



Separating wild versus stocking components in fish recruitment without identification data: a hierarchical modelling approach

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2 **identification data: a hierarchical modelling approach**

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Draft

38 Abstract

39 Salmonid juvenile stocking programs are often poorly monitored due to the lack of identification
40 between stocked and wild fish. In this study, a hierarchical Bayesian model is developed to take
41 advantage of spatio-temporal variations of stocking and wild recruitment for estimating these two
42 components despite the absence of identification data. It is first tested by means of simulated
43 data, and then applied to the 37 years abundance data set of the Atlantic salmon population of the
44 Allier catchment (France). Despite the absence of identification data, juvenile densities could be
45 estimated and split into wild and stocked components. We found that the stocked juveniles
46 contributed significantly to the total juvenile production, while the wild reproduction continued
47 to provide an important contribution. This approach is encouraging and promising from a
48 management advice perspective. It is flexible enough to accommodate for case study specificities
49 and shows that long term monitoring abundances can be useful to assess the impact of stocking
50 programs even in the absence of direct means of identifying stocked vs wild fish.

51

52 Key-words: Atlantic salmon, hierarchical Bayesian model, juveniles, stocking, density
53 dependence

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59 Résumé

60 Les programmes de repeuplement pour les populations de salmonidés sont souvent mal suivis.
61 Une des raisons principales étant l'absence de marquage pour distinguer les individus sauvages
62 des individus issus du repeuplement. Dans cette étude, la modélisation hiérarchique Bayésienne
63 est utilisée pour tirer parti des variations spatio-temporelles du recrutement issu des
64 repeuplements et du recrutement sauvage et ainsi estimer la contribution relative de ces deux
65 composantes en l'absence de données d'identification. Notre modèle est d'abord testé sur des
66 données simulées puis étendu à une série de données de 37 ans sur la population de saumon
67 Atlantique du bassin de l'Allier (France). En dépit de l'absence de données d'identification, les
68 densités de juvéniles ont été estimées et divisées composantes sauvage et repeuplement.
69 L'analyse rétrospective des densités de juvéniles met en évidence la contribution significative
70 des juvéniles déversés au printemps dans la production totale de juvéniles à l'automne.
71 L'approche de modélisation proposée dans cette étude est encourageante et prometteuse du point
72 de vue de la gestion. Les données de suivi long terme peuvent être utiles pour mesurer
73 rétrospectivement l'impact des programmes de repeuplement en dépit des insuffisances du
74 programme de suivi. Par ailleurs, le cadre de modélisation est suffisamment flexible pour
75 incorporer les spécificités de n'importe quel bassin versant rendant cette approche très
76 transférable.

77

78 Mots clés: densité dépendance, juvéniles, modélisation hiérarchique bayésienne, repeuplement,
79 saumon atlantique

80

81 1. Introduction

82

83 Over the past century, many exploited fish populations have declined significantly due to
84 environmental changes, overexploitation and human activities (Hilborn and Walters 1992; Pauly
85 et al. 2002; Blankenship and Leber 1995; Frank and Brickman 2001). Along with fisheries
86 regulations and habitat restoration (Hendry et al. 2003), stock enhancement is a recurrent
87 management tool used to reverse these trends (Molony et al. 2003). While assessing the
88 performance of stocked fish should be an essential component of enhancement program, this is
89 often overlooked (Waples et al. 2003).

90 The interactions and performance of hatchery fish versus wild fish have been extensively studied,
91 especially in salmonids. A diverse range of topics such as the competition between hatchery and
92 wild fish (Weber and Fausch 2003; Riley et al. 2004; Lafaille 2011; Tataru and Berejikian, 2011),
93 stocked density adjustment (Orciari et al. 1994; McMenemy, 1995), prior residency advantage
94 (Metcalf et al. 2003), and predation on stocked fish (Fresh et al. 2003; Henderson and Letcher
95 2003) have been studied. Due to the combined diversity (i) of the conditions under which these
96 studies are carried out (artificial, semi artificial or natural conditions) and (ii) of the associated
97 stocking programs (e.g. age and size of stocked fish, hatchery rearing conditions), there exists no
98 clear position regarding the interactions between hatchery reared and wild fish. At a population
99 scale, rivers with salmonid stocking programs have frequently failed to restore a self-sustaining
100 population (Fleming and Petersson 2001). In such a context, the necessity for monitoring the
101 effects of stocking programs to improve our understanding of their effects is reinforced. To be
102 most effective, one should be able to distinguish stocked fish from wild fish. While this is
103 possible by marking stocked fish (e.g. fin clipping, oxytetracycline immersion; Skalski et al.

104 2009) or by genetic assignment (Warnock et al. 2011), this is rarely done. In this case, can the
105 contributions of stocking versus wild recruitment still be appraised?

106 During the course of a stocking program, stocking intensity may change, intentionally or not,
107 according to spatio-temporal units. Wild production fluctuates in space and time, too. We
108 propose an approach that takes advantage of such spatio-temporal variations of stocking versus
109 wild recruitment for estimating their relative contribution from abundance data. We use Bayesian
110 hierarchical modelling (Royle and Dorazio 2008; Brun et al. 2011; Parent and Rivot 2013) as a
111 template for taking into account the spatio-temporal structure, while explicitly acknowledging
112 that the observable abundance comes from a mixture of fish of wild and hatchery origins. We
113 also incorporate biological knowledge regarding the wild recruitment process and the survival of
114 stocked juveniles to separate their relative contributions. We first present a generic model that
115 considers two nested spatial scales (i.e. electro-fishing at site and river section scale) and assess
116 its performance using simulated data. We then apply the model to estimate juvenile Atlantic
117 salmon (*Salmo salar*) densities in the Allier catchment, France (Fig. 1) over a study period of 37
118 years while assessing the relative contribution of wild reproduction, stocked eggs and stocked
119 juveniles to the total juvenile salmon production.

120

121 2. Materials and Methods

122

123 2.1 The generic model

124

125 Every year, juveniles densities are considered at the scale of a river reach (densities at this scale
126 are indicated by an upper-case D), within which a collection of sites are sampled every year
127 (densities at this scale are indicated by a lower-case d). At each local site, indices of abundances
128 are observed (typically by electro-fishing), providing information regarding juveniles densities
129 over successive generations (i.e. years). Densities are expressed in numbers of juvenile per square
130 metre of rearing habitat (e.g. runs, riffles and flats).

131 At both scales, total juvenile densities are made of 2 components:

- 132 i) Wild juveniles, defined as the progeny of adults from wild reproduction,
- 133 ii) Stocked juveniles, the survivors from the releases of hatchery produced fish.

134 Typically stocking occurs at an early stage (e.g. in spring for A. salmon) while the total juvenile
135 production is observed at a later stage (e.g. in autumn of the same year, or the following year).

136 Yearly densities at the river scale depend on the number of reproducing adults, denoted S , for the
137 wild component, and the number of fish released, J , for the stocked component.

138 Henceforth, the notation $a|bf(b)$ means the random variable a (whether unobservable or
139 observable) is distributed according to the probability distribution function (pdf) f conditional on
140 b . Indices indicate the year t and the electro-fishing site k . Superscript “ w ”, “ s ”, and “ T ”
141 designate the juvenile production components and their sum.

142

143 2.1.1 River scale densities

144

145 The total density of juveniles at the river scale for a given year D_t^T is the sum of two components:

146

147 (Eq. 1)
$$D_t^T = D_t^w + I_t^s \times D_t^s$$

148

149 Where I_t^s is the indicator of presence/absence of stocking in year t .

150

151 The annual wild density component D_t^w is conditional on the number of parent spawners S_t
152 according to a density-dependent model. In agreement with the current literature on stock-
153 recruitment relationships (Walters and Martell 2004), especially for salmonids (Michielsens and
154 McAllister 2004; Pulkkinen and Mäntyniemi 2013), a Beverton and Holt (1957) relationship for
155 deriving the wild juvenile density component D_t^w with Log-normal errors is chosen as a default
156 option:

157

158 (Eq. 2)
$$\log(D_t^w) | \mu_t^{D-w}, \sigma^{D-w} \sim \text{Normal}(\log(\mu_t^{D-w}), \sigma^{D-w})$$

159

160 (Eq. 3)
$$BH(a^w, Rmax_t^w, S_t, H) = \mu_t^{D-w} = \frac{a^w \times \frac{S_t}{H}}{1 + \frac{a^w}{Rmax_t^w} \times \frac{S_t}{H}}$$

161 Where σ^{D-w} is the standard deviation of the inter-annual fluctuations of D_t^w around its mean μ_t^{D-w}
 162 (log scale), H is the area of the juveniles rearing habitat in the river, a^w and $Rmax_t^w$ are the slope
 163 at the origin and the asymptote of the Beverton-Holt function respectively. $Rmax_t^w$ varies
 164 according to year due to interactions between the wild juveniles and varying number of their
 165 stocked counterparts (see Eq. 6 and 8). Note that in this generic model, all D_t^T , D_t^w , D_t^S and I_t^S are
 166 covariates for which values are known.

167 The stocked juvenile density component D_t^S depends on the initial number of juveniles stocked J_t .
 168 As for the wild component, it is assumed to be density dependent and modelled according to a
 169 Beverton-Holt type model with random and Log-normally distributed errors accounting for inter-
 170 annual variations (standard-deviation σ^{D-S}):

171

172 (Eq. 4)
$$\log(D_t^S) | \mu_t^{D-S}, \sigma^{D-S} \sim Normal(\log(\mu_t^{D-S}), \sigma^{D-S})$$

173

174 (Eq. 5)
$$\mu_t^{D-S} = BH(a_t^S, Rmax_t^S, J_t, H)$$

175

176

177 a_t^S and $Rmax_t^S$ are the slope at the origin and the asymptote of the Beverton-Holt function
 178 respectively. Both a_t^S and $Rmax_t^S$ are assumed to vary according to year because of the prior

179 residency of varying level of wild juveniles at the time of release of the stocked ones (see Eq. 7
180 and 11).

181 The wild juveniles are mixed together with their stocked counterparts from the date of release in
182 the river of the latter. We explicitly model the reciprocal interaction of these two juvenile
183 components.

184 First, we assume that the wild and stocked juveniles compete for the habitat available. This
185 competition is represented by apportioning the total carrying capacity parameter $Rmax$ into two
186 components $Rmax_t^w$ and $Rmax_t^s$ used in equations 3 and 5.

187

188 (Eq. 6)
$$Rmax_t^w = p_t^{Rmax} \times Rmax$$

189 (Eq. 7)
$$Rmax_t^s = (1 - p_t^{Rmax}) \times Rmax$$

190

191 The proportion coefficient is itself calculated as follows:

192 (Eq. 8)
$$p_t^{Rmax} = \frac{\mu_t^{w'}}{\mu_t^{w'} + \mu_t^{s'}}$$

193 With

194 (Eq. 9)
$$\mu_t^{w'} = BH(a^w, Rmax, S_t, H) \quad \text{and,}$$

195 (Eq. 10)
$$\mu_t^{s'} = BH(a^{s'}, Rmax, J_t, H)$$

196

197 Where $a^{s'}$ is the slope at the origin of the Beverton-Holt relationship for the wild juveniles in the
 198 absence of stocked juveniles and $a^{s'}$ is the slope at the origin of the Beverton-Holt relationship
 199 for the stocked juveniles in the absence of wild juveniles.

200 Second, even at low levels of stocking, the survival of the released fish should be negatively
 201 affected by the wild juveniles already in place. It was thus assumed that the slope at the origin of
 202 the Beverton-Holt relationship for the stocked juveniles $a^{s'}$ is reduced by a factor β_t^s equal to the
 203 (average) survival reduction suffered by the wild ones due to wild density-dependent regulation.

204 (Eq. 11) $a_t^s = a^{s'} \times \beta_t^s$ where,

205 (Eq. 12)
$$\beta_t^s = \frac{1}{1 + \frac{a^w}{Rmax} \times \frac{S_t}{H}}$$

206

207 A similar correction factor was not applied to the slope at origin of the wild Beverton-Holt
 208 relationship (Eq. 3) because, at the time of birth, the wild juveniles are alone in the river.
 209 Consequently, we consider there to be a potentially stronger effect of the wild fish on their
 210 stocked counterparts than the reverse due to their prior residency. Indeed, wild fish influence two
 211 parameters of the Beverton-Holt relationship of the stocked juveniles (a_t^s and $Rmax_t^s$), while the
 212 stocked fish influence only one parameter of the Beverton-Holt relationship of the wild juveniles
 213 ($Rmax_t^w$).

214

215 2.1.2 Local site densities

216

217 In a similar way to the river densities, the total juvenile density in each sampled site $d_{t,k}^T$ is
 218 comprised of 2 components:

219

220 (Eq. 13)
$$d_{t,k}^T = d_{t,k}^w + I_{t,k}^s \times d_{t,k}^s$$

221

222 Where $I_{t,k}^s$ is the indicator of the presence/absence of stocking in the site k during year t . Data are
 223 observed conditional to the total density $d_{t,k}^T$ at the site k . An observation process by electro-
 224 fishing, used in our illustrative case study, is described in the supplementary material. Other case
 225 specific observation processes could be used if needed.

226 Each component ($d_{t,k}^w$ and $d_{t,k}^s$) is drawn from a Log-normal distribution, for which the mean is
 227 the annual density at the river scale (D_t^w and D_t^s respectively, log scale).

228

229 (Eq. 14)
$$\log(d_{t,k}^w) | D_t^w, \sigma^{d-w} \sim \text{Normal}(\log(D_t^w), \sigma^{d-w})$$

230 (Eq. 15)
$$\log(d_{t,k}^s) | D_t^s, \sigma^{d-s} \sim \text{Normal}(\log(D_t^s), \sigma^{d-s})$$

231

232 Where σ^{d-w} and σ^{d-s} are the standard deviation parameters for the inter-site variations within the
 233 river for each component.

234

235 2.2 Simulation study

236

237 We used simulated data to assess the performance of the generic model described above.
238 Replicated data sets were generated according to the model (Eq. 1-9, supplementary material)
239 with values of the parameters and the covariates similar to those encountered in the Allier
240 catchment to better relate the analysis to the case study, (Table 1). The simulated data were then
241 used with the generic model for statistical inference, and the derived estimates for quantities of
242 interest were compared to their ‘true’ values.

243 Each replicated data set represents a time-period of 25 years, with 10 sites sampled each year. For
244 each replicate, the index of abundance observed at each local sampling site $A_{t,k}$ is drawn from a
245 Poisson distribution conditional on the local site density $d_{t,k}^T$ and a proportionality factor κ drawn
246 from a Gamma distribution (mean =270 and variance = 200, see supplementary material).

247

248 (Eq. 16)
$$A_{t,k} | d_{t,k}^{tot}, \eta, \kappa \sim Poisson(\kappa \times d_{t,k}^{tot})$$

249

250 For each year, adult abundance was generated using a uniform distribution with lower (100) and
251 upper (4500) bounds matching the range of observed adult salmon abundance in the Allier river
252 over the last 35 years (Dauphin et al. 2013). In order to evaluate the impact of stocking on the
253 statistical inference, three scenarios were tested: 1) absence of stocking, 2) constant stocking
254 (4×10^5 juveniles stocked every year) and 3) increasing stocking (0, 10^5 , 2×10^5 , 3×10^5 , 4×10^5
255 juveniles stocked at 5-year intervals). For each scenario, 20 replicated data sets were generated.

