceche di  
573 anguilla europea (*Anguilla anguilla* L.) per la gestione sostenibile di questa risorsa.  
574 Relazione finale MiPAF, VI Piano Triennale n. 6°21.
- 575 Crivelli, A. J., Auphan, N., Chauvelon, P., Sandoz, A., Menella, J.-Y., and Poizat, G. 2008.  
576 Glass eel recruitment, *Anguilla anguilla* (L.), in a Mediterranean lagoon assessed by a  
577 glass eel trap: factors explaining the catches. *In* Fish and Diadromy in Europe  
578 (ecology, management, conservation), pp. 79–86. Ed. by S. Dufour, E. Prévost, E.  
579 Rochard, and P. Williot. Springer Netherlands.  
580 [http://link.springer.com/chapter/10.1007/978-1-4020-8548-2\\_6](http://link.springer.com/chapter/10.1007/978-1-4020-8548-2_6) (Accessed 20  
581 December 2013).
- 582 Dekker, W. 2000a. A Procrustean assessment of the European eel stock, 57: 938–947.
- 583 Dekker, W. 2000b. The fractal geometry of the European eel stock. ICES Journal of Marine  
584 Science: Journal du Conseil, 57: 109–121.
- 585 Dekker, W. 2002. Monitoring of glass eel recruitment. Netherlands Institute of Fisheries  
586 Research. report C007/02-WD.
- 587 Dekker, W. 2003. Did lack of spawners cause the collapse of the European eel, *Anguilla*  
588 *anguilla*? *Fish Manage Ecol*, 10: 365–376.
- 589 Dekker, W. 2005. Report of the Workshop on National Data Collection for the European Eel,  
590 S\anga Säby (Stockholm, Sweden), 6–8 September 2005. Fiskeriverket Swedish  
591 Board of Fisheries, 282.
- 592 Dekker, W., Casselman, J., Cairns, D. K., Tsukamoto, K., Jellyman, D., and Lickers, H. 2003.  
593 Worldwide decline of eel resources necessitates immediate action: Québec Declaration  
594 of Concern. *Fisheries*, 28: 28.
- 595 Dekker, W., and Casselman, J. M. 2014. The 2003 Québec Declaration of Concern About Eel  
596 Declines—11 Years Later: Are Eels Climbing Back up the Slippery Slope? *Fisheries*,

597 39: 613–614.

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

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

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

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

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

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

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

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

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

- 623 (DIDSON) assessment of American shad (*Alosa sapidissima*) approaching a  
624 hydroelectric dam. *Canadian Journal of Fisheries and Aquatic Sciences*, 71: 545–558.
- 625 Hagstrom, O., and Wickström, H. 1990. Immigration of Young Eels to the Skagerrak-Kattegat  
626 Area 1900 to 1989. *Internationale Revue der gesamten Hydrobiologie und*  
627 *Hydrographie*, 75: 707–716.
- 628 Hanel, R., and Miller, M. J. 2014. Changes in Abundance of Anguillid Leptocephali in the  
629 Sargasso Sea. *Afs*. <https://afs.confex.com/afs/2014/webprogram/Paper16276.html>  
630 (Accessed 2 October 2014).
- 631 Hanel, R., Stepputtis, D., Bonhommeau, S., Castonguay, M., Schaber, M., Wysujack, K.,  
632 Vobach, M., *et al.* 2014. Low larval abundance in the Sargasso Sea: new evidence  
633 about reduced recruitment of the Atlantic eels. *Naturwissenschaften*, 101: 1041–1054.
- 634 Harrison, A. J., Walker, A. M., Pinder, A. C., Briand, C., and Aprahamian, M. W. 2014. A  
635 review of glass eel migratory behaviour, sampling techniques and abundance estimates  
636 in estuaries: implications for assessing recruitment, local production and exploitation.  
637 *Reviews in Fish Biology and Fisheries*: 1–17.
- 638 Hilborn, R., and Walters, C. J. 1992. *Quantitative Fisheries Stock Assessment*. Chapman and  
639 Hall, New York. 570 pp.
- 640 ICES. 2010. Report of the 2010 session of the Joint EIFAC/ICES Working Group on Eels.  
641 ICES CM 2010/ACOM:18. Hamburg.
- 642 ICES. 2012a. Report of the Joint EIFAAC/ICES Working Group on Eels (WGEEL). ICES  
643 CM 2012/ACOM:18. Copenhagen.
- 644 ICES. 2012b. Report of the Workshop on Eel and Salmon DCF Data (WKESDCF). ICES CM  
645 / ACOM:62. Copenhagen.
- 646 ICES. 2013. Report of the Joint EIFAAC/ICES Working Group on Eels (WGEEL). ICES CM  
647 2013/ACOM:18. Copenhagen.
- 648 ICES. 2014. Report of the Joint EIFAAC/ICES Working Group on Eels (WGEEL). ICES CM

