

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

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1	GEREM (Glass Eel Recruitment Estimation Model): A model to estimate
2	glass eel recruitment at different spatial scales
3	Authors: Drouineau, H. ^{1,*} ; Briand, C. ² ; Lambert, P. ¹ ; Beaulaton, L. ³⁴
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 Brieuc, 35042 Rennes, France
9	4 INRA, U3E (1036), Pôle Gest'Aqua, 65 rue de St Brieuc, 35042 Rennes, France
10	
11	*corresponding author: <u>hilaire.drouineau@irstea.fr</u> , 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 generally estimate recruitment at the river basin scale. With the aim of filling this gap, we 18 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 be consistent with the population scale. In this study, the model was applied to France, using 24

25 various recruitment indices obtained from 1960 to 2013. This provided trends and absolute recruitment estimates consistent with current expert knowledge. A sensitivity analysis was 26 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 recruitment. It could be used in the future to fix total allowable catches in countries such as 29 30 France where glass eels are fished commercially.

31

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

33

Introduction 2 34

35 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 36 37 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, 38 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.

The European eel population has been in drastic decline since the late 70s (Castonguay et al., 43

44 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 45

46 this population collapse have been suggested, including changes in oceanic conditions

(Castonguay et al., 1994), contamination and habitat degradation, parasitoids (Feunteun, 47

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 years in southern Europe to over 20 in northern Europe. In view of this, it is very difficult to 73 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 European regions, and relevant effort data are rarely reported, making silver eel catches 76 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).

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).

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 incorporate prior information, as well as quantifying uncertainty. To illustrate the model's 111 112 potential, we provide the results of an initial test on French EMUs. The possibility of using the model at European level is then discussed. 113

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

The model aims to estimate yearly absolute recruitment of glass eels using recruitment datacollected 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

125 with its own surface area: $S_{1,z},...,S_{n_z,z}$. 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).

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}*.

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

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

142
$$w_{c,z} = \frac{S_{c,z}^{\beta}}{\sum_{c_{z}=1}^{n_{z}} S_{c_{z},z}^{\beta}}$$
(3)

143 A β 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 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:

153
$$R(y) = R(y-1) \cdot e^{\epsilon(y)} \text{ with } \epsilon(y) \sim Normal(0, \sigma_R^2)$$
(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
$$\log\left(IA_{i,c}(y)\right) \sim N\left(\mu_{IA_{i,c}}(y), \sigma_{IA_{i}}^{2}\right) \text{ with } \mu_{IA_{i}}(y) = \log\left(q_{i} \cdot R_{c,z}(y)\right) - \frac{\sigma_{IA_{i}}^{2}}{2}$$
(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
$$\log\left(U_{i,c}(y)\right) \sim N\left(\mu_{U_{i,c}}(y), \sigma_{U_{i}}^{2}\right) \text{ with } \mu_{IA_{i}}(y) = \log\left(R_{c,z}(y)\right) - \frac{\sigma_{U_{i}}^{2}}{2}$$
(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 γ , 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 <i>et al.</i> , 2007). For β ,
176	used a uniform prior between 0.01 and 2 because, as previously mentioned, a β 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				

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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.

- 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).

236

237 **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

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 β at three different values: 0.5, 1 and 1.5.
253	

254 **4 Results**

255 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).

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 γ 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 intervals were observed for Somme, Vaccares, Bres, and SeGEMAC in certain years. For 269 270 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 $R_{cz}(y)$ 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 the logarithmic scale (since log(0) tends to negative infinity). 274 275 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 (Fig. 4 – Kendall τ = 0.87). The model confirms that recruitment has been on the decline since 277 278 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 279 280 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 kg/km² (credibility interval: [0.19, 1.26]) in 2010. The ratio was equal to 0.75 kg/km² in

284 2005 and 0.68 kg/km² in 2006. As a comparison, Cicotti (2006) estimated a ratio of around

285 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 noparticular 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 β 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

similar (Fig. 6). However, the value of β (S2) had a larger influence on results. Recruitment

297 was approximately 25% lower when setting β 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 β was set at 1.5 (but

299 β 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 β . β 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).

 β 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 β

309 increased, while, conversely, it increased for the Rhone-Mediterranea-Corsica zones.

310 Unsurprisingly, sensitivity to β 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 β 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 6.5km² catchment in a 129,586 km² zone, and the Somme is a 6,550 km²

316 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.

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

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

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.