256 The 500 adult abundances (20 replicates x 25 years) and the 20 κ values were the same for each
257 scenario. For each replicate, all unknown quantities were estimated by Bayesian inference (see
258 section 2.4).

259

260 2.3 Application to the Atlantic salmon population in the Allier River

261

262 2.3.1 Study site and data available

263

264 The Allier River is the main tributary of the Loire River (Fig. 1). It drains a 14310 km² catchment
265 and flows into the Loire River about 421 km from its source. To reach the first spawning area in
266 the Allier, adult salmon have to migrate for at least 700km from the mouth of the Loire. At the
267 end of the 19th century, professional and recreational salmon catches in the Loire-Allier
268 catchment declined severely from 15000-30000 to 3000-8000 adults per year (Bachelier 1963).
269 The Allier salmon population is now down to only a few hundred returning adults (Dauphin et al.
270 2013). Its conservation interest is reinforced by its unique genetic and phenotypic characteristics
271 (Prouzet 1990; Perrier et al. 2011). In response to its decline, the Allier salmon population has
272 been supplemented by stocking since the 1960's (Bachelier 1964). The stocking program has
273 been intensified over the last 30 years (Figs 2b and 2c). Similar to other salmonid enhancement
274 projects, the Allier stocking program lacks identification data for distinguishing the fish that are
275 released in the catchment from their wild counterparts. However, annual observations of the

276 abundance of the juvenile salmon in early fall (i.e. electro-fishing sampling) are available
277 together with the varying levels of stocking over time and space

278 Due to habitat quality differences (Cuinat 1988), and data collection constraints, the Allier can be
279 divided into three sections: between Vichy and Langeac, between Langeac and Poutès and
280 upstream from Poutès (Dauphin et al. 2013). In 1986, following the installation of a fish lift, the
281 section upstream from the Poutès dam became accessible to salmon and returning adults were
282 systematically counted. In 1997, another counting facility for returning adults was installed at
283 Vichy, downstream from any spawning habitat. At Langeac, adult salmon have been partially
284 counted from 2003 to 2008: the fish pass is not operational throughout the year, especially during
285 high flow events, so these counts represent a minimum abundance.

286 The adult counts, in association with red (nest) counts, were used to estimate annual spawner
287 abundances during the time frame of this study (1975 to 2011, see Dauphin et al. 2013 for
288 details). Minster and Bomassi (1999) mapped the different types of habitat available in the Allier
289 catchment. Using their results, the surface area of the habitat favourable to juvenile rearing in the
290 different river sections was calculated. In 2009, the two sections upstream from Langeac,
291 identified as potentially providing better juvenile rearing habitat (Cuinat 1988), were declared
292 “refuge area” and stocking in this area has been discontinued.

293 [Figure 1 about here]

294

295 Juveniles (released between May and July) and eggs (introduced in January or February in egg
296 incubators) were stocked from 1975 to 2011 (Figs 2b and c). Subsequent juvenile recruitment has

297 been monitored in autumn (late August to early October) by electro-fishing since 1975 at a
298 collection of sites distributed in the three river sections of the Allier. Two methods have been use.
299 From 1975 to 1990, a successive removal technique was implemented; from 1994 to 2011, a 5-
300 minute index of abundance technique was used (Prévost and Nihouarn 1999; Brun et al. 2011).
301 The successive removal technique is more demanding in terms of time and personnel thus only a
302 few sites were sampled every year (on average 5 sites per year). By contrast, the 5-minute index
303 of abundance technique is easier to implement in the field and more sites were sampled annually
304 (on average 30 sites per year, Fig. 2a).

305 The successive removal technique allows deriving precise estimates of abundance whereas the 5-
306 minute index provides a relative measure of abundance. Dauphin et al. (2009) demonstrated how
307 a calibration relationship between the two electro-fishing techniques can be obtained, allowing
308 conversion of the index into an absolute abundance estimate. Nine sites were sampled in the
309 Allier catchment in 1997, 2000 and 2001, first using the 5-minute index of abundance technique
310 and followed by the successive removal technique. The juvenile density data obtained from these
311 sites were then used to build a calibration relationship using a slightly modified version of the
312 model developed by Dauphin et al. (2009, see supplementary material).

313

314 [Figure 2 about here]

315 2.3.2 Modifications to the generic model

316

317 The generic model was adjusted to the specificities of the case study to account for:

318 i) differences between river sections (where index i representing one of the three river
319 sections was added to equations 1-16),

320 ii) the two types of juvenile stocking (egg incubators and juveniles release).

321

322 Additionally, potential differences in terms of recruitment processes between river sections was
323 addressed by adding a spatial effect to the density dependence relationships (eq. 3 and 5), and re-
324 written as:

325

326 (Eq. 17)
$$\mu_{t,i}^{D,w} = BH(a^w, Rmax_t^w, S_{t,i}, H_i) \times e^{\eta_i}$$

327 (Eq. 18)
$$\mu_{t,i}^{D,s} = BH(a^s, Rmax_t^s, J_{t,i}, H_i) \times e^{\eta_i}$$

328

329

330 The surface area of favourable habitat for juveniles in each river section H_i was calculated based
331 on a habitat assessment conducted in 1999 (Minster & Bomassi). The river section effect η_i
332 reflects differences in juvenile densities downstream and upstream from Langeac ($\eta_2 = \eta_3 = -\eta_1$;
333 Cuiat 1988). The river section effect for the wild component was assumed to apply to the annual
334 stocked juvenile density component. The number of annual spawners $S_{t,i}$ in each river section
335 was either known or estimated using the model described in Dauphin et al. (2013).

336 An early version of the model found that the residuals of the wild and stocking salmon density
337 components ($D_{t,i}^w$ and $D_{t,i}^s$) were correlated. To address this issue, during the years where both
338 wild and stocking recruitment occurred, equations 2 and 4 were re-written so that $D_{t,i}^w$ and $D_{t,i}^s$
339 were drawn from a multivariate normal distribution:

340

341 (Eq. 19)

342

343 $[Log(D_{t,i}^w), Log(D_{t,i}^s)] | \mu_{t,i}^{D-w}, \mu_{t,i}^{D-s}, \rho^D, \sigma^{D-w}, \sigma^{D-s} \sim Normal([Log(\mu_{t,i}^{D-w}), Log(\mu_{t,i}^{D-s})], \Sigma^D)$

344

345 Where ρ^D is the correlation coefficient in the variance-covariance matrix Σ^D :

346 (Eq. 20)
$$\Sigma^D = \begin{pmatrix} \sigma^{D-w^2} & \rho^D \cdot \sigma^{D-w} \cdot \sigma^{D-s} \\ \rho^D \cdot \sigma^{D-w} \cdot \sigma^{D-s} & \sigma^{D-s^2} \end{pmatrix}$$

347

348 The additional type of stocking was addressed by rewriting equations 1 and 13 as the sum of
 349 three components instead of two. The total density in a river section and an electro-fishing site
 350 scale were therefore written as:

351

352 (Eq. 21)
$$D_{t,i}^T = D_{t,i}^w + I_{t,i}^s \times D_{t,i}^s + I_{t,i}^e \times D_{t,i}^e$$

353

354 (Eq. 22)
$$d_{t,i,k}^T = d_{t,i,k}^w + I_{t,i,k}^s \times d_{t,i,k}^s + I_{t,i,k}^e \times d_{t,i,k}^e$$

355

356 Where $I_{t,i}^e$ is the indicator of presence/absence of egg stocking in river section i , and $I_{t,i,k}^e$ is the
 357 presence/absence indicator of egg stocking affecting the site k during year t in the river section i
 358 where site k was located.

359

360 The stocked egg density component $D_{t,i}^e$ was considered differently than the two other
 361 components (see also the discussion section on this issue). It depended on the number of
 362 incubators used each year in each river section $N_{t,i}^{inc}$, an average survival parameter s^e , the
 363 number of eggs stocked in any given incubator j , $E_{t,i,j}$ and the rearing habitat surface area for
 364 juveniles in each river section H_i and follows a Log-normal distribution:

365

366 (Eq. 23)
$$\log(D_{t,i}^e) | \mu_{t,i}^{D,e}, \sigma^{D,e} \sim Normal(\log(\mu_{t,i}^{D,e}), \sigma^{D,e})$$

367

368 Where $\sigma^{D,e}$ is the standard deviation parameter for the inter-annual fluctuations around the mean

369 $\mu_{t,i}^{D,e}$:

370

371 (Eq. 24)
$$\mu_{t,i}^{D,e} = s^e \times \sum_{j=1}^{N_{t,i}^{inc}} \frac{E_{t,i,j}}{H_i}$$

372

373 The total number of egg incubators $N_{t,i}^{inc}$ varied between 1 and 6 according to year t . From 1975
 374 to 1996, there were only three years (1977, 1979 and 1984) during which very limited numbers of
 375 eggs were stocked (Fig. 2b) with different methodologies but with no electro-fishing sites in
 376 proximity to the eggs stocking location. Hence, eggs stocked before 1996 were excluded from the
 377 analysis.

378

379 During their first year of life, the dispersal of juvenile salmon from their incubation site is limited
 380 (Einum et al. 2008; Foldvik et al. 2010; Teichert et al. 2011). Beall et al. (1994) found that, by
 381 October, 89 % of juveniles were within 1600m downstream from the egg nest where they
 382 originated. We used this distance to calculate the surface area $H_{t,j}^{inc}$ of the patch potentially
 383 colonized by the juveniles produced by each incubator. Given that the Allier River is much wider
 384 than the brook considered by Beall et al. (1994), this likely resulted in an overestimate of the area
 385 influenced by the incubators. The mean density on the patches influenced by egg incubators can
 386 be calculated by raising the average density at the river section scale $D_{t,i}^e$ by a factor
 387 corresponding to the ratio of the total habitat area H_i in a given river section i over the restricted
 388 habitat area directly influenced by the incubators installed in the same river section, $\sum_{j=1}^{J_i} I_{t,i,j}^{inc} \times$
 389 $H_{i,j}^{inc}$, where J_i is the total number of egg incubators in a river section i and $I_{t,i,j}^{inc}$ is an indicator that
 390 a given incubator is in activity or not on year t . Due to their respective locations, every electro-
 391 fishing site can only be affected by one incubator. At a site k potentially influenced by an egg
 392 incubator, the local density resulting from the j stocked eggs $d_{t,i,k}^e$ was then distributed according
 393 to a Log-normal distribution:

394

395 (Eq. 25) $\log(d_{t,i,k}^e) | D_{t,i}^e, H_i, I_{t,i,j}^{inc}, H_{i,j}^{inc}, \sigma^{d-e}$

$$Normal\left(\log\left(D_{t,i}^e \times \frac{H_i}{\sum_{j=1}^{J_i} I_{t,i,j}^{inc} \times H_{i,j}^{inc}}\right), \sigma^{d-e}\right)$$

396

397 Where σ^{d-e} is the standard deviation associated with the inter-site variations within a river section
 398 for any given year.

399 The wild and stocked components $d_{t,i,k}^w$ and $d_{t,i,k}^s$ are Log-normally distributed, their mean (log
 400 scale) being the annual densities in the river sections ($D_{t,i}^w$ and $D_{t,i}^s$ respectively):

401

402 (Eq. 26) $\log(d_{t,i,k}^w) | D_{t,i}^w, \sigma^{d-w} \sim \text{Normal}(\log(D_{t,i}^w), \sigma^{d-w})$

403 (Eq. 27) $\log(d_{t,i,k}^s) | D_{t,i}^s, \sigma^{d-s} \sim \text{Normal}(\log(D_{t,i}^s), \sigma^{d-s})$

404

405 Where σ^{d-w} and σ^{d-s} are the standard deviation parameters associated to the inter-site variations
 406 within a river section for any given year.

407 The electro-fishing data $A_{t,i,k}$ were observed conditional to the total density $d_{t,i,k}^{tot}$ following an
 408 observation process very similar to the one presented in Brun et al. (2011). This model
 409 incorporates a joint modelling of the two electro-fishing techniques, derived from Dauphin et al.
 410 (2009) and detailed in the supplementary material.

411

412 2.4 Bayesian inference

413

414 Statistical inference was conducted in the Bayesian framework. The same approach was used for
 415 the simulated data and the Allier River case study. Little-informative and independent prior

416 probability distributions were assigned to the model parameters (Table 1) to ensure that posterior
417 inferences would primarily reflect the information brought by the data. The only exception is the
418 slope of the Beverton-Holt density dependence relationship a^w . This relationship can be
419 described as the average number of fall juveniles produced by one adult Atlantic salmon in the
420 Allier River catchment when the spawner density is low. The prior used for this parameter
421 corresponds to a Beta distributed variable multiplied by 8000. This figure is a gross estimate of
422 the average fecundity per spawner in the Allier River (i.e. number of eggs after accounting for the
423 female:male sex-ratio), the Allier spawners being comprised mainly of large individuals having
424 spent two or three winters at sea. The majority of the large salmon are females (sex-ratio
425 fluctuating between 60 and 80%, Minster and Bomassi 1999; CNSS, 2014, unpublished data).
426 The survival of wild eggs to fall juveniles was more likely to be low (Aprahamian et al., 2003).
427 To reflect this, a $Beta(0.1,2.18)$ distribution was used, with a mean of 0.044 and probability
428 levels decreasing monotonically from 0 to 1. Priors were assigned on precisions τ instead of
429 standard deviations σ ($\tau = 1/\sigma^2$). A hierarchical structure was implemented for all the juvenile
430 salmon precisions (τ^{D-w} , τ^{d-w} , τ^{D-s} , τ^{d-s} , τ^{D-e} , τ^{d-e}) which were all independently drawn from a
431 Gamma distribution ($Gamma(\mu^\tau \times \beta^\tau, \beta^\tau)$, see Table 1 for description of the parameters and
432 their priors). The correlation factor ρ^D between the wild and stocked recruitment was given an
433 $Uniform(-1,1)$ prior distribution.

434

435 The joint posterior distribution of all the models unknowns (i.e. unobservable quantities and
436 observables in the case of missing data) was approximated using MCMC sampling (Gelman *et al.*
437 2003). All computations were carried out with the OpenBUGS software (version 3.2.2; Thomas
438 *et al.* 2006; Spiegelhalter *et al.* 2007) and R (version 3.1.2, www.r-project.com). To test for the

439 convergence of the MCMC sampling on all the model parameters, the Gelman-Rubin (Brooks
440 and Gelman 1998) diagnostics as implemented by OpenBUGS was used based on three chains
441 with contrasting starting points. These diagnostics indicated good mixing of the MCMC chains
442 after 10^6 iterations. One in every 100 iteration was retained to obtain a sample of 20,000 values.
443 The first 10,000 were discarded and the remaining 10,000 values were then used to approximate
444 posterior distributions of all the model unknowns. The fit of the generic model to the data in each
445 of the 3 scenarios tested was assessed by looking at the differences between the posterior mean of
446 total and relative density estimates and their true value and quantified using root mean square
447 error (RMSE, Table 3, Janssen and Heuberger, 1995). The case study model fit was assessed
448 using standardized Pearson residuals and χ^2 discrepancies (see supplementary material).