- 649 2014/ACOM:18. Rome.
- 650 ICES. 2015. EU request on criteria for CITES non-detriment finding for European eel  
651 (*Anguilla anguilla*). In ICES Advice 2015, book 9. ICES. ICES.
- 652 Jacoby, D., and Gollock, M. 2014. *Anguilla anguilla*. In The IUCN Red List of Threatened  
653 Species. Version 2014.2. <http://www.iucnredlist.org>.
- 654 Jessop, B. M. 2000. Size, and exploitation rate by dip net fishery, of the run of American eel,  
655 *Anguilla rostrata* (LeSueur), elvers in the East River, Nova Scotia. *Dana*, 12: 43–57.
- 656 Johnson, N. L., Kotz, S., and Balakrishnan, N. 1997. Discrete Multivariate Distributions.  
657 Wiley-Interscience. 328 pp.
- 658 Kettle, A. J., Asbjørn Vøllestad, L., and Wibig, J. 2011. Where once the eel and the elephant  
659 were together: decline of the European eel because of changing hydrology in  
660 southwest Europe and northwest Africa? *Fish and Fisheries*, 12: 380–411.
- 661 Koops, M. A., Young, A., and Cairns, D. K. 2014. Meta-Population Dynamics in the  
662 American Eel and the Importance of Larval Distribution. *Afs*.  
663 <https://afs.confex.com/afs/2014/webprogram/Paper16645.html> (Accessed 9 October  
664 2014).
- 665 Lambert, P. 2008. Évaluation des effets possibles de différents niveaux de réduction des  
666 impacts sur le temps de restauration du stock d'anguille européenne. Convention de  
667 partenariat Onema-Cemagref. <http://cemadoc.irstea.fr/cemoa/PUB00028119>.
- 668 Moriarty, C., and Dekker, W. 1997. Management of the European Eel. *Irish Fisheries Bulletin*,  
669 15: 1–125.
- 670 Ohlssen, D. I., Sharples, L. D., and Spiegelhalter, D. J. 2007. Flexible random-effects models  
671 using Bayesian semi-parametric models: applications to institutional comparisons. *Stat*  
672 *Med*, 26: 2088–2112.
- 673 Prouzet, P., Bouvet, J.-C., Bru, N., and Boussouar, A. 2007. Quantification de la biomasse  
674 saison-nière de civelles (*Anguilla anguilla*) dans l'estuaire de la Loire et estimation du

- 675           taux d'exploitation saisonnier de la pêche professionnelle pour les saisons de pêche  
676           2003 à 2005. Rapport Ifremer – projet Indicang <http://www.ifremer.fr/indicang/boite->  
677           bassins-versants/pdf/rapport-saison-bv-loire.pdf, Rapport Ifremer – projet Indicang  
678           <http://www.ifremer.fr/indicang/boite-bassins-versants/pdf/rapport-saison-bv-loire.pdf>.
- 679 R Development Core Team. 2011. R: A Language and Environment for Statistical Computing.  
680           <http://www.R-project.org/>.
- 681 Schmidt, J. 1923. Breeding places and migrations of the eel. *Nature*, 111: 51–54.
- 682 Sorensen, P. W. 1986. Origins of the freshwater attractant(s) of migrating elvers of the  
683           American eel, *Anguilla rostrata*. *Environmental Biology of Fishes*, 17: 185–200.
- 684 Stan Development Team. 2013. Stan: A C++ Library for Probability and Sampling, Version  
685           1.3. URL <http://mc-stan.org/>.
- 686 Tesch, F.-W. 1980. Occurrence of eel *Anguilla anguilla* larvae west of the European  
687           continental shelf, 1971–1977. *Environmental Biology of Fishes*, 5: 185–190.
- 688 Tesch, F. W. 2003. *The Eel*. Blackwell Publishing.
- 689 Tzeng, W.-N. 1984. An estimate of the exploitation rate of *Anguilla-japonica* elvers  
690           immigrating into the coastal waters off Shuang-Chi River, Taiwan. *Bulletin of the*  
691           Institute of Zoology, Academia Sinica, 23: 173–180.
- 692 Vogt, J., and Foisneau, S. 2007. European river and catchment database, version 2.0 (CCM2)  
693           analysis tools. Report. Luxembourg : Publications Office of the European Union.  
694           <http://www.envia.bl.uk/handle/123456789/4533> (Accessed 2 October 2014).
- 695 Vollestad, L. A. 1992. Geographic variation in age and length at metamorphosis of maturing  
696           European eel - Environmental effects and phenotypic plasticity, 61: 41–48.
- 697 Westerberg, H. 1998. Oceanographic aspects of the recruitment of eels to the Baltic Sea.  
698           *Bulletin Français de la Pêche et de la Pisciculture*: 177–185.
- 699 Westerberg, H., and Wickström, H. 2014. Baltic Eel Recruitment and Escapement;  
700           Quantitative Estimates from Survey Data. *Afs*.