The modelling approach used in GEREM could form the basis for a patch-based population 343 dynamics model (Wu and Levin, 1997) for the whole eel continental phase, similar to the 344 345 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 homogeneous in terms of eel sub-population characteristics and anthropogenic pressure. In 347 348 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, 2013). The nested spatial scales, ranging from distribution area to recruitment zones, 351 352 subpatches, and river catchments would appear to be especially relevant in addressing the fractal geometry of the eel population (Dekker, 2000b). 353

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 β . Currently, the model estimates for the β parameter encompasses the power

360 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

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 β 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.

Experiments have shown that energy reserves and highly efficient swimming of American 369 glass eels allow them to sustain active swimming over long distances (Wuenschel and Able, 370 371 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. 372 373 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 between different zones. The second is active navigation within a zone, which is probably 375 376 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 β . 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

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

386 similar, irrespective of β values. However, overall recruitment was sensitive to β (25% lower

387 when setting β 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). Hyperstability can arise when fishermen modify their behaviour as a function of abundance 395 396 (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 hyperstability. It has been observed at European level that most commercial CPUE collected 398 399 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 (Lambert, 2008; Moriarty and Dekker, 1997). Estimating recruitment is of particular 410 411 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 412 413 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 414 415 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 in the data, even for the Somme catchment, where absolute estimates are based on an expert 417 418 assessment of exploitation rate.

419 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 420 was around 538 tonnes, approximately 76% of total European recruitment, resulting in a glass 421 422 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 423 total European recruitment, and an exploitation rate of 26%. GEREM estimates for the same 424 period were similar, with a median of 1,490 tonnes in 1993 (credibility interval 784 to 5,020 425 tonnes), although this only applies to France. 426

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 and discharge relationship may not have been appropriate. New series and absolute 446 recruitment estimates could prove valuable in improving estimates made by the model. 447 448 The estimated overall recruitment displayed very large credibility intervals (Fig. 4). This can 449 be explained by several factors. Firstly, the uncertainty attached to β due to the limited levels 450 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 451 452 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 priors. However, it would be possible to use similar standard deviations for similar types of 454 455 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 456 the future, if estimates of uncertainty on those data-series were provided, they could be used 457

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.

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

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

Should this model be applied to the whole of Europe, the main limitation would once again be 470 the limited amount of absolute number estimates. Such an application would require 471 aggregation of EMUs into larger zones. ICES eco-regions (Celtic Sea, Atlantic coast, 472 473 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 474 475 valuable source of information, as proposed by Dekker (2002, 2005) and ICES (2012b, 2014). Standardisation of some monitoring programs throughout Europe could provide similar 476 477 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

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512

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708 8 Tables

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

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

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

EMU	Catchment area (km ²)
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

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
- 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 ²) (%zone)	River length (km)	Index short name	Туре	Extent (missing data)	Ref
Seine – Artois	Bresle	748 (0.6%)	72	Bres	Ι	1994 – 2010	(Beaulaton <i>et al.</i> , 2014)
Seine – Artois	Somme	6,550 (5.7%)	245	Somme	А	1992-2012 (1)	
Bretagne	Vilaine	10,500 (34%)	218	Vil	А	1971 – 2011	(Beaulaton et al., 2014)
Loire	Loire	117,000 (92%)	1013	LoGERMA	A	2004 – 2006	(Prouzet <i>et al.</i> , 2007)
Loire	Loire			Loi	Ι	1930 – 2008	(Beaulaton et al., 2014)
Loire	Sèvre Niortaise	3,650 (2.9%)	159	SevN	Ι	1962 – 2008 (25)	(Beaulaton et al., 2014)
Garonne	Charente	9,855 (10%)	381	ChGEMAC	ĊA	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 1961	(Beaulaton and Briand, 2007) (Beaulaton et al
Garonne	Garonne			GiCP	Ι	2008 (1)	(Dedulaton et al., 2014)
Garonne	Garonne	16.000		GiSc	Ι	1992 – 2013	(Beaulaton et al., 2014)
Adour	Adour	16,880 (83%)	309	AdGERMA	AA	1999 – 2005 1966 –	(Bru <i>et al</i> ., 2006) (Beaulaton et al
Adour	Adour			AdCP	Ι	2008 (6)	(Deciditation et al., 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 $\mu_{U_{ic}}$ while solid lines represent the
- 723 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
- 726 median
- 727 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
- 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).
- **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).
- 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.
- 739