449

450

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451 3. Results

452

453 3.1 Simulation study

454

455 For all scenarios, the information contained in the data led to a significant update of the prior
456 distributions of all parameters governing the model. Overall, there was good agreement between
457 their posterior probability distributions and their true values. There were some differences within
458 and between scenarios about the precision and the accuracy of the estimates.

459 In the two stocking scenarios (constant and increasing), for almost all parameters in each
460 replicate the 95% posterior probability intervals encompassed the true values of the parameters
461 (248/280, the total 280 corresponds to the 20 replicates \times 7 parameters \times 2 scenarios, Fig. 3). No
462 systematic pattern of inaccuracy in the parameters estimates was revealed, except for those
463 controlling the inter-annual and inter-site variability of the stocking component: $\sigma^{D.s}$ and $\sigma^{d.s}$
464 which tended to be under- and over-estimated respectively. Relative to the no stocking scenario,
465 the slope of the stock recruitment relationship a^w had a similar uncertainty in the scenario with
466 increasing stocking and in the scenario with constant stocking (Fig. 3). The 95% posterior
467 probability intervals of the annual total juvenile densities D_t^{tot} encompassed the true value in the
468 vast majority of years, with no systematic pattern of inaccuracy (Table 2). The posterior medians
469 of D_t^T were comprised between 0.5 and 1.5 times the true value in 84% of the cases in the no
470 stocking scenario. In the scenarios with constant and increasing stocking this percentage was
471 89% and 82% respectively (Fig. 4a,b,d; Table 2).

472 The ability of the model to identify the wild vs. stocking component of the juvenile production
473 was assessed by considering the relative contribution of the wild component $D_t^r = D_t^w / D_t^T$ (Fig.
474 4c,e). The 95% posterior probability interval encompassed the true value in most of the years
475 cumulated over the replicated data sets and the years of each stocking scenario (92% and 89% of
476 D_t^r for the constant and increasing stocking scenarios respectively). For the two scenarios with
477 stocking, the medians of the posterior distributions of D_t^r (relative to the true value) fluctuated
478 within a range similar to D_t^T . In the constant stocking scenario, there was a 0.3 probability to
479 observe the medians of the posterior distributions of D_t^r to be lower or higher than 0.5 or 1.5
480 folds the true value (Table 2), versus a 0.15 probability in the increasing stocking scenario. In
481 both stocking scenario, extreme values could not be totally dismissed and there was a small
482 percentage (about 1%, Table 2) of the D_t^r medians that were at least 5 folds smaller or higher than
483 the true value. In the two stocking scenarios, there was some confusion between the wild and
484 stocking inter-annual and inter-site standard deviation components, but their identification was
485 improved under the increasing stocking scenario (Fig. 4). The RMSEs for D_t^T were smaller than
486 the RMSEs for D_t^r (Table 3) indicating a better estimation of the total densities than the relative
487 contribution.

488 [Figures 3 and 4 about here]

489 [Table 2 and 3 about here]

490

491 3.2 Case study

492

493 All the parameters of the model were significantly updated from their prior distributions (see
494 Table 1). χ^2 discrepancies and associated p-values for the model did not reveal inconsistencies
495 between the model and the data from the three river sections as all p-values are close to 0.5
496 (Table S3). The average survival of the eggs from the incubators until the first autumn was low
497 (5.9% on average, Table 1). Significant differences were found between the river sections
498 upstream and downstream from Langeac regarding the juvenile productivity ($P(\eta_1^D \leq 0) < 10^{-6}$;
499 Table 1). This was reflected in the slope and asymptote parameters of the Beverton-Holt function
500 (Fig. 5): the two river sections upstream from Langeac were on average two times more
501 productive than the river section downstream from Langeac. The average maximum juvenile
502 density downstream from Langeac was 0.079 juveniles.m⁻² while the average maximum juvenile
503 density was 0.171 juveniles.m⁻² in the river sections upstream from Langeac. During the years
504 with juvenile stocking, the percentage of the habitat used by wild juvenile salmon p_t^{Rmax}
505 fluctuated between 5% and 97%, reflecting the annual variance in terms of number of spawners
506 returning to each river section and number of juveniles stocked (Fig. 6).

507 Downstream from Langeac, when the number of spawners tended towards 0, one spawner
508 produced on average approximately 478 surviving juveniles the following fall compared with an
509 average of 1040 surviving juveniles in the section upstream from Langeac. The average slope at
510 the origin of the stocked juvenile Beverton-Holt relationship, i.e. the survival of stocked juvenile
511 at lower stocking intensity, was affected in a similar way: downstream from Langeac it the slope
512 at the origin averaged 0.438 versus 0.949 upstream from Langeac. The reduction factor reflecting
513 the effect of the number of wild juveniles on the slope at the origin of the stocked juveniles
514 Beverton-Holt relationship β_t^S was on average, 0.60, 0.47 and 0.75 for the Vichy-Langeac,
515 Langeac-Poutès and upstream of Poutès river sections respectively (Fig. 7). For the latter section

516 the stocked juvenile survival is increased until stocking stopped. In the two other river sections
517 the effect on the stocked juveniles' survival varied little over the time-series.

518 The various standard deviation parameters were estimated fairly precisely (CVs ranging from
519 0.046 to 0.205), the standard deviation associated with the inter-annual variations of the stocked
520 egg component at the river section scale σ^{D-e} was more uncertain (CV=0.409; see Discussion
521 section). The relative magnitude of the estimates show that the inter-annual variability of the
522 average juveniles densities of the wild component at the river section scale σ^{D-w} was the lowest,
523 whereas the between-sites variability of the stocked eggs component σ^{d-e} was the highest. The
524 two standard deviations associated with the stocked juveniles' component were of similar
525 magnitude. Additionally, there was a positive correlation between the variance of the wild and
526 stocked juvenile recruitment ($\rho^D = 0.43$).

527

528 [Figures 6 and 7 about here]

529

530 3.2.2. Wild and stocked juveniles densities

531 The model allowed estimating the annual total densities for each river section, and for each of the
532 three components when relevant (Fig. 8), and calculations of their relative contributions (Fig. 9).
533 Note there was no stocked eggs component upstream from Poutès because no egg incubators
534 were used in this river section throughout the time-series considered.

535 The total juvenile density, its components and their relative contribution were often uncertain.
536 This is not surprising given the lack of reliable data for identifying the origin of the juveniles
537 electro-fished in the autumn. However, it was possible to identify interesting patterns of
538 variations over time and some important differences between the three river sections. For
539 example, the density estimates showed that:

540 (i) in the two river sections where eggs were stocked, their contribution to the total juvenile
541 density was low (Figs 9c and 9f).

542 (ii) the contribution of stocked juveniles increased significantly during the mid-1990's (Figs
543 9b, 9e and 9h), coincident with a marked augmentation of the releases (Figs 2b and 2c).
544 During the first part of the time series, juvenile salmon production was almost entirely
545 from wild reproduction.

546 (iii) the highest densities of the wild component were obtained in the intermediate river
547 section (Langeac-Poutès); the lowest densities were observed in the lower section (Vichy-
548 Langeac, Fig. 8).

549 (iv) downstream from Poutès (sections 1 and 2), wild juvenile densities appeared to be lower,
550 on average, following the low values observed in the mid-1990's (Fig. 8).

551 (v) total juvenile density tended to increase over the last five years of the time-series in the
552 lower river section (Vichy-Langeac) whereas the total juvenile density decreased in the
553 two other river sections. This recent increase in the total juvenile salmon density in the
554 lower section reflected an increased contribution of stocked juveniles following from the
555 augmentation of the numbers of juveniles released (Fig. 2). Our model assumed that the

556 carrying capacity of the habitat was shared by the wild and stocked juvenile salmon
557 components. This was reflected by the annual variation of the proportion of the carrying
558 capacity used by the wild juveniles p^{Rmax} (Fig. 8). In the downstream section of the
559 Allier, this proportion has been stable from the mid-1990's to the present. In the river
560 section upstream of Poutès, the proportion of wild juveniles increased as the stocking
561 effort diminished in this part of the catchment.

562

563

[Table 1 about here]

564

565

[Figure 5 about here]

566

567

[Figure 8 and 9 about here]

568

569 4. Discussion

570

571 Enhancement programs are often poorly monitored and consequently, it is difficult to assess their
572 impact (Waples et al. 2003). Ideally, the evaluation of the contribution of stocked fish to the
573 population would require using marked fish. Unfortunately, as illustrated by our Allier River case
574 study, this information is often not available. The proposed generic model and its hierarchical
575 spatio-temporal structure, coupled with the explicit consideration of the components contributing
576 to the juvenile salmon production attempts to separate them despite the absence identification
577 data. We evaluated the performance of our generic model using simulated data, due to lengthy
578 computation time, only 20 replicates were run for each scenario tested (absence of stocking,
579 constant stocking and increasing stocking). In the three scenarios we tested, we found that the
580 different parameters governing the model were fairly accurately estimated with varying levels of
581 uncertainty. The most uncertain estimations were for the slope a^w and asymptote R_{max} of the
582 Beverton and Holt relationship but these are notoriously challenging parameters to estimate due
583 to the high variability of recruitment (Walters and Korman, 2001). More importantly, with
584 regards to our primary objective, i.e. the assessment of wild vs stocking components, the model
585 does allow for separate estimates. Although these estimations can be imprecise (depending on the
586 scenario, the data set in a given scenario, and the year in a given data set), it was not misleading
587 as the 95% posterior probability intervals, in most instances, comprise the true values of the
588 density components (Fig. 3-4, Table 2).

589 The generic model was modified to account for the specificity of our case study of the Atlantic
590 salmon population of the Allier River. This allowed to take advantage of the data sets available

591 and the, rather unintentional, experimental design they were associated to. Consequently, despite
592 the absence of distinguishing marks, the total juvenile densities could be separated into three
593 components (wild and stocked juveniles, stocked eggs) and the relative contribution of each was
594 assessed by year and river section. The biological knowledge incorporated in the model regarding
595 wild recruitment processes and stocked juvenile survival likely contributed to the model's
596 performance, although it is difficult to appraise precisely the associated benefits.

597 This biological knowledge translated into different assumptions introduced in our model. Some
598 of them reflected local information specific to the Allier, e.g. the spatial heterogeneity in the
599 quality of the habitat for salmon juvenile recruitment (below and above Langeac). We also relied
600 on a generic formulation of the wild recruitment, the survival of the stocked fish and their
601 interactions, which would balance realism and parsimony. For instance, we used a Beverton-Holt
602 relationship for the density-dependent processes involved in the wild recruitment and in the
603 survival of the stocked juveniles, as this seems to be the option of choice for stock-recruitment
604 modelling in general (Walters and Martell 2004), and for Atlantic salmon in particular
605 (Michielsens and McAllister 2004). It is worth noting that the rather informative prior used for
606 the slope at the origin of the Beverton-Holt curve was significantly updated a posteriori by the
607 data, so that its somewhat arbitrary definition did not strongly influence the results. Regarding the
608 interactions between the wild and stocked juveniles, the current literature tends to indicate that
609 there is a prior residency advantage to the wild juveniles who have been holding their territories
610 for several months when stocked juveniles are released (Henderson and Letcher 2003; Metcalfe
611 et al. 2003; Kvingedal and Einum 2011; Costas et al. 2013). Additionally, it has been documented
612 that stocked juveniles have lower survival due to the differences between their rearing
613 environment (hatchery) and where they are stocked (Einum and Fleming 2001), thus reinforcing

614 the idea that they do not compete efficiently with their wild counterparts. However, the
615 interaction between wild and stocked is likely to be case specific depending on how the stocked
616 fish are reared and when they are released. To accommodate this variability we assumed no bias
617 in the reciprocal interactions between the wild and stoked components in the sharing of the
618 available carrying capacity. Although our hypotheses are open to discussion, there were no
619 indications of their inadequacy as applied to the data in the Allier River case study. For each
620 component and river section, both the yearly and site specific density residuals were scrutinized
621 by checking they were independent and with 0 means. These checks (results not shown) revealed
622 no inconsistency between the model and the data. Regardless of the specificities of the biological
623 hypotheses used for our case study in the Allier River, the important point was that the flexibility
624 of the generic model proposed, combined with its implementation by means of MCMC sampling
625 (with OpenBUGS), allows one easily modify these hypotheses, if needed.

626 The modelling of the contribution of the egg incubators to the total juvenile density is much
627 cruder than for the other two components. In the model, the juvenile salmon emerging from the
628 egg incubators were considered supplementary production that had no significant influence on
629 total population abundance and was not influenced by the other production components through
630 density dependent processes. This modelling choice was dictated mostly by two considerations.
631 First, the paucity of data precluded the use of more refined modelling involving more unknown
632 parameters without entering into problems for their identification when proceeding to their
633 estimation. Indeed, there was rarely an electro-fishing site in proximity to an egg incubator each
634 year (over the 37 years time-series only 24 electro-fishing surveys occurred nearby an egg
635 incubator). Consequently, there was little information to appraise the average densities at the
636 river section scale resulting from the incubators and this was reflected in the poor estimation of

637 their inter-annual variability (σ^{D-e} , Table 1). Second, even more refined modelling would not
638 have changed the overall assessment that the contribution of the incubators in a river section was
639 low. Indeed, this result is essentially due to the assumption (justified in the Materials and
640 Methods section) that the area influenced by the incubators was small in comparison to the total
641 surface area available for juvenile production. In addition, the electro-fishing operations available
642 to assess the contribution of the incubators revealed contrasting results in terms of local densities
643 rather than, suggesting a systematic and strong effect of the egg stocking. Finally, it is worth
644 noting that, the contribution of the egg incubators, although low, was most likely overestimated
645 because (i) the area influenced by an incubator was probably overvalued (see Materials and
646 Methods section) and (ii) the survival of the juveniles issuing from the incubators was not
647 assumed to be constrained by any negative density dependent feedback.

648 The potential of the proposed modelling approach was demonstrated by the retrospective analysis
649 of the juvenile salmon densities in three river sections of the Allier River using an extensive
650 electro-fishing data set collected over a 37 year time-series. The results are valuable for fisheries
651 management. At the general level, they model clearly showed the significant contribution of the
652 spring stocking of juvenile stages to the total juvenile salmon production in autumn, from the
653 mid-1990' when the number of juveniles stocked annually increased markedly (Fig. 2), at the
654 same time, reproduction of wild fish continued to provide an important contribution to the total
655 production of Atlantic salmon in the river (Figs 9a, 9d and 9g).

656

657 Whereas the inability to identify the contribution of stocking to recruitment in fish populations is
658 a common situation, our study and proposed modelling approach yielded encouraging results
659 from a management advice perspective. It showed that long term abundance data can be useful to

33

660 retrospectively investigate the impact of stocking programs despite deficiencies in monitoring.
661 Experiments using in situ marked stocked fish would still be most valuable to validate our
662 approach.

663

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1 Figure captions

2

3 Figure 1: The Loire and the Allier river and the location of the three Atlantic salmon adults counting stations at Vichy, Langeac and
4 Poutès (CARTHAGE Database).

5

6 Figure 2: Number of electric fishing sites sampled annually (a), total number of eggs (b) and 0+ juveniles (c) stocked annually in each
7 of the three sections of the Allier river. In (b) filled squares indicate the successive removal technique and filled dots indicate the 5
8 minutes sampling technique.

