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

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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):

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

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):

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

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 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

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 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 *et al.*, 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

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 β 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 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
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 kg/km^2 (credibility interval: [0.19, 1.26]) in 2010. The ratio was equal to 0.75 kg/km^2 in
284 2005 and 0.68 kg/km^2 in 2006. As a comparison, Cicotti (2006) estimated a ratio of around
285 0.01 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 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 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
296 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).

307 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
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 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
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 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.

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 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
384 to provide valuable data in the near future. In the absence of any further data, comparing
385 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).
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 β 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 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.

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

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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-walk standard-deviation	$\sigma_R^2 \sim InverseGamma(0.01,0.01)$	1.001
σ_{U_i} : standard-deviation of observation for absolute index i	$\sigma_{U_i}^2 \sim InverseGamma(0.01,0.01)$	min 1.000 max 1.001
σ_{AI_i} : standard-deviation of observation for relative index i	$\sigma_{AI_i}^2 \sim InverseGamma(0.01,0.01)$	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
β : power parameter of the relation between catchment surface and proportion of the recruitment	$\beta \sim Unif(0.01,2)$	1.000
p_z Proportion of recruitment in zone z	$\begin{bmatrix} p_1 \\ \vdots \\ p_{nb_z} \end{bmatrix} \sim Dirichlet \begin{bmatrix} \alpha_1 \\ \vdots \\ \alpha_{nb_z} \end{bmatrix}$	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.	
γ Dirichlet concentration parameter (a value below 1 leads to sparse distributions while a value above 1 leads to dense distributions)	$\gamma \sim Unif(0.3,10)$	1.001

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
 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 ²) (%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) (Bertand, 2009; Briand <i>et al.</i> , 2012)
Garonne	Seudre	855 (0.9%)	68	SeGEMAC	A	2007 – 2008	(Beaulaton and Briand, 2007)
Garonne	Garonne	78,870 (81%)	647	GiGEMAC	A	1999	(Beaulaton <i>et al.</i> , 2014)
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 β estimated by the model

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

739