- 701 <https://afs.confex.com/afs/2014/webprogram/Paper15498.html> (Accessed 2 October  
702 2014).
- 703 Wuenschel, M. J., and Able, K. W. 2008. Swimming ability of eels (*Anguilla rostrata*, *Conger*  
704 *oceanicus*) at estuarine ingress: contrasting patterns of cross-shelf transport? *Marine*  
705 *Biology*, 154: 775–786.
- 706 Wu, J., and Levin, S. A. 1997. A patch-based spatial modeling approach: conceptual  
707 framework and simulation scheme. *Ecological Modelling*, 101: 325–346.

708 **8 Tables**

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

Parameters	priors	Rhat
$\sigma_R$ : recruitment random-walk standard-deviation	$\sigma_R^2 \sim InverseGamma(0.01,0.01)$	1.001
$\sigma_{U_i}$ : standard-deviation of observation for absolute index $i$	$\sigma_{U_i}^2 \sim InverseGamma(0.01,0.01)$	min 1.000 max 1.001
$\sigma_{AI_i}$ : standard-deviation of observation for relative index $i$	$\sigma_{AI_i}^2 \sim InverseGamma(0.01,0.01)$	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
$\beta$ : 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 $z$	$\begin{bmatrix} p_1 \\ \vdots \\ p_{nb_z} \end{bmatrix} \sim Dirichlet \begin{bmatrix} \alpha_1 \\ \vdots \\ \alpha_{nb_z} \end{bmatrix}$	min 1.001 max 1.002
	with $\alpha_1 = \dots = \alpha_{nb_z} = \frac{1}{nb_z} \cdot \gamma$ and $nb_z$ the number of zones.	
$\gamma$ 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

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

---

EMU	Catchment area (km <sup>2</sup> )
Seine – Artois	114,293
Bretagne	30,561
Loire	127,813
Garonne	97,340
Rhone – Mediterranea – Corsica	129,586
Adour	20,228

---

712



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

Catchment characteristics		Recruitment indices					
Zone	Catchment	Area (km <sup>2</sup> ) (%zone)	River length (km)	Index short name	Type	Extent (missing data)	Ref
Seine – Artois	Bresle	748 (0.6%)	72	Bres	I	1994 – 2010	(Beaulaton <i>et al.</i> , 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 <i>et al.</i> , 2014)
Loire	Loire	117,000 (92%)	1013	LoGERMA	A	2004 – 2006	(Prouzet <i>et al.</i> , 2007)
Loire	Loire			Loi	I	1950 – 2008	(Beaulaton <i>et al.</i> , 2014)
Loire	Sèvre Niortaise	3,650 (2.9%)	159	SevN	I	1962 – 2008 (25)	(Beaulaton <i>et al.</i> , 2014)
Garonne	Charente	9,855 (10%)	381	ChGEMACA		2007 – 2008	(Bertand, 2009)
Garonne	Seudre	855 (0.9%)	68	SeGEMAC	A	2007 – 2008	(Bertand, 2009; Briand <i>et al.</i> , 2012)
Garonne	Garonne	78,870 (81%)	647	GiGEMAC	A	1999	(Beaulaton and Briand, 2007)
Garonne	Garonne			GiCP	I	1961 – 2008 (1)	(Beaulaton <i>et al.</i> , 2014)
Garonne	Garonne			GiSc	I	1992 – 2013	(Beaulaton <i>et al.</i> , 2014)
Adour	Adour	16,880 (83%)	309	AdGERMAA		1999 – 2005	(Bru <i>et al.</i> , 2006)
Adour	Adour			AdCP	I	1966 – 2008 (6)	(Beaulaton <i>et al.</i> , 2014)
Rhone – Mediterranea – Corsica	Vaccarès	6.5 (<0.1%)	245	Vaccares	A	2004 – 2011	(Crivelli <i>et al.</i> , 2008)

## 719 9 Figures

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

721 **Fig. 2.** Estimated (black solid lines) and observed (grey line and points) absolute estimates.

722 Dashed lines represent 95 % credibility intervals for  $\mu_{U_{i,c}}$  while solid lines represent the  
723 median.

724 **Fig. 3.** Estimated (black solid lines) and observed (grey line and points) relative indices.

725 Dashed lines represent 95 % credibility intervals for  $\mu_{IA_{i,c}}$  and solid lines represent the  
726 median

727 **Fig. 4.** Estimated French glass eel recruitment in tonnes (bottom panel) and in log-scale (top

728 panel). Solid line indicates the median while dashed lines represent the corresponding

729 credibility interval (95%). Darker grey line represents Elsewhere-Europe WGEEL index

730 (ICES, 2013) while light grey line represents the catches estimated by Briand et al. (2008).

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

732 **Fig. 6.** Recruitment (median) estimated by the model when fitting the model on altered

733 datasets according to S1 (left panel) and S2 (right panel).

734 **Fig. 7.** Zone recruitments estimated by the model for the last year when the model is fitted on

735 altered datasets according to S1 (top panel) and S2 (bottom panel). Bars represent the median

736 while vertical segments represent the 97.5 % quantile of the a posteriori distributions

737 **Fig. 8.** Medians (circles) and 2.5 and 97.5 % quantiles (segments) of  $\beta$  estimated by the model

738 when the model is fitted on altered datasets according to S1.

739