9

10 Figure 3: Posterior distributions of the main parameters of the generic model for each data simulation scenarios (no stocking, constant
11 stocking and increasing stocking) and for 20 replicated data sets per scenario. The median (black dot), the 2.5th -97.5th posterior
12 distribution interval (thin black segment) and 25th-75th posterior distribution interval (thick black segment) are represented. The grey
13 dashed lines are the actual values of these parameters.

14 Figure 4: Posterior distribution of the ratios estimated/true value of the total densities D^T (a , b and d) and of the proportion of wild
15 over total densities $D^{rel} = D^w/D^T$ (c and e) for the 10 replicated data sets for the 3 data simulation scenarios (no stocking, constant
16 stocking and increasing stocking). Note the use of a Log scale for the y axis. The dark thick lines are the medians and the light dashed
17 lines are the 2.5th and 97.5th percentiles of each replicates. The horizontal red dashed line is the reference line (estimated = true). The
18 vertical black dashed line in figure e and f indicates the beginning of stocking in the increasing stocking scenario.

19

20

21

22 Figure 5: Average density dependence relationships between (a) the potential spawners density of a given year t and the wild 0+
23 juvenile density the following year $t+1$ and between (b) the juvenile stocking density in spring and the stocked 0+ juvenile density in
24 the fall. Spatial differences between downstream and upstream from Langeac are represented by two grey curves (dark and light)
25 corresponding to the average relationship downstream and upstream from Langeac. Plain grey dots and squares correspond to annual
26 estimates (posterior median) for the three river sections. The dashed line in panel (b) represent 100% survival. All densities are in fish
27 per square meter of favorable habitat.

28

29 Figure 6: Posterior distributions of the proportion of R_{max} used by the wild component $p^{R_{max}}$ for each year by river section (Vichy-
30 Langeac *a*, Langeac-Poutès *b* and; upstream Poutès *c*). The grey dots indicate years with no stocking. Boxplots indicate 2.5th, 25th, 50th
31 (median), 75th and 97.5th percentiles. The vertical dashed line indicates the removal of Poutès dam.

32

33 Figure 7: Posterior distributions of the reduction factor on the slope at the origin of the Beverton-Holt relationship for stocked 0+ β_t^s
34 for each year by river section (Vichy-Langeac *a*, Langeac-Poutès *b* and upstream Poutès *c*). Boxplots indicate 2.5th, 25th, 50th (median),
35 75th and 97.5th percentiles. The vertical dashed line indicates the removal of Poutès dam.

36

37 Figure 8: Posterior distributions of $D_{t,i}^T$ (panels *a*, *e* and *i*) and its 3 components $D_{t,i}^W$ (panels *b*, *f* and *j*), $D_{t,i}^S$ (panels *c*, *g* and *k*), and $D_{t,i}^E$
38 (panels *d* and *h*) for each year by river sections (Vichy-Langeac, Langeac-Poutès and upstream Poutès). Dark grey indicate years with
39 stocking and light grey years with no stocking. Boxplots indicate 2.5th, 25th, 50th (median), 75th and 97.5th percentiles. The vertical
40 dashed line indicates the removal of Poutès dam.

41

42 Figure 9: Posterior distributions of the relative contributions of each components (wild, stocked 0+ and stocked eggs) of the 0+
43 juvenile total densities for each year by river section (Vichy-Langeac *a*, *b*, *c*; Langeac-Poutès *d*, *e*, *f* and; upstream Poutès, *g*, *h*). Dark

44 grey indicate years with stocking and light grey years with no stocking. Boxplots indicate 2.5th, 25th, 50th (median), 75th and 97.5th
45 percentiles. The vertical dashed line indicates the removal of Poutès dam.

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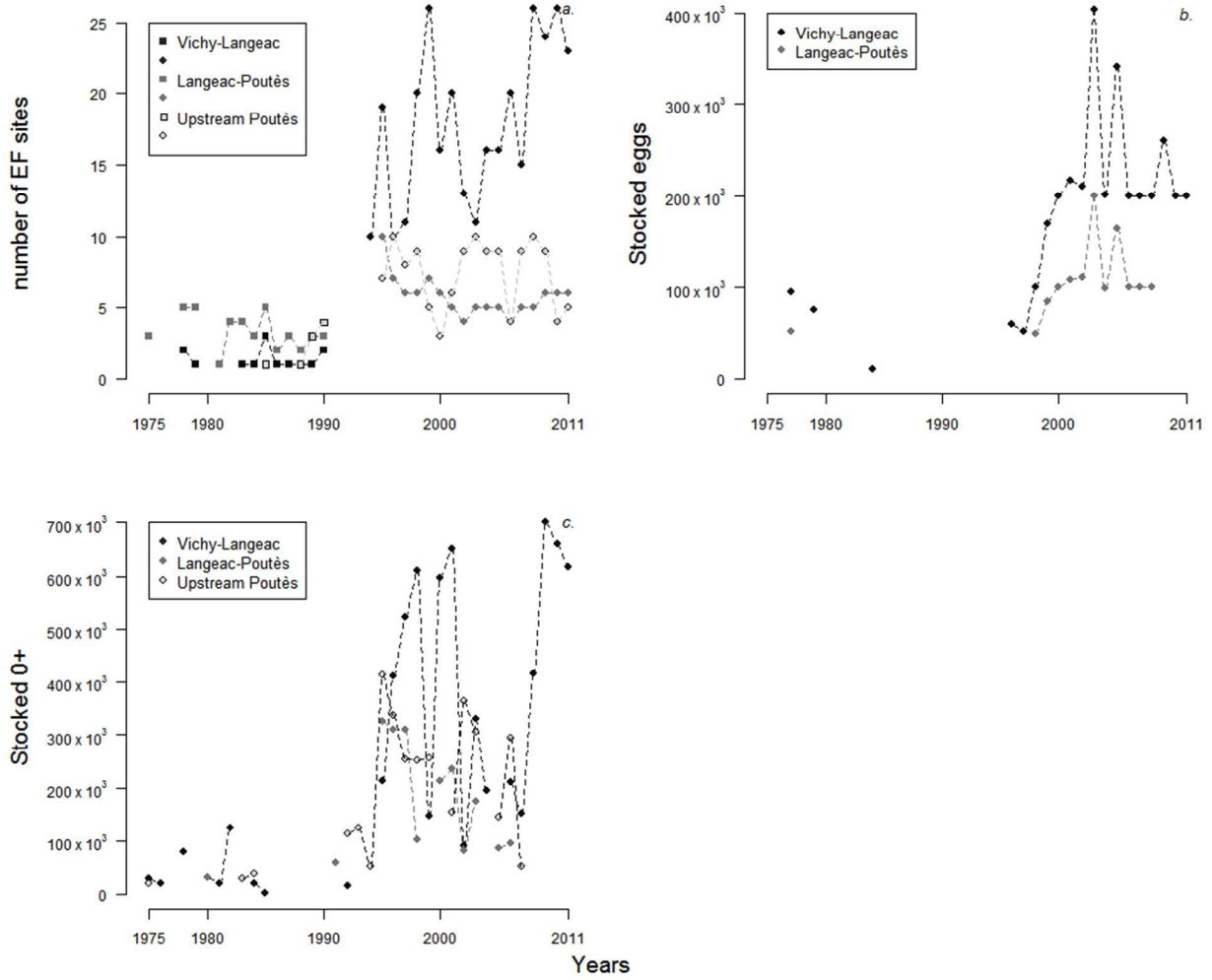


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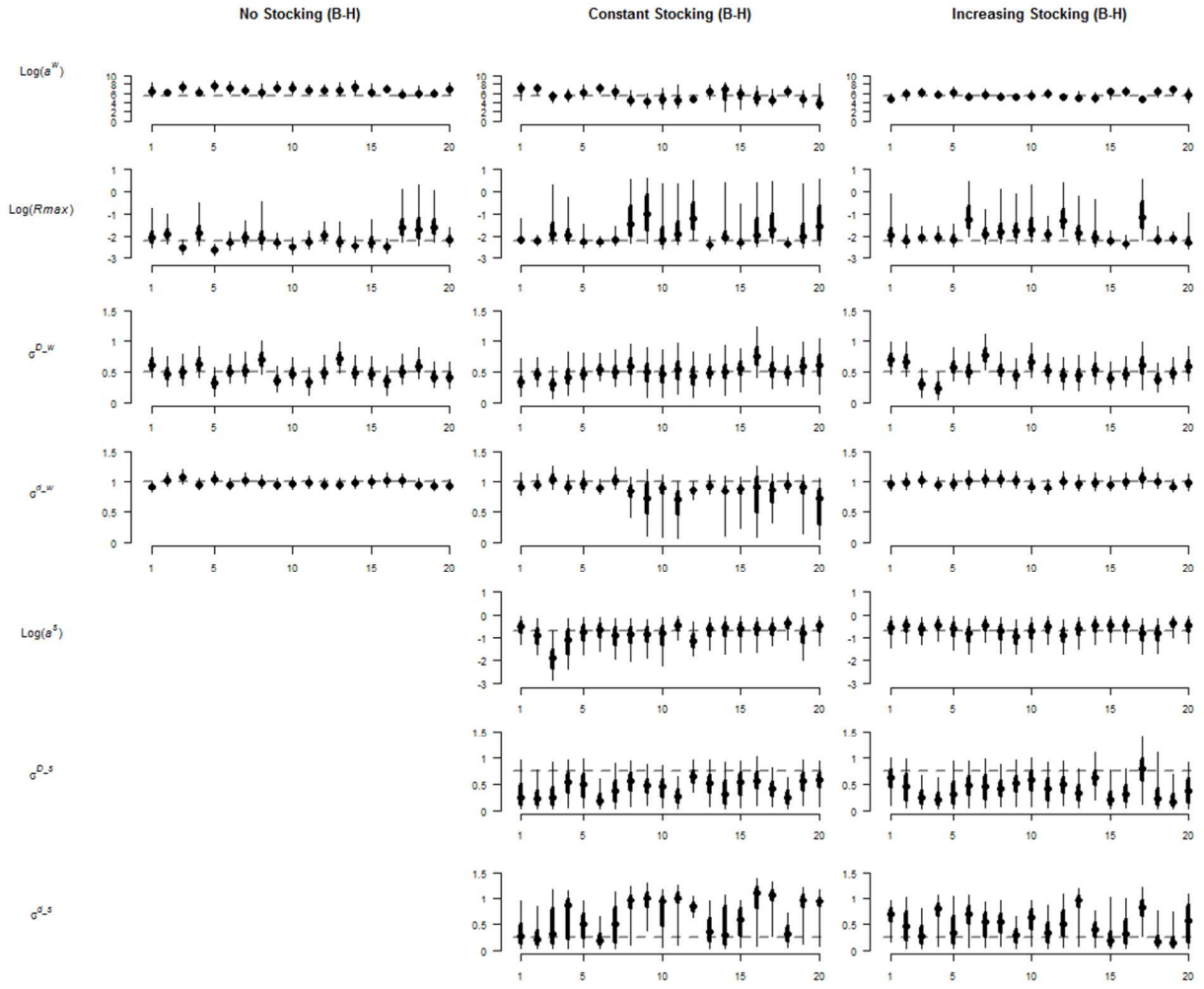
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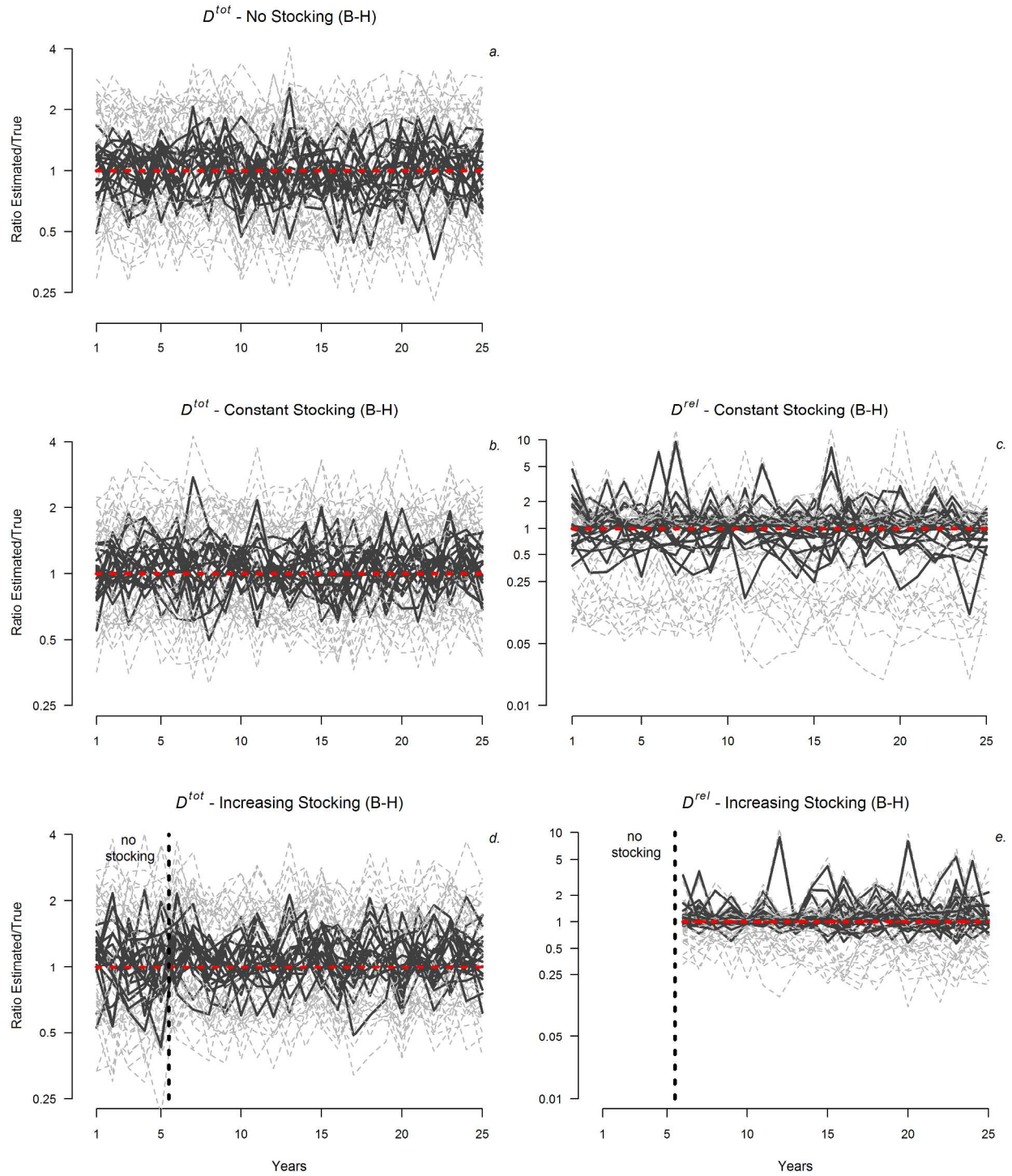
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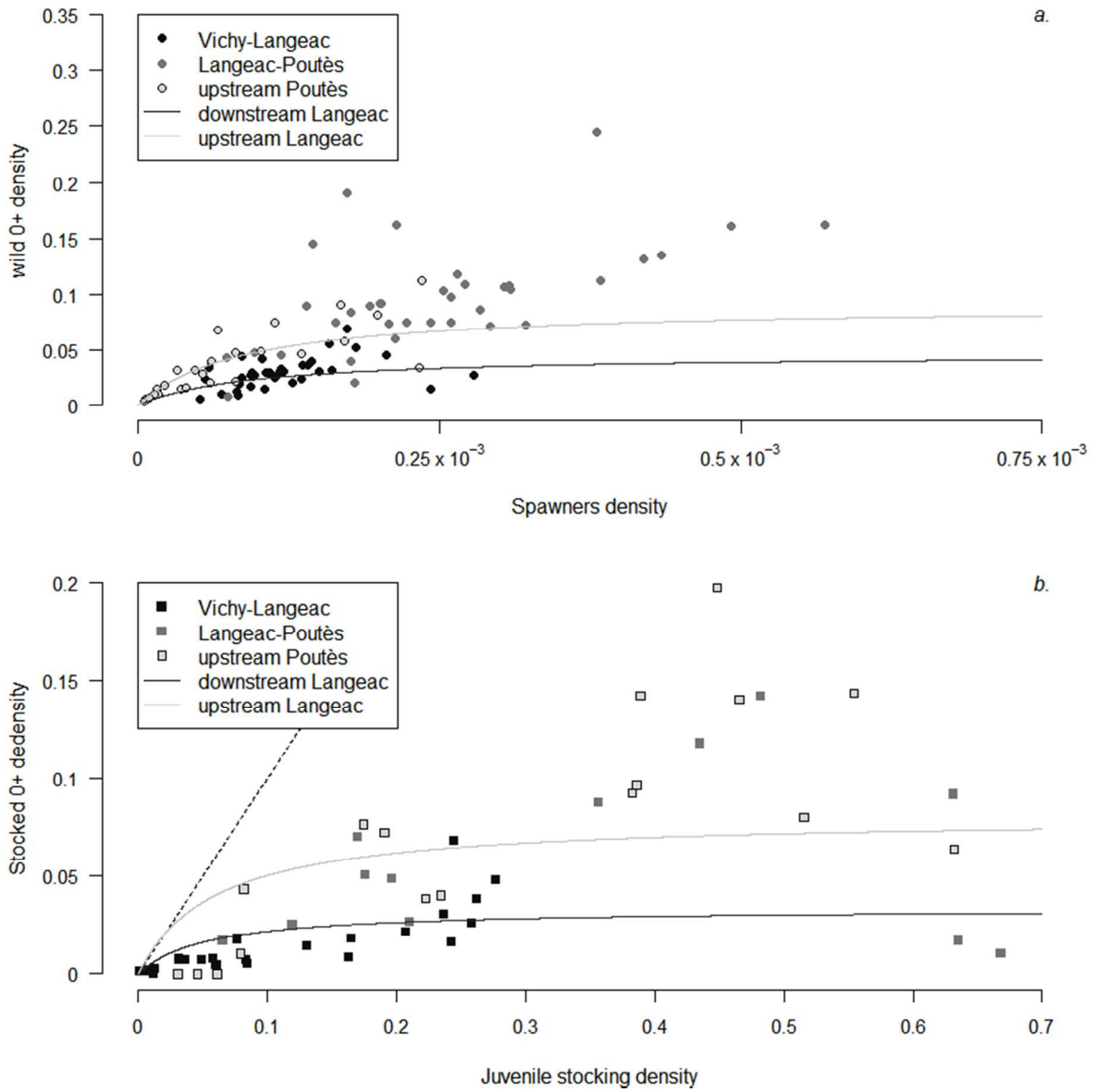


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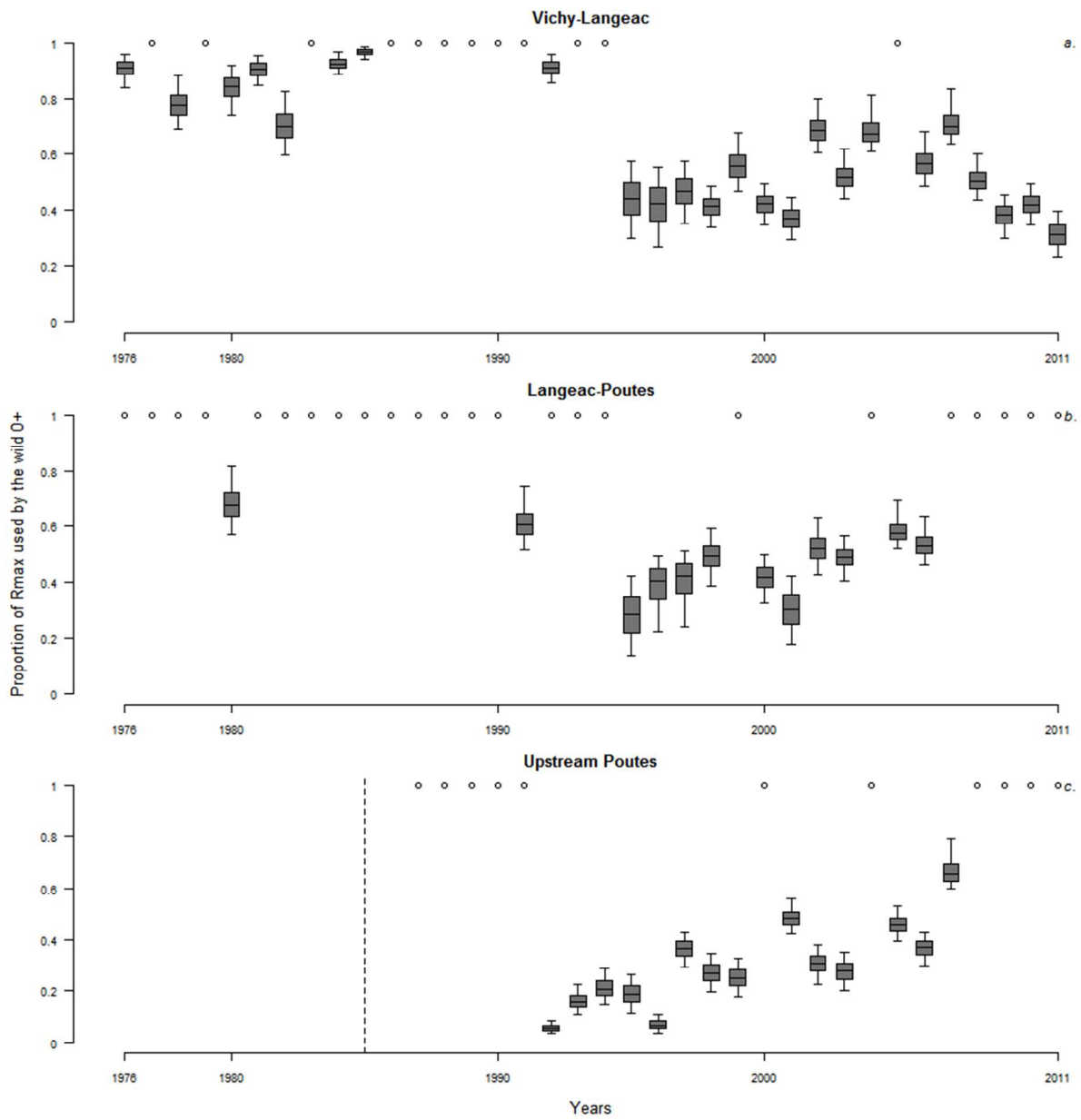
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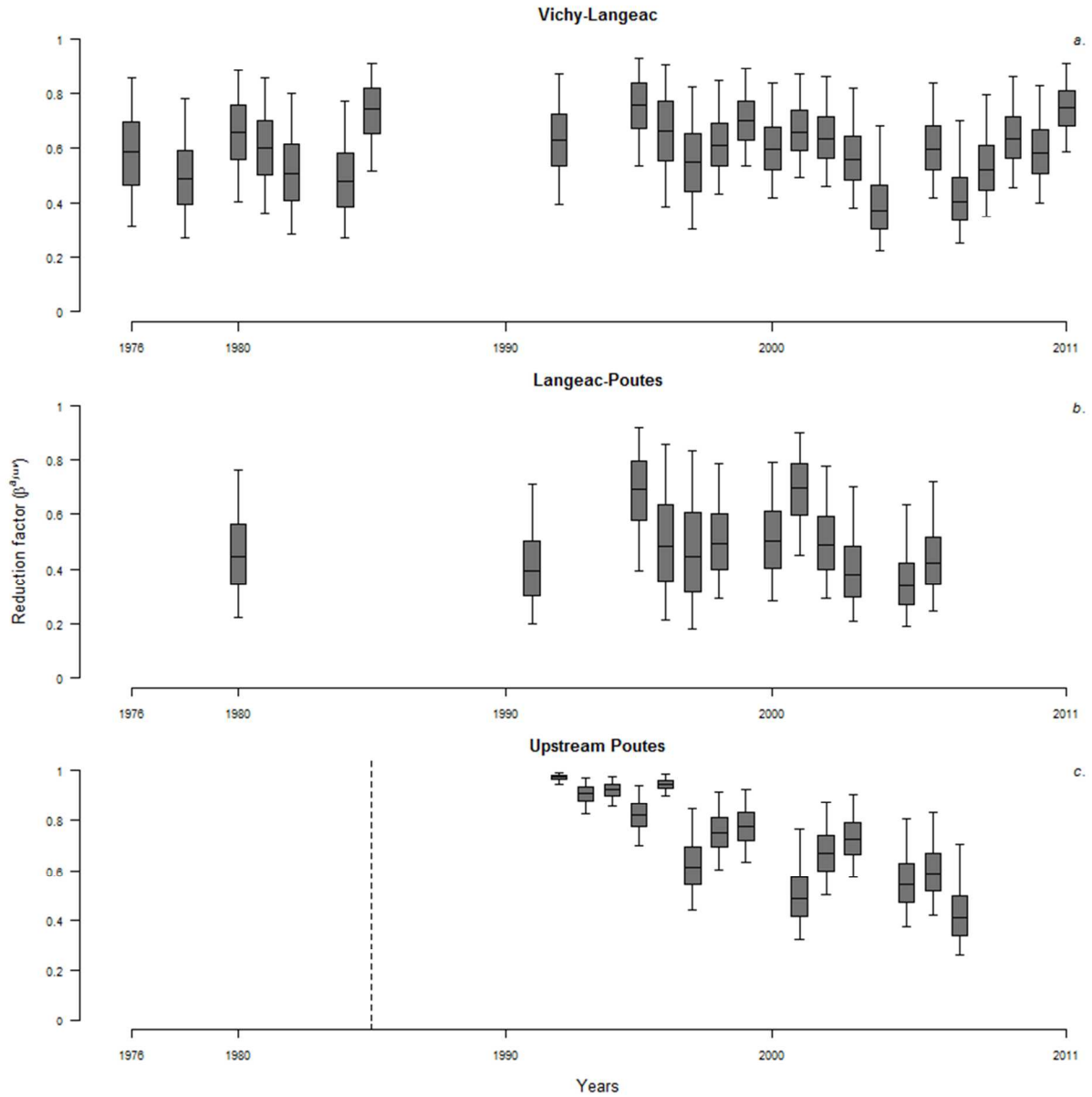
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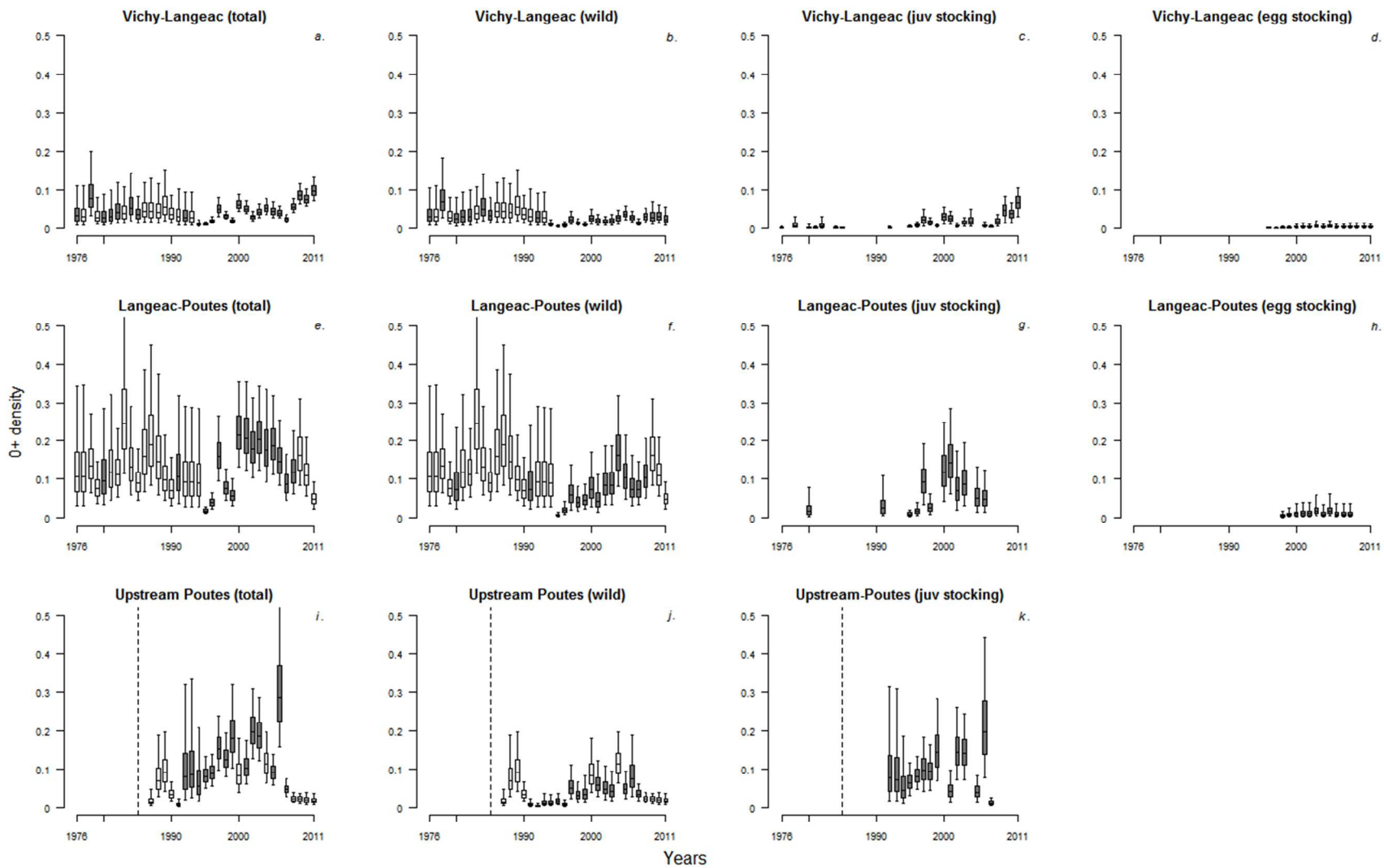


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82 Fig. 6

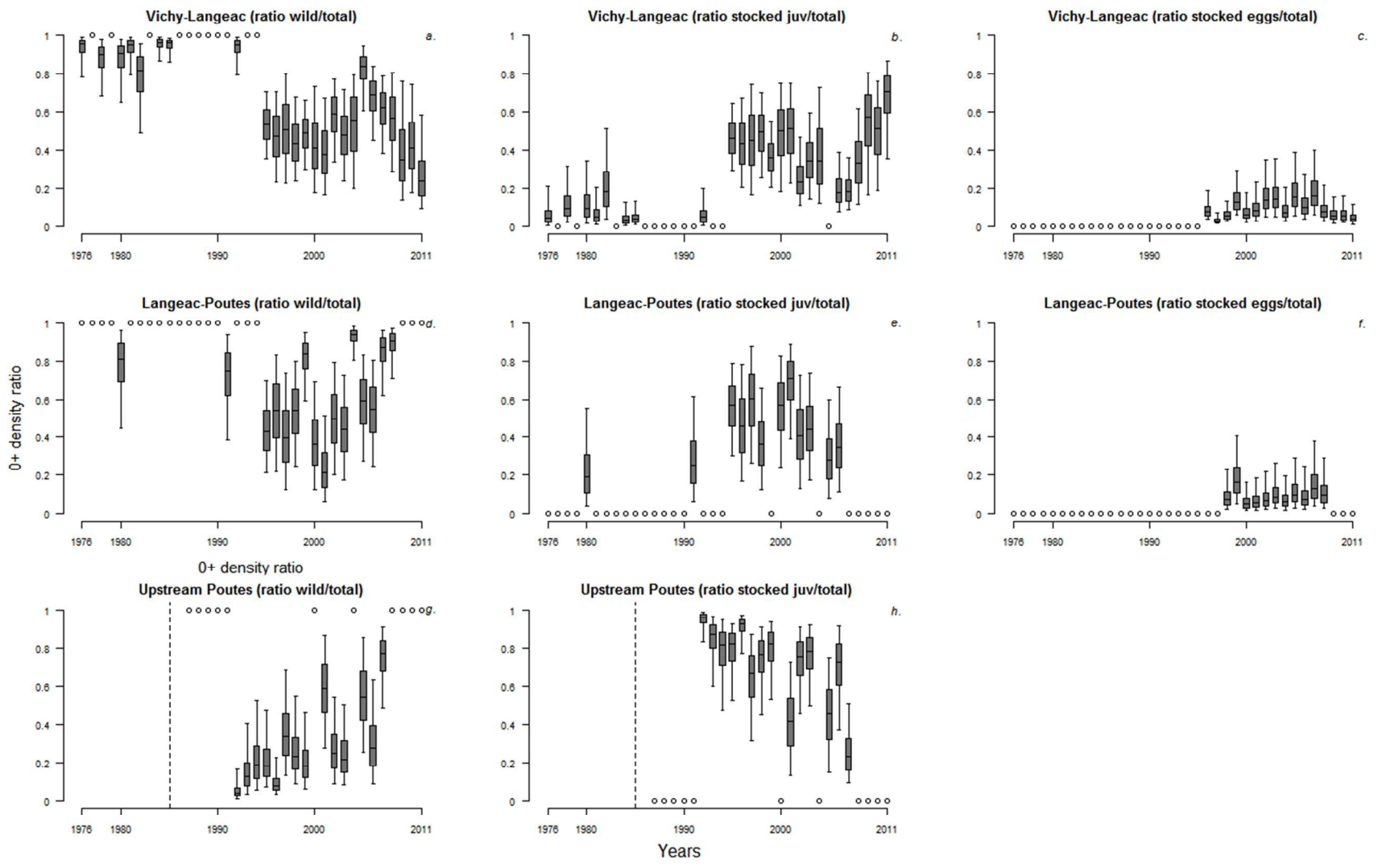


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87 Fig. 8



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Table .1: Prior distributions of the parameters of the model and summary statistics of their associated posterior distribution for the Allier case study (sd: standard deviation). The normal distribution are parameterized with mean and precision. The Gamma distributions are parameterized with shape and inverse-scale.

Parameters	Description	Value used to simulate data	Prior			Posterior						
			Distribution	Mean	sd	Mean	sd	2.5%	25%	50%	75%	97.5%
s^e	Stocked eggs survival parameter	-	$Beta(2,2)$	0.5	0.224	0.0594	0.0325	0.0288	0.0418	0.0519	0.0667	0.136
$\alpha^w/8000$	Average slope of the wild 0+ density dependence relationship	0.031	$Beta(0.1,2.18)$	0.044	0.113	0.0920	0.0295	0.0459	0.0716	0.0882	0.108	0.161
α^s	Average slope of the stocked 0+ density dependence relationship	0.5	$Beta(2,2)$	0.5	0.224	0.631	0.196	0.205	0.497	0.652	0.784	0.940
$Rmax$	Asymptote of the density dependence relationship	0.111	$Unif(0,2)$	1	0.577	0.195	0.148	0.0807	0.100	0.116	0.138	0.403
η_1	Spatial effect on 0+ density dependence relationship for the Vichy Langeac section	-	$Normal(0,0.01)$	0	10	-0.382	0.0985	-0.572	-0.447	-0.383	-0.317	-0.187
ρ^D	Correlation factor between 0+ wild and stocking recruitment		$Unif(-1,1)$	0	0.577	0.429	0.294	-0.171	0.224	0.446	0.650	0.933
μ^τ	Average precision		$Gamma(0.01,0.01)$	1	10	4.09	4.88	0.851	1.55	2.36	4.32	19.5
β^τ	Average inverse-scale of the precisions distribution		$Gamma(0.01,0.01)$	1	10	0.581	0.659	0.0163	0.130	0.362	0.791	2.40

Table 2: Probabilities to observe the 95% posterior distribution of estimated D^T and D^r encompassing their true values and probabilities to observe the medians of estimated D^T and D^r within an arbitrary interval of their true values times a multiplicative factor in 3 simulation study scenarios (no stocking, constant stocking and increasing stocking). Probabilities are calculated over 500 values (25 years \times 20 replicates) except for D^r in the increasing stocking scenario where percentages are calculated over 400 values (there is no stocking during the first 5 years: 20 years \times 20 replicates).

	No stocking	Constant stocking		Increasing stocking	
	D^T	D^T	D^r	D^T	D^r
95% posterior distribution overlapping the true value	0.94	0.93	0.92	0.93	0.89
Median inside of the 0.66 and 1.5 folds the true value interval	0.84	0.89	0.70	0.82	0.85
Median inside of the 0.5 and 2 folds the true value interval	0.98	0.99	0.86	0.98	0.94
Median inside of the 0.2 and 5 folds the true value interval	1	1	0.99	1	0.99

Table 3: Mean and standard deviation (sd) of root mean square error (RMSE) computed over 20 replicates for total densities (D^T) and relative contribution of the wild juveniles (D^r)

RMSE (mean \pm sd)	No stocking	Constant stocking	Increasing stocking
$\text{Log}(D^T)$	0.292 ± 0.037	0.253 ± 0.041	0.278 ± 0.035
$\text{Logit}(D^r / D^T)$	-	1.186 ± 0.277	1.052 ± 0.228

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1 Supplementary material

2 Electro-fishing calibration relationship

3

4 1. Introduction

5

6 To evaluate 0+ juvenile densities of Atlantic salmon, two different types of electro-fishing
7 techniques have been used in the Allier catchment throughout the time series considered in
8 this project (1975 to 2011). From 1975 to 1990, a successive removal sampling technique was
9 used: 2 electric fishing pass were carried out with no time limit. From 1994 to 2011 the
10 successive removal method was replaced by a single timed pass (fixed duration of 5 minutes)
11 sampling technique.

12

13 In order to be able to use the two data sets together to estimate local densities throughout the
14 time series, in 1997, 2000 and 2001, 9 sites (Fig. S1) were sampled using both techniques in
15 order to build a calibration relationship (Crozier and Kennedy, 1994). A 5 minutes pass was
16 carried out first and followed by 2 removal passes. In addition, the area of the site was
17 measured and fish collected had their lengths measured.

18

19 To estimate the parameters of this relationship a model developed by Dauphin et al. (2009) was
20 slightly modified to fit to the data available.

21

22 2. Model

23

24 All sites were assumed to be exchangeable and for every site sampled, the 0+ juvenile density
25 d_i was assumed to follow a Gamma distribution with a common mean d^{moy} and inverse scale
26 parameter β^d .

27

28 (Eq. S1)
$$d_i | d^{moy}, \beta^d \sim \text{Gamma}(d^{moy} \times \beta^d, \beta^d)$$

29

30 Each site was first sampled using the 5 minutes index of abundance (IA) A_i technique. The IA A_i
31 is assumed to follow a Negative Binomial distribution:

32

33 (Eq. S2)
$$A_i | \lambda_i^A, \varphi \sim \text{Negative Binomial}(\lambda_i^A \times \varphi, \varphi)$$

34

35 Where φ is the inverse scale parameter and λ_i^A is the mean of the distribution which is
36 deterministically linked to the density d_i :

37

38 (Eq. S3)
$$\lambda_i^A = \kappa \times d_i$$

39 Where κ is a factor of proportionality between the IA and the density d_i . The 5 minutes sample
40 was followed by two successive removal fishing pass, the remaining 0+ juveniles in the site is:

41

42 (Eq. S4)
$$n_i^{tot} = N_i^{tot} - A_i$$

43

44 Where N_i^{tot} is the total number of fish present in the site before any sampling occurred. The
45 total number of fish N_i^{tot} is directly related to the 0+ juvenile density and is assumed to follow a
46 Poisson distribution.

47

48 (Eq. S5)
$$N_i^{tot} | \lambda_i^N \sim \text{Poisson}(\lambda_i^N)$$

49

50 Where λ_i^N is calculated as the product of the site's surface S_i and the 0+ juvenile density d_i

51

52 (Eq. S6)
$$\lambda_i^N = S_i \times d_i$$

53 The number of 0+ juvenile caught during the first successive removal pass C_i^1 is assumed to
54 follow a Binomial distribution

55

56 (Eq. S7)
$$C_i^1 | p_i, n_i^{tot} \sim \text{Binomial}(p_i, n_i^{tot})$$

57

58 Where n_i^{tot} is the number of fish remaining after the 5 minutes timed pass and p_i is the
59 probability of capturing 0+ juveniles at site i . The number of fish remaining after the first
60 removal pass is:

61

62 (Eq. S8)
$$N_i^1 = n_i^{tot} - C_i^1$$

63

64 Like the first removal pass, the number of 0+ juvenile caught during the second successive
65 removal pass C_i^2 is assumed to follow a Binomial distribution:

66

67 (Eq. S9)
$$C_i^2 | p_i, N_i^1 \sim \text{Binomial}(p_i, N_i^1)$$

68

69 In our calibration model, the probability of capturing 0+ juvenile is assumed to be the same
70 during the two successive removal passes. The probabilities of capture each site p_i were
71 assumed to be exchangeable and to follow a normal distribution (logit scale):

72

73 (Eq. S10)
$$\text{Logit}(p_i) | \mu^p, \sigma^p \sim \text{Normal}(\text{Logit}(\mu^p), \sigma^p)$$

74 Where μ^p is the mean probability of capturing 0+ juveniles and σ^p the standard deviation (logit
75 scale).

76 The structure of conditional dependency of the relations described in equations S1-10 can be
77 graphically summarized in a Directed Acyclic Graph (DAG) (Fig. S2).

78

79 All parameters of the model were given little-informative and independent prior distributions
80 (Table S1) in order to obtain posterior inferences reflecting the information brought by the
81 data. The full data set used in this calibration model can be found in Table S2. The joint
82 posterior distribution of all unknowns (i.e. parameters and latent variables) conditionally on all
83 the observed data was approximated using MCMC sampling. All computations were carried out
84 with the OpenBUGs software (version 3.2.1). In order to test the convergence of the MCMC
85 sampling, three chains with contrasted starting points were used. The Gelman-Rubin statistic as
86 calculated in OpenBUGs indicated good mixing of the MCMC chains after 2.10^6 iterations. An
87 additional sample of 8000 values (8.10^6 iterations, but only retaining one out a hundred) was
88 used to provide estimates of the joint posterior distributions of all parameters.

89

90 3. Results & Discussion

91

92 All posterior distributions of the model parameters revealed a significant updating from the
93 data (Table S1). The 9 sites sampled for this calibration exercise presented contrasted densities
94 ranging from 0.052 to 0.52 0+ salmon juvenile per square meter (Fig. S3). The average
95 probability of capturing a 0+ juvenile over all sites μ^p is 0.50 but with important variations
96 across sites ($\sigma^p = 1.09$, p_i ranging from 0.17 to 0.78).

97 On Figure S3, the 5 minutes IA to density relationship average relationship is represented
98 alongside with the density estimates of the 9 calibration sites. The relationship is extended to
99 IAs values up to 300 which are the maximum values observed in the Allier catchment over the
100 last 30 years. It is important to notice that no calibration sites presented an IA higher than 159
101 and therefore the relationship is more speculative for IAs above this value. However, the 9 sites
102 sampled for this calibration exercise present contrasted density over the mainly encountered
103 range of IAs in the Allier catchment making this model a good tool to provide 0+ salmon
104 juvenile density estimates based on the 5 minutes IAs.

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111 Table S1: Prior distributions of the main parameters of the model ($\varepsilon = 10^{-3}$) and their
 112 associated posterior distribution.

parameters	Prior distribution	Posterior distribution						
		mean	sd	2.5 th	25 th	median	75 th	97.5 th
d^{moy}	$Gamma(\varepsilon, \varepsilon)$	0.325	0.262	0.177	0.248	0.296	0.360	0.632
β^d	$Gamma(\varepsilon, \varepsilon)$	6.48	3.67	1.25	3.79	5.86	8.53	15.3
κ	$1/Gamma(\varepsilon, \varepsilon)$	274	16.5	243	262	273	285	307
μ^p	$Inv. Logit(Normal(0, \varepsilon))$	0.499	0.096	0.305	0.438	0.500	0.561	0.690
σ^p	$Uniform(0,10)$	1.09	0.353	0.624	0.850	1.02	1.25	1.99

113

114 Table S2: Summary of data available in the 9 sites used for the calibration relationship:
 115 5minutes index of abundance, 0+ caught during the first and second removal pass and surface
 116 of the site.

Site	A_i	C_i^1	C_i^2	S_i
Vabres	52	222	68	1210
Pontgibert radier	131	83	34	464
St-Arcons aval pont	159	296	60	751.2
St-julien des Chazes chapelle	120	221	132	1134.3
La Vialette camping	61	140	45	828
Truchon	15	50	21	1854
Monistrol camping	82	136	121	2880
Chambon de Blassac RD	21	21	14	752
Lavoûte-Chilhac camping	21	46	31	1192.5

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122 Figure S1: Partial map of the Allier catchment. The 9 sites sampled for the calibration
123 relationship are indicated by a plain dot.

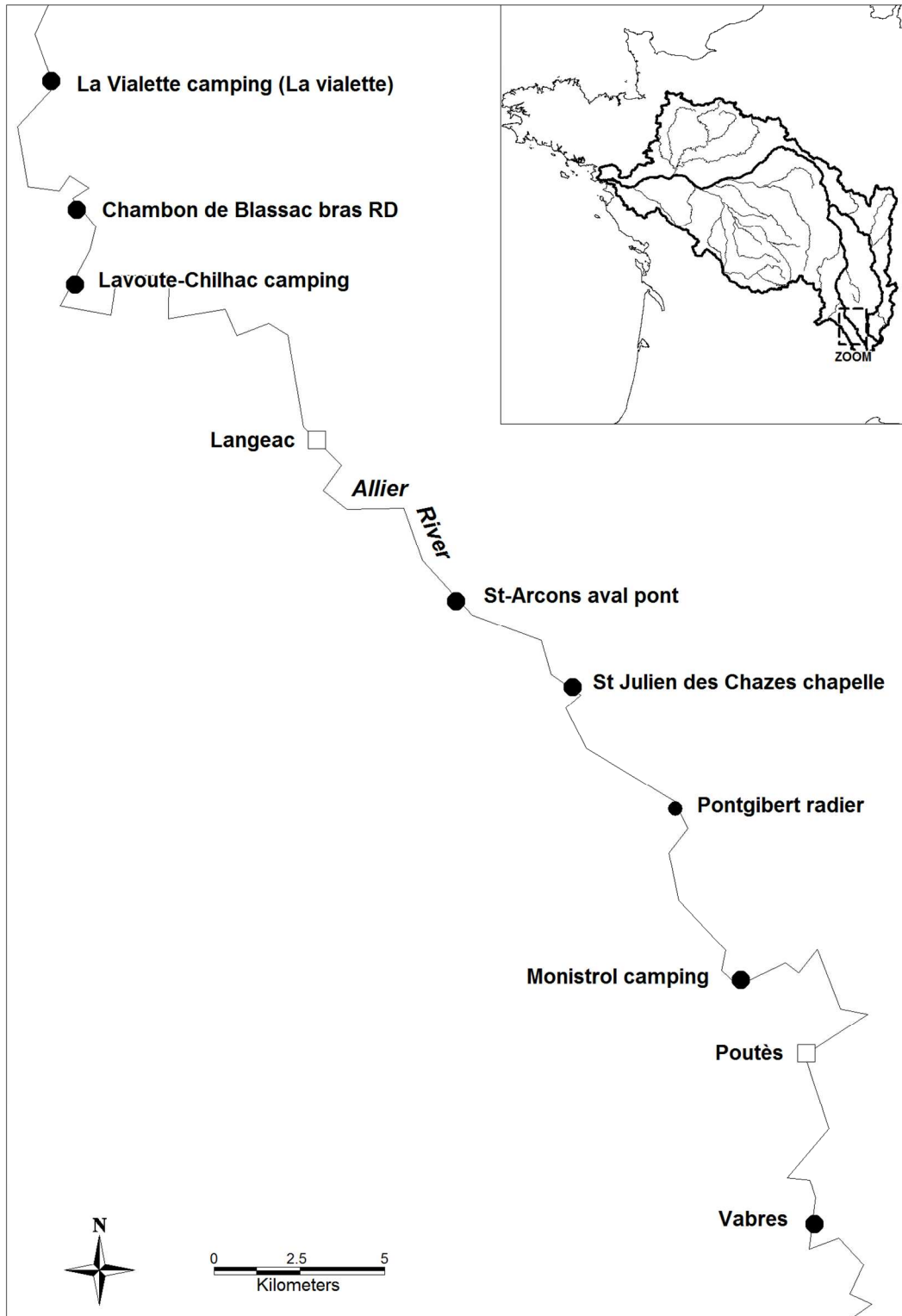
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125 Figure S2: Directed Acyclic Graph (DAG) of the model used to estimate densities of the sites
126 studied. Squares represent fixed quantities. All observed quantities are greyed. Arrows
127 represent the parent-child dependencies between the different nodes: single arrows represent
128 probabilistic relationship between the parent(s) and child nodes, dashed arrows indicate
129 deterministic relationship. The frame represents a repetition of structure over sites. Nodes
130 outside the frame are unknown parameters constant across sites.

131

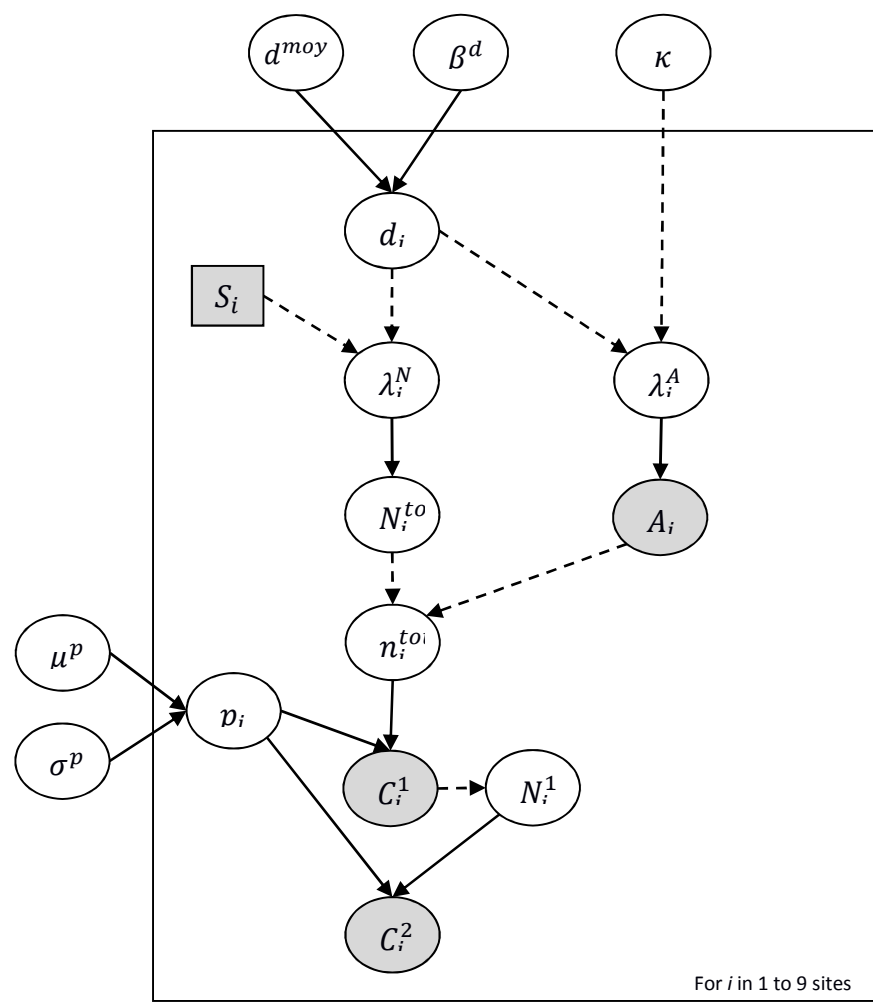
132 Figure S3: 0+ juveniles density estimates vs 5 minutes index of abundance for the 9 sites
133 sampled with the two electric fishing techniques. Boxplots indicate 2.5th, 25th, median, 75th and
134 97.5th quantiles. The plain and dashed red lines indicate the 2.5th, median and 97.5th quantiles
135 of predicted densities for 5 minutes index of abundance only ranging from 1 to 300.

136



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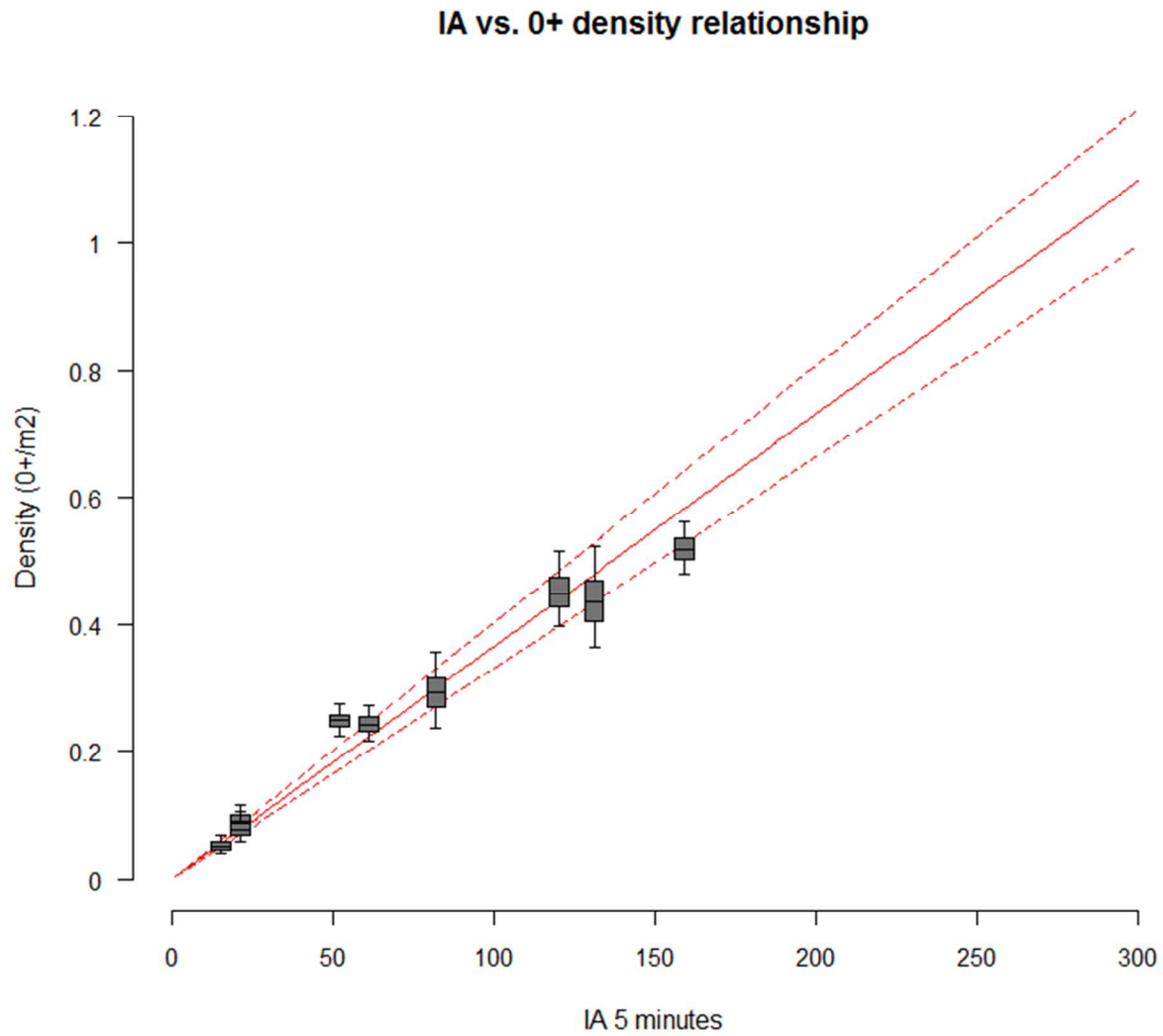
138 Fig S1



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140 Fig. S2

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143 Fig. S3

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149 Posterior checking

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151 A standardized Pearson residuals is defined as:

152 (Eq. S11)
$$r_i(\theta) = \frac{y_i - E(y_i|\theta)}{\sqrt{\text{Var}(y_i|\theta)}}$$

153 Where X_i is an observation and θ the set of parameters conditioning observation X_i . It has
154 mean 0 and variance 1. Residuals were computed for each index of abundance and first
155 successive removal pass observation. All residuals for each observation are summarized in
156 figure S4. The average residuals for the index of abundance is -0.0513 and 0.152 for the first
157 successive removal pass. There are a small number of index of abundance residuals that show
158 lower values than the rest. They are associated with very low abundance: when juvenile density
159 is low, the abundance index tends to be lower than expected according to the calibration
160 model. This is somewhat artefactual in the sense that, given the structure of the model, when
161 the abundance index is null (i.e. no fish caught over 5 minutes), its underlying expectation is
162 necessarily positive (see equations S1 to S3). Note also that the smallest index of abundance
163 observation in the calibration model (table S2) is 15, so there is no hard data to test the validity
164 of the model relating abundance indices to densities at very low densities.

165 Additionally to the Pearson residuals and following the approach proposed by Gelman et al.
166 (1996), the consistency between the assumed model and the data was checked by means of
167 posterior predictive assessment techniques. These techniques extend classical goodness-of-fit

168 tests in the Bayesian setting by averaging over the posterior distribution of unknown quantities
169 of the model. The omnibus chi-square statistic, a measure of discrepancy between the model
170 and the data, was used (see Gelman et al. 2003 for detailed description).

171 (Eq. S12)
$$\chi^2(X, \theta) = \sum_t \frac{(X_t - E(X_t | \theta_t))^2}{\text{Var}(X_t | \theta_t)}$$

172 with X being any observable quantity and θ the set of unknown parameters controlling the
173 probability distribution of X . For each river section (Vichy-Langeac, Langeac-Poutès and
174 upstream of Poutès), the realised discrepancies $\chi^2(A_i, \theta^A)$ and $\chi^2(C_i^1, \theta^{C1})$ computed with the
175 observed values of the 5 minutes index of abundance A_i and, the first successive removal pass
176 C_i^1 were compared to the corresponding posterior predicted discrepancies $\chi^2(A_{rep_i}, \theta^A)$ and
177 $\chi^2(C_{rep_i}^1, \theta^{C1})$. The later were computed with a posteriori replicated data (A_{rep_i} and
178 $C_{rep_i}^1$) as simulated by the model. The chi-square discrepancy statistics did not reveal any
179 inconsistency between the model and the data (Table S3).

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187 Table S3: Bayesian p-values of chi-square statistics based on data replication technique for each
 188 river section.

Observation	$P(\chi^2(X^{rep}, \theta) \geq \chi^2(X, \theta))$			
	Vichy-Langeac	Langeac-Poutès	Upstream Poutès	All together
5 minutes index of abundance A_i	0.527	0.511	0.504	0.519
first successive removal pass C_i^1	0.526	0.473	0.524	0.492

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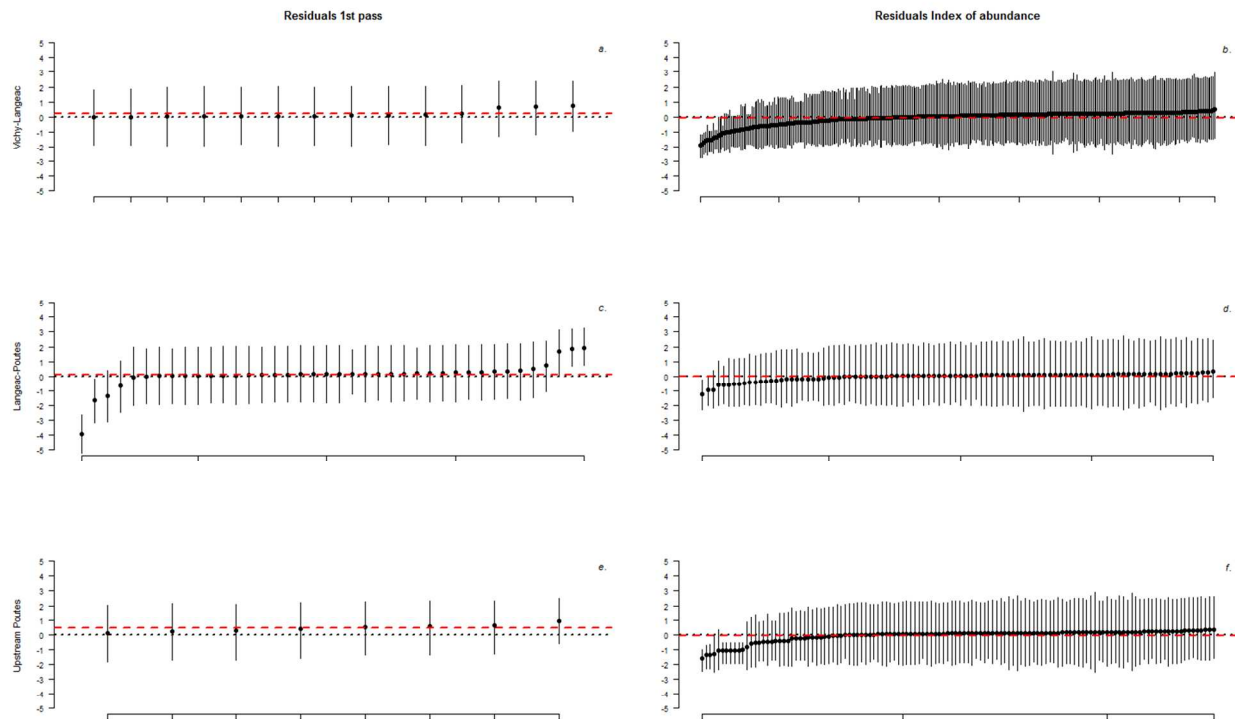
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202 Figure S4: Posterior distribution of the standardized Pearson residuals ordered by their median
203 value for the first successive removal pass (left panels) and 5 minutes index of abundance (right
204 panels) observations for Vichy-Langeac (*a*, *b*), Langeac-Poutès (*c*, *d*) and upstream of Poutès (*e*,
205 *f*) river sections. The dots indicate the median residual for each observation and the segments
206 indicate the 95% posterior distribution of the residual. The black dashed lines indicate the 0
207 reference, the red lines indicate the average residual for each panel.
208



209

210 Fig. S4

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225 Additional Figures

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228 Figure S5: Average density dependence relationships between (a) the potential spawners
229 density of a given year t and the wild 0+ juvenile density the following year $t+1$ and between (b)
230 the juvenile stocking density in spring and the stocked 0+ juvenile density in the fall. Spatial
231 differences between downstream and upstream from Langeac are represented by two grey
232 curves (dark and light) corresponding to the average relationship downstream and upstream
233 from Langeac. Plain grey dots and squares correspond to annual estimates (posterior median)
234 for the three river sections. The dashed line in panel (b) represent 100% survival. All densities
235 are in fish per square meter of favorable habitat.

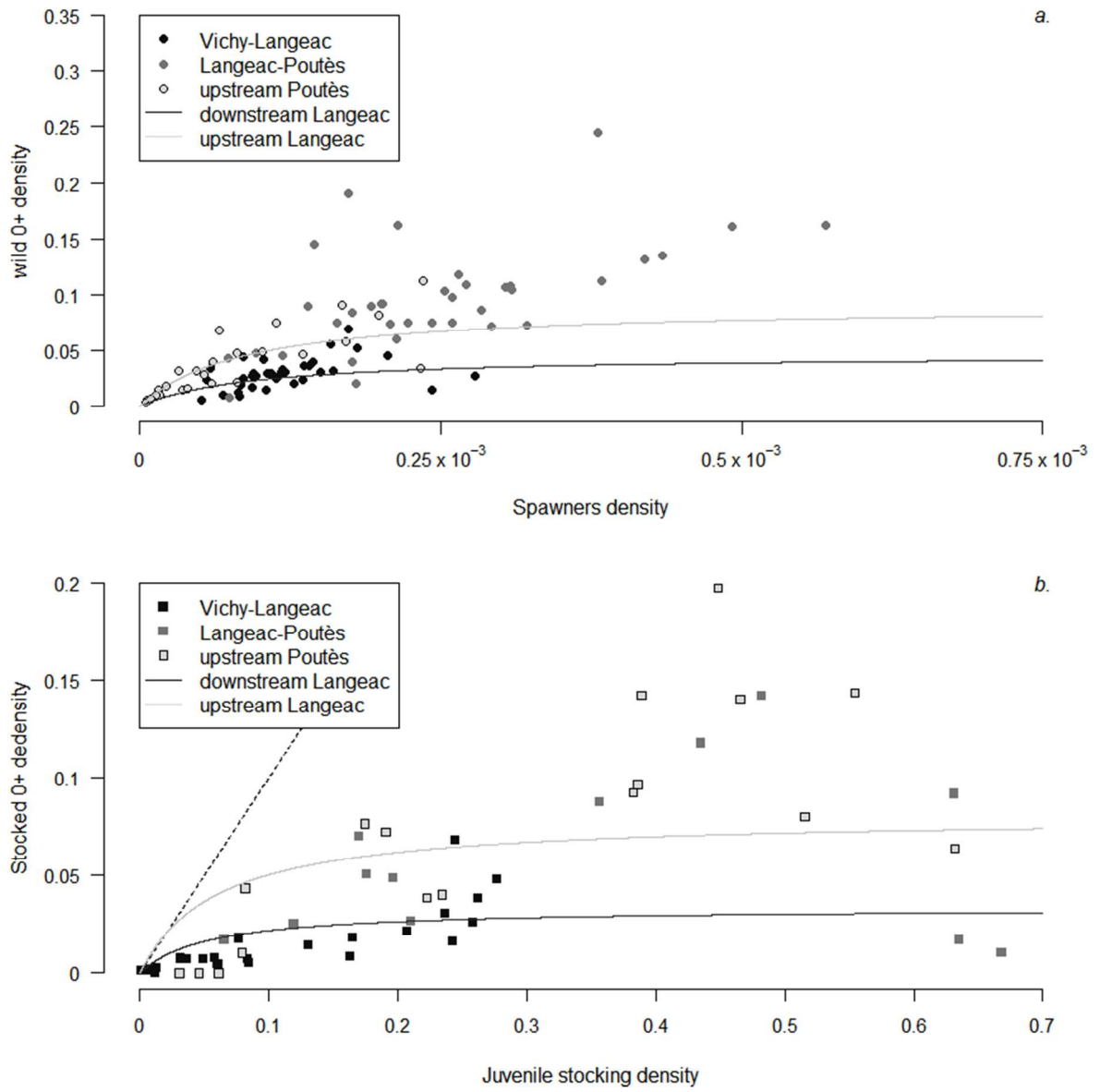
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237 Figure S6: Posterior distributions of the proportion of R_{max} available to wild component
238 $p_t^{R_{max}}$ for each year by river section (Vichy-Langeac a , Langeac-Poutès b and; upstream Poutès
239 c). The grey dots indicate years with no stocking. Boxplots indicate 2.5th, 25th, 50th (median),
240 75th and 97.5th percentiles. The vertical dashed line indicates the opening of Poutès dam.

241

242 Figure S7: Posterior distributions of the reduction factor of the slope at the origin of the
243 Beverton-Holt relationship for stocked 0+ β_t^S for each year by river section (Vichy-Langeac a ,
244 Langeac-Poutès b and upstream Poutès c). Boxplots indicate 2.5th, 25th, 50th (median), 75th and
245 97.5th percentiles. The vertical dashed line indicates the opening of Poutès dam.

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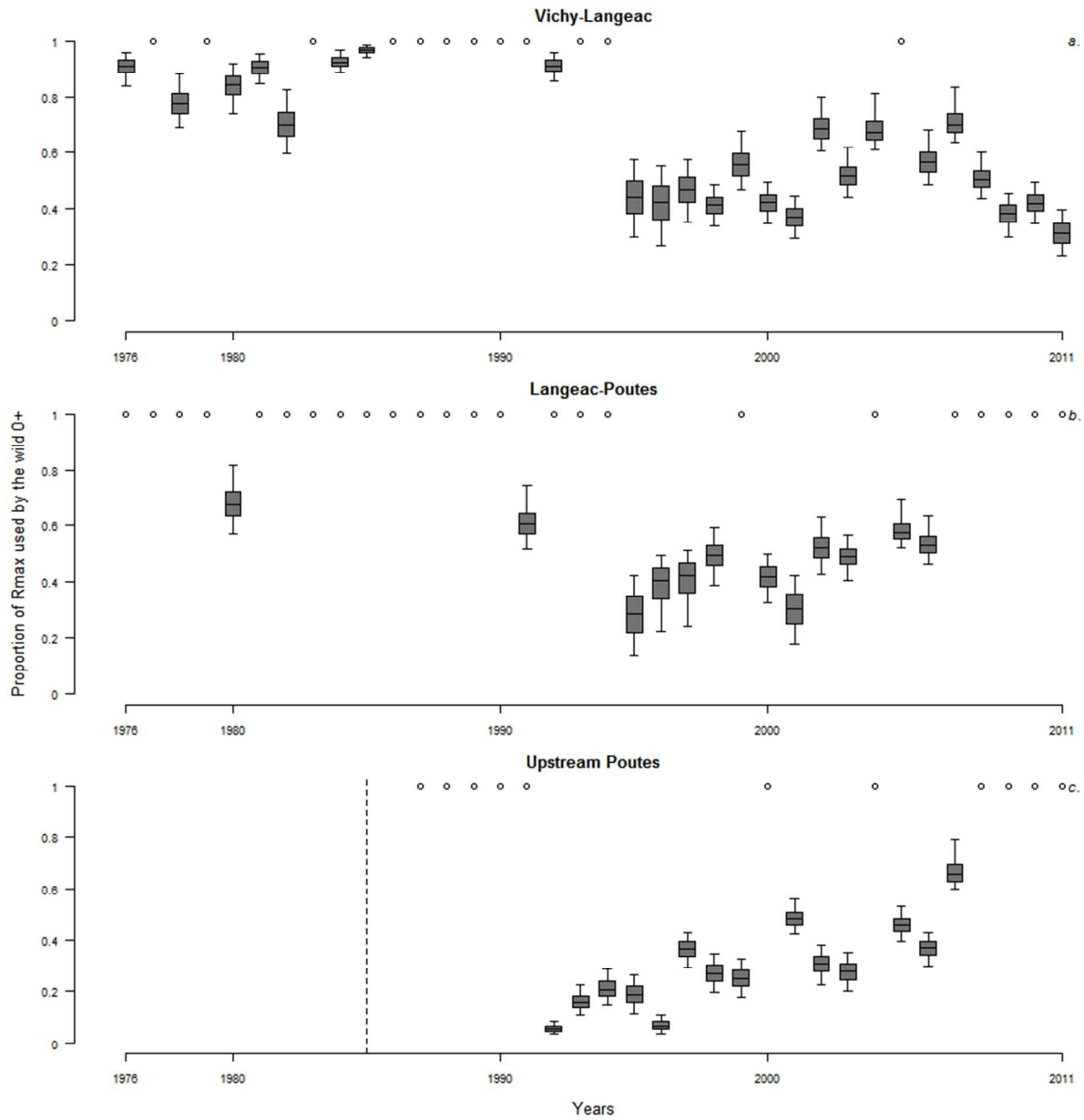
249 Fig. S5

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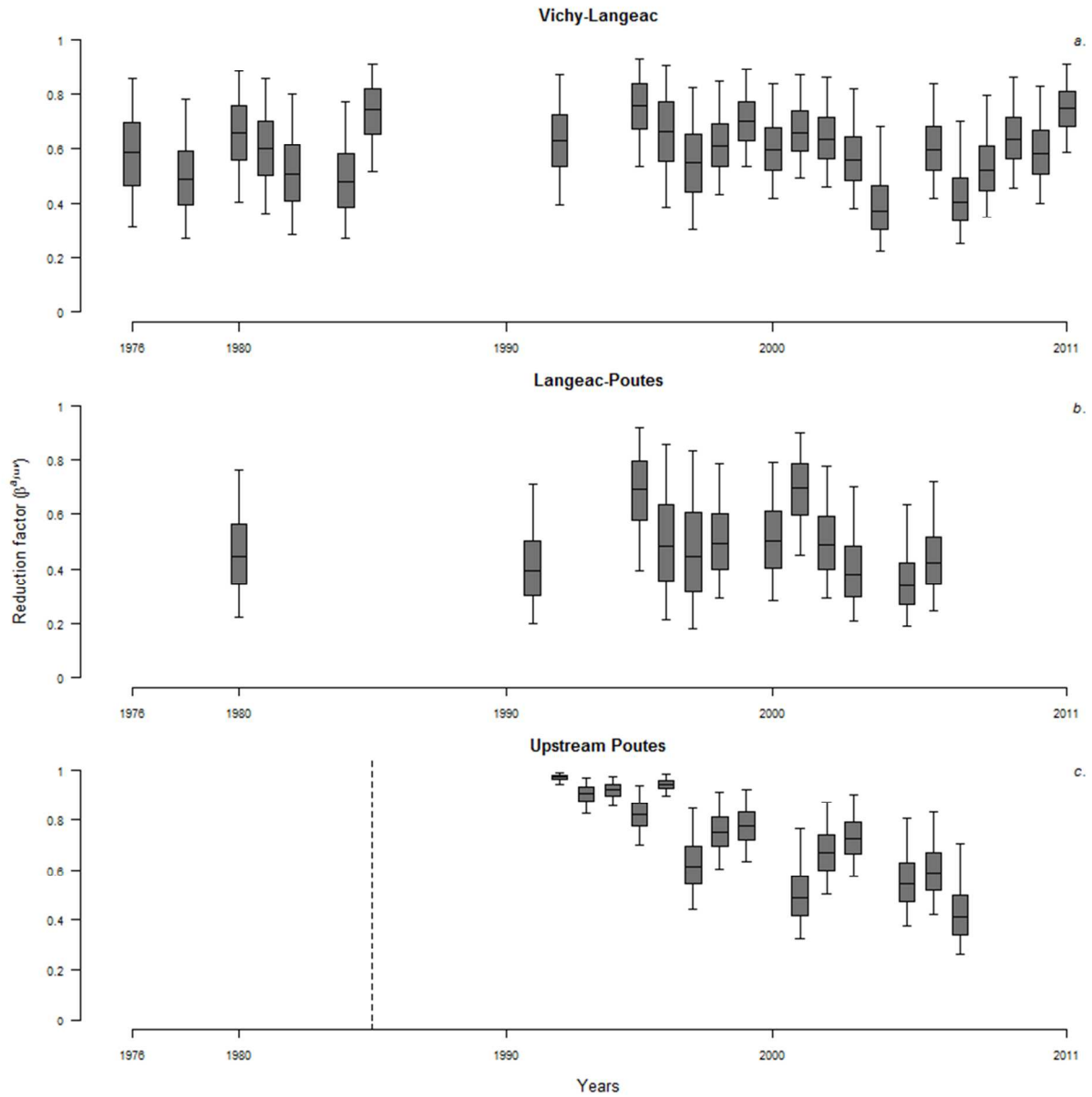
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255 Fig. S6



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